Great tits take greater risk towards humans and sparrowhawks in urban habitats than in forests

Running title: Urban great tits take greater risk

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Abstract

Urban animals often take more risk towards humans than their non-urban conspecifics do, but it is unclear how urbanization affects behavior towards non-human predators. Responses to humans and non-human predators may covary due to common mechanisms enforcing a phenotypic correlation. However, while increased tolerance towards humans may be advantageous for urban animals, reduced vigilance towards non-human predators that can pose actual threat may be costly. Therefore, urban animals may benefit from showing specific responses to different threat levels, such as humans versus non-human predators, or hostile versus non-hostile humans. To test these alternatives, we compared responses (latencies to return to nest) of urban and forest-breeding great tits (*Parus major*) to familiar hostile and unfamiliar humans as well as one of their common predators, the sparrowhawk (*Accipiter nisus*). We found that urban birds were more risk-taking towards both humans and sparrowhawk than forest birds. However, responses to sparrowhawk did not correlate with responses to humans either within or across habitats. This suggests that higher risk-taking of urban compared to forest-dwelling great tits towards sparrowhawk may be threat-specific response to lower predation risk rather than a spillover effect of increased tolerance to humans. Furthermore, birds responded similarly to unfamiliar and familiar (potentially dangerous) humans in both habitats, suggesting that great tits may not adjust their risk-taking to the threat represented by individual humans. These findings indicate that urban birds may flexibly adjust their risk-taking to certain, but not all, types of threat.

Keywords: urbanization, avian anti-predator behavior, behavioral spillover, predator discrimination

Introduction

Urban areas differ from natural habitats in a number of ecological characteristics (Sol et al., 2013; Seress & Liker, 2015), one of the most obvious being the high abundance of humans. Wild animals usually perceive humans as threat, responding to their proximity with similar behaviors that they show towards predators, for example with alarm calls and mobbing or with avoidance such as flight or hiding (Blumstein, 2014; Frid & Dill, 2002; Geffroy et al., 2015). Such anti-predatory behaviors may have an energetic cost and can also lead to missed opportunities, because they are in trade-off with behaviors such as foraging and offspring provisioning. Therefore, fleeing is only advantageous if not fleeing is even more costly (Lima, 1998; Frid & Dill, 2002; Coleman et al., 2008). Humans in cities seldom pose direct threat to free-living animals like birds (Clucas & Marzluff, 2012), thus greater risk-taking (e.g. reduced avoidance) towards humans can be advantageous in urban habitats. Reduced flight responses have been observed in many urban animals (Samia et al., 2015), including birds (Vincze et al., 2016; Myers & Hyman, 2016; Carrete & Tella, 2017; Møller et al., 2015), mammals (Uchida et al., 2016; McCleery, 2009) and reptiles (McGowan et al., 2014; Lapiedra et al., 2017).

Risk-taking towards humans is often suggested to correlate with other forms of risk-taking behavior, such as aggressiveness (risk-taking towards a conspecific opponent; Scales et al. 2011; Myers and Hyman 2016), neophobia and exploration (risk-taking towards novel stimuli; Bókony et al., 2012; Carrete and Tella, 2017), and anti-predator behavior (risk-taking towards non-human predators; Bókony et al., 2012; Carrete and Tella, 2017; Myers and Hyman, 2016). Such phenotypic correlation across different situations is often called ‘behavioral syndrome’ (Sih et al., 2004; Herczeg & Garamszegi, 2012; but see Dingemanse et al., 2012). The correlation between responses to humans and responses to non-human predators is often considered to be particularly strong, as it is frequently assumed that animals perceive humans as a type of predator (Beale & Monaghan, 2004; Frid & Dill, 2002).

Consequently, some authors interpret responses towards humans as a measure of general anti-predator response (Stankowich & Blumstein, 2005); for example, they consider the relatively low flight initiation distances (Møller, 2012; Jiang & Møller, 2017) and higher docility during handling (Møller & Ibáñez-Álamo, 2012) by urban compared to non-urban birds as decreased general anti-predatory behavior. This ‘general risk-taking’ hypothesis predicts that as animals increase their risk-taking towards humans in urban habitats, their risk-taking towards non-human predators also becomes greater (Geffroy et al., 2015). This may happen by differential colonization, when cities are colonized by a subset of individuals that have above-average general risk-taking (Møller 2010), for example due to differences in pace-of-life syndromes (Sol et al., 2018; Charmantier et al., 2017). Also, local micro-evolutionary adaptation in cities may lead to intrinsic differences in general risk-taking between urban and non-urban populations (Sprau & Dingemanse, 2017; Holtmann et al., 2017; Carrete & Tella, 2010). Furthermore, habituation to human disturbance may also be transferred to other type of threats, resulting in reduced general risk-taking (McCleery, 2009).

However, such a correlation between risk-taking towards humans and risk-taking towards non-human predators may not be adaptive in cities, because greater risk-taking driven by tolerance to humans may result in higher mortality by predators if predation pressure is high (i.e. human-mediated behavioral spillover, Geffroy et al. 2015). In such circumstances, urban animals may benefit from ‘breaking down’ the phenotypic correlation between risk-taking behaviors and showing differential responses to different types of threat. The ability to recognize distinct types of predators and respond in specific ways to them has been demonstrated in a number of species (Greene & Meagher, 1998; Zuberbühler et al., 1997; Zuberbühler, 2001; Suzuki, 2011; Suzuki, 2012; Pongrácz & Altbäcker, 2000). Birds appear to be good at estimating the level of threat by different types of predators and adjusting the intensity of their anti-predator behaviors to it (Edelaar & Wright, 2006; Templeton et al., 2005; Curio et al., 1983). As humans in cities are seldom hostile toward birds (Clucas & Marzluff, 2012), whereas non-human predators, particularly those specialized on birds, represent a high level of danger, the ‘threat-specific risk-taking’ hypothesis predicts that urban individuals take greater risk specifically towards humans while remaining vigilant towards non-human predators that pose real danger to them. Animals can achieve this by individual behavioral plasticity such as habituation and learning (Vincze et al., 2016; McCleery, 2009; Weaver et al., 2018), but also by evolving predator discrimination (Carthey & Blumstein, 2018).

In our study, we aimed to contrast the general risk-taking hypothesis and the threat-specific risk-taking hypothesis by comparing responses to humans and to a non-human predator. What makes this challenging is that predictions of the threat-specific risk-taking hypothesis depend on the level of predation pressure in urban habitats. A number of empirical studies reported high predator abundance or high nest predation rates in urban compared to non-urban habitats (Haskell et al., 2001; Jokimäki & Huhta, 2000) or stronger anti-predator behavior in urban than in non-urban populations (Coleman et al., 2008; Bókony et al., 2012), suggesting high predation pressure. In such conditions, urban animals are expected to be tolerant of humans but not of non-human predators. However, other studies found low abundance of predators or low predation risk (Møller & Ibáñez-Álamo, 2012; McCleery et al., 2008) as well as weak anti-predator behaviors (McCleery, 2009) in urban habitats, suggesting that the effect of urbanization on predation pressure can vary among species or localities, or with other factors such as age (Seress et al., 2011). If predation pressure is low in cities, the threat-specific risk-taking hypothesis predicts that urban animals should take greater risk towards humans and predators alike. Although this latter prediction is identical to what the general risk-taking hypothesis predicts, the underlying mechanisms are different. Thus, it is possible to confront the two hypotheses if, beside comparing the average behavior of animals between urban and non-urban habitats (Weaver et al., 2018), the correlation between responses to humans and to non-human predators within habitats is also tested (Myers & Hyman, 2016; Carrete & Tella, 2017). The general risk-taking hypothesis predicts that individuals that take more risk towards humans will also take more risk towards predators both across and within habitats. In contrast, the threat-specific risk-taking hypothesis predicts the within-habitat 'breakdown' of this phenotypic correlation, because responses to humans and predators should be adjusted independently from each other to the fine-scale variation of danger in the microhabitat of each individual. Several species exhibit such urban breakdown of correlation between risk-taking behaviors, e.g. between neophobia and exploration (Riyahi et al., 2017) or between intraspecific aggression and risk-taking towards humans (Scales et al., 2011). Two recent studies found that non-urban birds that were more tolerant of humans were also more risk-taking in response to natural predators, while urban conspecifics did not show such correlation (Carrete & Tella, 2017; Myers & Hyman, 2016), supporting the 'threat-specific risk-taking' hypothesis. However, in both studies, risk-taking towards humans was quantified via flight initiation distances (i.e. avoidance), whereas risk-taking towards predators was quantified by mobbing behavior (i.e. aggression) elicited by a predator dummy or by heterospecific alarm calls. Because urbanization may select for changes in aggressive behaviors (Myers and Hyman 2016, Sprau and Dingemanse 2017), testing whether the avoidance of non-human predators (i.e. a non-aggressive response) is related to avoidance of humans within different habitats could make an important contribution to validating the breakdown of phenotypic correlation and thereby understanding how animals adapt to urban environments. The only study we know of that quantified responses to humans and to non-human predators using similar behaviors along the urban-rural gradient did not report formal tests of the breakdown of phenotypic correlation (Weaver et al., 2018).

Threat-specific behavior can also go beyond differentiating between humans and non-human predators, as it may also be advantageous to discriminate between individual enemies of the same species, such as individual humans. Although the majority of humans, especially in cities, are neutral towards wild animals like birds in their environment (Clucas & Marzluff, 2012), some people still pose a threat to wildlife by hunting, pest control or various other forms of repeated disturbance. Under such conditions, it pays off to recognize hostile humans and show increased anti-predator behaviors towards these specific individuals (Nordell et al., 2017; Levey et al., 2009; Lee et al., 2011) while tolerating other humans that represent lower threat, avoiding the cost of flight from them. Accordingly, differential responses towards more threatening and less threatening people have been found in a number of bird species living in anthropogenic habitats, including corvids (Lee et al., 2011; Marzluff et al., 2010), pigeons (Belguermi et al., 2011) and small passerines (Levey et al., 2009; Vincze et al., 2015). However, no study to our knowledge has tested whether urban-dwelling individuals are actually better at this discrimination than conspecifics living in non-urban habitats where humans are seldom present (Vincze et al., 2015).

Our present study investigated the behavior of urban and non-urban great tits (*Parus major*), asking four questions: 1) Do urban and forest birds differ in their responses to human disturbance? 2) Do urban and forest birds differ in their responses to familiar hostile versus unfamiliar humans? 3) Do urban and forest birds differ in their responses to one of their principal natural predators, the Eurasian sparrowhawk (*Accipiter nisus*)? 4) Are the responses to humans and responses to sparrowhawk correlated, across habitats and within either of the two habitat types? We predicted reduced responses to humans and greater discrimination of hostile and non-hostile humans by urban birds. We also predicted that, in case of general risk-taking, we would find reduced responses to sparrowhawk in urban birds and also a positive phenotypic correlation between the responses to different threats in both habitats. Conversely, in case of threat-specific responses, we would find no such phenotypic correlation in urban birds. Great tits inhabit both human settlements and forests, and often breed in artificial nest boxes; therefore they provide an excellent study system to investigate these questions.

Methods

This study was conducted as part of a series of field experiments in April to July, 2013 in four study sites in Hungary (Preiszner et al., 2017; Bókony et al., 2017). The two urban sites were in the cities of Veszprém (47°05’17”N, 17°54’29”E) and Balatonfüred (46°57’30”N, 17°53’34”E); the former consisted of smaller parks, cemeteries and university campuses, whereas the latter consisted of one larger (ca. 9 ha) park surrounded by an urban matrix with residential areas and roads with heavy traffic, in cities with residential human population density of 495.2 and 278.9 people/km^2, respectively (data from the Hungarian Central Statistical Office). The two forest study sites were deciduous forests at Vilma-puszta (47°05’06”N, 17°51’51”E), characterized by sessile oak (*Quercus robur*) and flowering ash (*Fraxinus ornus*), and near Szentgál (47°06’39”N, 17°41’17”E), characterized by beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*), surrounded by a rural matrix, both ca. 3 km away from the closest human settlement. At each site we monitored great tits breeding in artificial nest boxes that were placed on trees. Throughout the breeding season, we checked the nest boxes twice a week and recorded the number of eggs and/or nestlings at each visit. To avoid inducing nest desertion, we never removed incubating females from their nests during nest checks (Dubiec, 2011). When the nestlings were 5-9 days old (day 1 being the day when the first nestling hatched), we captured one parent with a string-operated trap door on their nest (described in detail in Seress et al. 2017); this trapping method does not harm the parents, and has no significant effect on the survival and body condition of nestlings (Seress et al., 2017). Upon capture, we ringed the birds with a unique combination of a metal ring and 3 plastic color rings and recorded their sex based on plumage characteristics, and released them near their nest after a standard, 10-15 minutes long measurement routine. The color rings ensured that we could distinguish the two parents on video recordings. To minimize stress, we always trapped only one of the two parents before the tests, or neither of them in case of 15 pairs where one or both parents had already been ringed in previous years.

Between 8 and 16 days (mean ± *SD,* urban birds: 12.15 ± 1.69; forest birds: 13.17 ± 1.38) of nestling age, we conducted two behavioral tests that quantified the birds' responses to humans (questions 1, 2 and 4) and to a sparrowhawk (questions 3 and 4). These two tests took place in randomized order, each on a different day (1 to 5 days apart from each other, mean ± *SD* = 1.78 ± 1.16 days). Tests have been performed at varying time of the day, between 7:12 and 18:49 (mean ± *SD* = 11:15 ± 178 minutes). Both tests consisted of three main phases (Figure 1): a 15 minutes long (mean ± *SD* = 932 ± 77 sec) pre-stimulus phase and two test phases, each 20 minutes long (1224 ± 52 sec and 1237 ± 59 sec for the first and the second test phase respectively). Both test phases were further divided into two equal-length periods: the first with a stimulus present (stimulus period) and the second after removing the stimulus (post-stimulus period, see below). The tests were recorded by a camera (GoPro Hero 2; 7 × 5.5 × 5 cm), which was concealed in a black plastic box that was 15 cm from the nest entrance and was permanently attached to the nest box, installed before the breeding season so birds were already familiar with its presence. In a former experiment we have validated that this box hid the camera effectively, as further familiarization to the camera did not have any effect on the birds' return latency after nest disturbance (Seress et al., 2017). Due to logistic constraints as well as to avoid too much disturbance for ethical reasons, we kept the length of each daily test ≤ 1 hour, and we never conducted the two tests on the same day at the same nest, and we conducted each test only once at each nest. While this approach did not allow us to test within-individual repeatability and within-individual correlation of the two forms of risk-taking behavior (as suggested by Dingemanse et al., 2010; Dingemanse et al., 2012), it still allowed us to test the within-site and across-site phenotypic correlation of the two responses (Myers & Hyman, 2016; Davidson et al., 2018; Scales et al., 2011; Bókony et al., 2012; Riyahi et al., 2017).

All procedures were in accordance with the ASAB/ABS Guidelines for the Use of Animals in Research and with Hungarian laws, licensed by the Middle Transdanubian Inspectorate for Environmental Protection, Natural Protection and Water Management (permission number: 31559/2011).

Human disturbance test

At the beginning of the pre-stimulus phase, the experimenter checked the nest content, placed the camera in the hiding box, started the recording, and left the vicinity of the nest. Both test phases (Figure 1) started with a stimulus period during which one person was standing under the nest box, but not looking at it, for 10 minutes (595 ± 24 sec), followed by a 10-minute long (638 ± 73 sec) post-stimulus period during which no person was standing under the nest box or in its vicinity. Two different persons were present in the two stimulus periods: one person was ‘unfamiliar’, i.e. someone who never visited the vicinity of the nest before the test, whereas the other person was ‘familiar hostile’, i.e. someone who regularly checked the nest box (7 to 16 times, mean ± *SD* = 12.74 ± 1.61, from egg laying, including the start of the human disturbance test) and participated in the trapping of one parent. We believed that this disturbance was enough for the birds to perceive this person as potentially dangerous and get sensitized to them, as for other passerines even four encounters were enough to specifically recognize and mob the person who checked the nest (Levey et al., 2009). The stimulus persons were of varying gender, build, clothing and hairstyle; the familiar hostile persons, i.e. the researchers conducting the field work, also wore various clothes during nest checks. The order of the two persons was randomized between the two test phases. Both persons announced their arrival and their departure audibly to the camera, thereby the start and end of each stimulus phase was identifiable from the video recordings.

Sparrowhawk test

The sparrowhawk test followed a protocol largely similar to the human disturbance test, with a pre-stimulus phase and two test phases (Figure 1). Before checking the contents of the nest box and starting the pre-stimulus phase, the experimenter placed a tripod below the nest box, with the tripod's top ca. 3 m away from the entrance, which remained there until the end of the test. We considered this distance to be short enough for the birds to perceive approaching and entering the nest box in presence of the stimulus as risky (i.e. even though being inside the nest box may be safe, approaching it when a predator is nearby is likely dangerous). The experimenter left the proximity of the nest and only returned briefly at the start and end of each stimulus period to place or remove the stimulus under the nest. The first test phase was a 'dove phase', during which a mounted collared dove (*Streptopelia decaocto*) was present on the tripod for the 10 minutes of the stimulus period (608 ± 42 sec), whereas the second test phase was a 'sparrowhawk phase' during which a mounted sparrowhawk was present on the tripod for the 10 minutes of the stimulus period (611 ± 33 sec). Both stimuli were followed by a 10-minute (627 ± 36 sec) post-stimulus period, during which no dummy was present on the tripod. The order of the two stimuli was fixed, with the dove always preceding the sparrowhawk. We decided on fixed order because we expected the sparrowhawk to be a lot more threatening than the collared dove, and thus there would be strong carry-over effects in the second phase if the sparrowhawk was presented first (Bell, 2013). We used sparrowhawk as the predator stimulus because it preys primarily on small passerines, including great tits (Newton & Marquiss, 1982; Götmark & Post, 1996; Zawadzka & Zawadzki, 2001) and also frequently breed in both urban and non-urban habitats (Thornton et al., 2017). We used the collared dove as control because it is a granivorous species (thus not perceived by tits as potential predator or competitor) that is common in both urban and non-urban habitats in Hungary, and is close in size to the sparrowhawk. We had two dove mounts and two sparrowhawk mounts, which were randomly alternated between tests. At the start and end of each stimulus period, the placement and the removal of the mount was announced audibly by the experimenter.

Data processing

We only used data from tests conducted with the first annual brood of each pair, because seasonal effects can influence nest defense behavior in great tits (Curio et al., 1984) and we had too few data from second broods to statistically control for seasonal effects. We excluded 8 human disturbance tests and 10 sparrowhawk tests from the analyses due to technical problems (i.e. poor image or sound quality, premature camera failure). We also omitted 1 human disturbance test where one of the stimulus periods was extremely short (<7 minutes) and 3 sparrowhawk tests where the stimulus period was extremely long (>13 minutes) due to the experimenter arriving at incorrect times. Furthermore, we also excluded the human disturbance test of 9 individuals and the sparrowhawk test of 16 individuals that never appeared on the video over the course of the entire test; and the human disturbance test of 9 individuals and the sparrowhawk test of 6 individuals that were inside the nest at the start of the stimulus period and did not emerge for at least 2 minutes. We decided to exclude these data points because it would not have been possible to express their responses to the stimulus (see below), and we do not know whether these birds perceived any disturbance in the stimulus phase. Thus, we ended up with different sample sizes for the two tests: in the human disturbance test we analyzed the data of 47 males and 39 females from 50 nesting attempts, whereas in the sparrowhawk test we could use 40 males and 34 females from 43 nesting attempts. We tested the correlation between the two responses for a subset of individuals where both tests could be analyzed (33 males and 22 females from 36 nesting attempts).

We quantified the individuals' behavior in the pre-stimulus phase and each of the two test phases with their return latency, i.e. the time elapsed between the start of the phase and the first time the bird entered the nest box. We did not calculate separate return latencies for the stimulus and post-stimulus periods of the test phases, because the majority of birds did not enter the nest box during the stimulus period (83.7% of birds in both stimulus periods of the human disturbance test; 68.9% of birds in the stimulus period of the sparrowhawk phase; Table 1), resulting in too little variation in the behaviors in these periods for meaningful analyses. Birds that did not visit the nest until the beginning of the next test phase or the termination of the test were assigned maximal latencies, according to the phase's length (901 seconds for pre-stimulus phases, 1261 seconds for test phases; we used the latter number rather than 1201 because, due to the slight variation in the test phase length, there were five birds that entered the nest more than 1200 seconds after the beginning of the test phase); note that these maximal latencies were used as censored observations in the analyses, as explained below. We assumed that longer latencies indicate lower level of risk-taking, likely due to stronger fear of the stimulus (but see *Cautionary remarks*).

A few (1 to 7; mean ± *SD* = 2.93 ± 1.56) days before the human disturbance and the sparrowhawk tests, we conducted 3 other behavioral tests, described in detail in Preiszner et al. (2017). These tests began with a 30-minute baseline observation period each, which we used in our current analyses to quantify the birds' provisioning behavior when no threatening stimulus (tripod, mount, or human) was present at the nest (apart from the very short presence of the experimenter at the beginning of the test to install and start the camera). We calculated a 'baseline return latency' from the 3 × 30 minutes of these observations as each bird's average return latency, i.e. the time elapsed until the first return into the nest box averaged over the three observations (13%, 10% and 6% of birds did not return to the nest during the 30 minutes in the first, second and third baseline observations, respectively; these birds were given a latency of 1800 sec). We used this baseline provisioning behavior because it was estimated from a broader time range (90 minutes over several days) compared to the pre-stimulus behavior (15 minutes right at the test start), thus it may more accurately represent persistent characteristics such as territory quality in regards of food (Tremblay et al., 2005) and intrinsic foraging abilities of the parents (Cole et al., 2012). By contrast, pre-stimulus behavior may more accurately represent the immediate inner state of the parents.

Statistical analyses

All analyses were run in R (version 3.3.0; R Core Team 2016), using the ‘irr’ (Gamer et al., 2012), ‘coxme’ (Therneau, 2012), ‘car’ (Fox et al., 2010), ‘MASS’ (Venables & Ripley, 2002) and ‘lsmeans’ (Lenth, 2016) packages. First, to validate that return latency is an individually consistent variable, we tested the repeatability of return latencies by comparing the pre-stimulus phases of the two tests using Spearman’s rank correlation and the intraclass correlation coefficient (ICC; Nakagawa and Schielzeth 2010). These pre-stimulus latencies are likely influenced by both the birds’ motivation to feed their offspring and their sensitivity to short disturbance at the beginning of the test. Birds that did not enter the nest during one or both pre-stimulus phases were excluded from the ICC analysis because this method requires normally distributed residuals, which would be violated if we used the maximal values for those latencies we could not measure. All data were used for the Spearman’s rank correlation.

To test our research questions, we built Cox’s proportional hazards models (henceforth Cox models), with maximal latencies used as censored observations. For each question, we ran a separate model and extracted pre-planned comparisons from the model's estimates as follows. For our first 3 research questions, each model included a focal interaction, along with a set of potentially confounding variables that may influence return latency, and bird ID nested in pair ID as random factors. The focal interaction estimated the birds' mean behavior (i.e. their log hazards ratio, expressing their chances of returning to the nest) in each phase at each site. We then removed statistically non-significant confounding variables with $P > 0.1$ via stepwise backwards model selection, but never omitted our focal interaction. For factors with more than two levels and their interactions, we calculated P-values with simultaneous (type 2) analysis-of-deviance tests. This model-reduction procedure enhanced model fit (ΔAIC > 6) and reduced estimation uncertainty while retaining all important parameters with estimates qualitatively similar to the full models (Supplementary Tables S1-4). The full models including all considered confounding variables and the final models that contain only the statistically significant ($P < 0.05$) and marginally non-significant ($0.05 < P < 0.1$) confounding variables besides our focal interaction are presented in the supplementary material (Supplementary Tables S1-4). From the estimates of the final models, we calculated the birds' behavioral response, i.e. the difference between test phases, for each site. Finally, we compared these behavioral responses between the two habitat types by calculating the difference in response between the two forest sites versus the two urban sites (Figure 1). All these differences were derived from the parameter estimates and errors estimated by each model as linear contrasts of least-squares means (Lenth, 2016). We used this approach rather than including habitat type as a fixed effect and site as a random effect because variance estimations of random effects with few levels are unreliable (Piepho et al., 2003; Bolker et al., 2008), whereas including both habitat type and site as fixed effect would have resulted in a model with high collinearity between these two factors (Dormann et al., 2013). Note that pre-planned comparisons are a powerful approach for testing *a priori* hypotheses (Ruxton &

Beauchamp, 2008). Whenever we evaluated multiple comparisons at the same time (e.g. responses for four sites), we corrected the P-values for the number of contrasts using the false discovery rate (FDR) method (Pike, 2011). For further information on the calculation of linear contrasts, see the Supplementary R script. We describe the details specific to each question below.

Question 1: Do urban and forest birds differ in their responses to human disturbance?

In this model, we included site × phase as the focal interaction, where "phase" was a 3-level factor (pre-stimulus phase, first test phase, second test phase). From the estimates of this model, we calculated the response to human disturbance as the difference between the pre-stimulus phase and the two phases with humans. Furthermore, the initial model also included the following confounding variables: baseline return latency, trapping status (i.e. whether the individual bird was trapped or not before the test), trapping status × phase interaction (to test whether trapped birds are more sensitive to humans), number of nest checks preceding the human disturbance test (as more checks may make the birds more sensitized to humans), test order (i.e. whether the human disturbance test was before or after the sparrowhawk test), nest height from the ground (in centimeters), the bird's sex, number of nestlings, age of nestlings (number of days from the hatching of the first chick in the nest), calendar date (number of days from the 1st of January) and time of day (number of minutes since midnight).

Question 2: Do urban and forest birds differ in their responses to hostile versus unfamiliar humans?

In this model, we included site × person as the focal interaction, where "person" was a 2-level factor (familiar or unfamiliar). Response to hostile versus unfamiliar humans was calculated as the difference between the unfamiliar and familiar person phases. The initial model also included the following confounding variables: baseline return latency, pre-stimulus return latency, trapping status, trapping status × person interaction (to test whether trapped birds were sensitized to the familiar hostile person specifically), number of nest checks, test order, nest height from the ground, sex, number of nestlings, age of nestlings, calendar date and time of day, as well as the phase × site × person interactions ("phase" in this case was a 2-level factor, i.e. first or second test phase). By the latter interaction we aimed to test whether the birds' discrimination between persons depended on the order the people were presented, and whether this order effect differed between sites.

Question 3: Do urban and forest birds differ in their responses to sparrowhawk?

In this model, we included site × stimulus as our focal interaction, where "stimulus" is a 2-level factor (dove or sparrowhawk). Response to sparrowhawk was calculated as the difference between the dove and sparrowhawk phases. The initial model included the following confounding variables: pre-stimulus return latency, baseline return latency, trapping status, nest height from the ground, test order, sex, number of nestlings, age of nestlings, calendar date and time of day.

Question 4: Are the responses to humans and responses to sparrowhawk correlated?

To test our fourth question, we used a subset of birds (N = 55 birds from 36 nests) for which we had data from both tests. We could not directly test the relationship between the response to humans and the response to sparrowhawk with a Cox model, because we had censored latencies in both variables (i.e. the only information we have on some birds is that they did not return during the entire phase; such information can be adequately handled in the dependent variable of Cox models but not in the predictor variables). Therefore, first we tested the relationship between return latencies in the human disturbance test and in the sparrowhawk phase of the sparrowhawk test with Spearman rank correlation. However, this analysis does not take into account the control variables (i.e. behavior in the pre-stimulus phase of the human disturbance test and in the dove phase) and pseudo-replication (i.e. two latencies for each individual in the human disturbance test and two birds per nest). To handle these issues in a more complex analysis, we estimated each bird's response to each stimulus as its residual latency in the test phase relative to its latency in the respective control phase, as follows. We expressed the birds' response to human disturbance (regardless whether the person was familiar hostile or unfamiliar) by building a Cox model with return latency in the test phases (two phases per bird) as dependent variable and pre-stimulus return latency as fixed effect (covariate). This model contained no random factors because it was not used for significance testing but for estimating the relationship between the individuals' behaviors in non-disturbed and disturbed situations. We extracted the martingale residuals (Therneau et al., 1990) for each bird in each test phase from this model (henceforth 'residual return speed'; note that larger residuals belong to faster returns, i.e. shorter latencies). To similarly express the birds' response to sparrowhawk, we built a Cox model with return latency in the sparrowhawk phase as dependent variable and return latency in the dove phase as fixed effect (covariate), and then extracted the martingale residuals (one for each bird) from this model. To test whether there was a linear relationship between the responses elicited by the two types of threat across all birds, we built a linear mixed-effects model with residual return speed in the human disturbance test as the dependent variable (two data points per bird), residual return speed in the sparrowhawk test as fixed effect (covariate), and bird ID nested in pair ID as random factors. We tested whether the regression slope differed among sites using a similar model that also included site as fixed factor and its interaction with the covariate. Additionally, we included sex, trapping status, nest height, number of nestlings, age of nestlings, and phase (first or second person) as fixed effects in our initial model, and removed them stepwise until only statistically significant ($P < 0.05$) and marginally non-significant ($0.05 < P < 0.1$) confounding variables remained. From the final model, we estimated the slope of regression (i.e. relationship between the two responses) for each site; then we compared the two forest slopes with the two urban slopes by calculating a single linear contrast (see Supplementary R script) to test whether the relationship between the two responses differed between the two habitat types.

Results

Return latencies in the pre-stimulus phase were significantly correlated between the human disturbance test and the sparrowhawk test using all birds (Spearman's $\rho = 0.288$, P = 0.032, N = 55). Among birds that returned to their nest in both pre-stimulus phases, we found fairly high and significant repeatability between the two pre-stimulus phases (ICC = 0.51, $F_{30,31} = 3.08$, P = 0.001, N = 31, Supplementary Figure S1). Both estimates indicate consistent variation among individuals in their return latency after the brief disturbance of test start (i.e. their risk-taking in a mildly risky situation).

Question 1: Do urban and forest birds differ in their responses to human disturbance?

Overall, the birds responded to the presence of humans, as they returned to the nest later in the test phases than in the pre-stimulus phase (Supplementary Table S1, Figure 2A)., This response was stronger in trapped birds than in non-trapped birds (linear contrast: 0.953 ± 0.346, z = 2.76, P = 0.006; Supplementary Table S1, Table 2A). The difference between the pre-stimulus and test phases (i.e. response to human disturbance) was significant for both trapped and non-trapped birds in all sites except for Balatonfüred, the site with the lowest sample size for this test, where it was marginally non-significant for the trapped and non-significant for the non-trapped birds (Table 2A, Figure 2A).

Response to human disturbance was significantly greater in forest than in urban sites, i.e. forest-dwelling birds increased their latencies in the test phases compared to the pre-stimulus phase to a greater extent than urban birds did (Table 2A, Figure 2A). Notably, none of the forest birds entered the nest during the stimulus periods (i.e. when a human was standing under the nest box), whereas 42% of urban birds entered the nest in the presence of at least one of the two humans (χ^2 test: $\chi^2_1 = 18.36$, $P < 0.001$; Table 1). There was no significant difference in return latencies between the first and the second test phases (Supplementary Table S5).

Question 2: Do urban and forest birds differ in their responses to hostile versus unfamiliar humans?

Return latencies did not differ significantly between the familiar hostile and unfamiliar persons' phases in any of the four sites (Table 2B), and there was no significant difference between urban and forest habitats in the response to hostile versus unfamiliar humans (Table 2B, Figure 2B). There was a marginally non-significant phase × person interaction (Supplementary Table S2), but none of the pairwise comparisons were significant following FDR correction (Supplementary Table S6; Supplementary Figure S2). Trapped birds returned later than non-trapped birds, but the trapping status × person interaction was non-significant (Supplementary Table S6).

Question 3: Do urban and forest birds differ in their responses to sparrowhawk?

Return latencies were longer in the sparrowhawk phase than in the dove phase in all four sites (Table 2C, Figure 2C); these differences were statistically significant in Veszprém and Szentgál (the city and forest site, respectively, with the largest sample size) (Table 2C). Responses to sparrowhawk (i.e. contrasts between the two phases) tended to be greater in forest than in urban habitats, i.e. forest birds delayed their return in the sparrowhawk phase compared to the dove phase to a greater extent than urban birds did (Table 2C, Figure 2C). In this test, one forest bird at Vilma-puszta was an outlier (Figure 2C) that did not return in the dove phase; after removing this outlier the difference between forest and urban birds' responses increased and became statistically significant (contrast ± SE = 1.220 ± 0.550; z = 2.22; P = 0.027). Furthermore, only 3 out of 27 forest birds (11%) entered the nest while the sparrowhawk dummy was present, whereas 43% of urban birds did so (χ^2 test: $\chi^2_1 = 6.515$, P = 0.011; Table 1).

Question 4: Are the responses to humans and responses to sparrowhawk correlated?

Across all birds we found a weak but significant correlation between the return latencies in the human disturbance and the sparrowhawk tests (Spearman's $\rho = 0.233$, $P = 0.014$ N= 55. individuals); however, when we controlled for "baseline behaviors" and pseudo-replication, this correlation was no longer significant (regression slope: $b \pm SE = 0.12 \pm 0.14$, $t_{18} = 0.87$, $P = 0.396$, $N = 55$ birds). Within each of the four study sites, the correlation between responses to humans and responses to sparrowhawk was not significant either with simple Spearman correlations (Szentgál: $\rho = -0.034$, $P = 0.860$; Vilma-puszta: $\rho = 0.165$, $P = 0.648$; Balatonfüred: $\rho = 0.291$, $P = 0.275$; Veszprém: $\rho = 0.095$, $P = 0.494$; Figure 3A) or with the mixed model of residuals (Table 3, Figure 3B). Importantly, the regression slopes did not differ significantly between urban and forest sites (linear contrast: -0.248 ± 0.428; t = -0.58; P = 0.570).

The other predictors of return latencies were also different between the two test situations. Trapped birds returned later than non-trapped birds in the human disturbance test (Supplementary Tables S1, S2, S4) but not in the sparrowhawk test (Supplementary Table S3). Return latencies in the sparrowhawk test were longer at later times of the day, and somewhat also later in the season (Supplementary Table S3), whereas birds with longer latencies in the baseline observation also had longer latencies in the human disturbance test (Supplementary Table S1). In both tests, birds with fewer nestlings returned later (Supplementary Table S1, S2, S3).

Discussion

In the present study we found that great tits took more risk towards humans in the cities than in the forests, but birds in neither habitat discriminated between familiar hostile and unfamiliar persons. Furthermore, urban great tits showed weaker avoidance responses towards a sparrowhawk than forest great tits did, but there was no correlation between the birds' response to humans and response to sparrowhawk either across or within sites. We discuss each of these findings in detail below.

Question 1: Do urban and forest birds differ in their responses to human disturbance?

Our results suggest that great tits take more risk towards humans than their forest-dwelling conspecifics. This agrees with numerous studies showing that urban animals take more risk towards humans than non-urban animals (Samia et al., 2015). Personality-dependent habitat choice may be an important driver of this difference, as a recent study on great tits found that the distribution of individuals in an urban-suburban area was explained by their risk-taking towards humans, but the birds did not flexibly adjust their avoidance behavior to the level of urbanization (Sprau & Dingemanse, 2017). Nevertheless, we cannot exclude the possibility that habituation or other forms of behavioral plasticity play a major role in the greater risk-taking responses in urban great tits compared to conspecifics living in forests. One aspect of our results that supports that great tits do respond flexibly to changes in the level of human disturbance is that trapped birds showed greater avoidance of humans than non-trapped birds

(Supplementary Table S1), fitting well with an experimental study in which we found that trapping made great tits more vigilant (Seress et al., 2017). This result in great tits corroborates similar findings on other species that even a brief experience with a hostile human can sensitize animals to subsequent human disturbance (Levey et al. 2009; Marzluff et al. 2010; Vincze et al. 2015). In a similar way, encounters with non-hostile people may facilitate habituation, especially in urban habitats (Vincze et al., 2016).

Question 2: Do urban and forest birds differ in their responses to hostile versus unfamiliar humans?

Whether a person was previously hostile or had no previous encounter with the birds had very little if any effect on the great tits' behavior in the human disturbance test. This lack of differentiation between the familiar hostile and unfamiliar person indicates that great tits either did not recognize the people or perceived them as equally threatening. Although the ability to recognize individual humans is often associated with particularly intelligent species such as corvids (Marzluff et al., 2010; Lee et al., 2011), it has also been demonstrated in other birds like passerines and pigeons (Levey et al., 2009; Vincze et al., 2015; Belguermi et al., 2011). Great tits often perform well in learning and problem-solving tasks (Sasvári, 1979; Preiszner et al., 2017), thus, if individual recognition of humans is part of a more general set of cognitive abilities, great tits are likely to have the cognitive capacity for it. Instead, we suggest that differentiating between humans might have little ecological relevance for both urban and forest great tits, for two reasons. First, recognizing individual humans may be the most relevant in habitats with low but non-negligible human population density (such as farmlands) where repeated encounters with the same individual humans are likely (Vincze et al., 2015). In forest habitats, encounters with humans are very uncommon, whereas in cities, only few of the many people may be encountered repeatedly, at least in public areas like our study sites. Second, as great tits are perceived as pleasant birds by the public, hostility towards them is probably rare in both habitat types. Some species where the ability to differentiate between hostile and non-hostile humans was demonstrated, such as pigeons (Belguermi et al., 2011) and house sparrows (Vincze et al., 2015), have long evolutionary history with humans who have often persecuted them as pests, thus recognizing hostile people may be more beneficial for them.

Question 3: Do urban and forest birds differ in their responses to sparrowhawk?

The finding that both urban and forest birds increased their return latency in the sparrowhawk phase compared to the dove phase indicates that our treatments were successful: the birds reacted to the sparrowhawk mount as if it was a predator. Although the order of stimuli in this test was fixed (the dove always preceded the sparrowhawk), we think it is unlikely that the difference between the responses to the two stimuli was due to an order effect, for two reasons. First, if there was an order effect, e.g. birds generally took less risk (due to becoming more fearful or less motivated to feed) during the second test phase than the first, we should have found a similar pattern in the human disturbance test as well, but instead we found no difference between the responses in the first and second phases (Supplementary Table S5). Second, we often heard great tit alarm calls in our video recordings during the sparrowhawk phase (in 27 out of 43 tests) but extremely rarely in the dove phase (in 3 out of 43 tests), indicating a specific anti-predatory behavior elicited by the sparrowhawk mount.

Urban birds tended to show a weaker avoidance response to the sparrowhawk, i.e. they were more likely to enter their nest while the raptor dummy was present, and they did not increase their return latency compared to the dove phase as strongly as forest birds did. The higher risk-taking of urban birds might be explained by sparrowhawk attacks being less frequent in cities. For example, some censuses indicate that raptors like sparrowhawks are less common in urban habitats (Møller & Ibáñez-Álamo, 2012), possibly because they are more sensitive to human disturbance than smaller prey species (Møller, 2012). Furthermore, even predators that are abundant in urban habitats can pose a lower level of threat to certain prey, for example by shifting their diet in cities, preferring easier and/or more abundant prey (Rodewald et al., 2011). Although we do not have data on great tit predation rates by sparrowhawks at our study sites, our earlier research indirectly suggests that urban sparrowhawks in our area might preferentially hunt for house sparrows (Bókony et al., 2012; Seress et al., 2011). Alternatively, it is possible that the weaker avoidance response to sparrowhawk is due to a human-mediated spillover effect, i.e. that urban birds became less vigilant towards humans, and thereby their vigilance towards non-human predators also decreased (Geffroy et al., 2015). We would expect such an effect if responses to humans and to non-human predators are forced by common mechanisms into a phenotypic correlation, as predicted by the general risk-taking hypothesis. This possibility is discussed next.

Question 4: Are the responses to humans and responses to sparrowhawk correlated?

The general risk-taking hypothesis predicts that responses to humans and to non-human predators are driven by common intrinsic mechanisms, and therefore should be correlated not only across habitats but also within habitats. This was not supported by our results: although urban birds on average took more risk than forest birds both towards sparrowhawks and towards humans, the correlation between the two behaviors was weak at best and not significant either in our total sample or within any of the urban or the forest sites. The weak correlation in the total sample that disappeared in the more complex analysis is likely to be simply the result of between-habitat differences (i.e. generally longer latencies in forest birds). Furthermore, the correlation was not stronger in forest sites than in urban sites, which does not support the breakdown of phenotypic correlation.

An explanation for these results may be that, in our great tit populations, responses to humans and responses to sparrowhawk are truly unrelated to each other regardless of habitat type (but see *Cautionary remarks* below). According to this explanation, avoidance of humans may be affected by different behavioral and ecological characteristics than avoidance of sparrowhawks, and the two behaviors may have decreased in urban great tits for different reasons: the former because tolerance of human disturbance is necessary for survival and reproduction in urban habitats, and the latter because sparrowhawk attacks on great tits may be less common in cities. The fact that trapping status significantly affected the birds' responses in the human disturbance test (Supplementary Table S1-S2) but not in the sparrowhawk test (Supplementary Table S3) further supports the idea that birds adjusted their risk-taking towards humans based on their earlier experiences with humans but this did not influence their response to the sparrowhawk. These findings fit well with the threat-specific predator-discrimination abilities of great tits, which react with distinct alarm calls and different behaviors to snakes and avian nest predators (Suzuki, 2011; Suzuki, 2012), and mob faster-moving predators like sparrowhawks from greater distances than slower predators like owls (Curio et al., 1983). Such flexibility may be due to learning; for example, rabbits can learn not to fear humans or cats depending on early-life experiences (Pongrácz et al., 2001).

In contrast to our results, two earlier studies found that non-urban birds (song sparrows *Melospiza melodia* and burrowing owls *Athene cunicularia*, respectively) with shorter flight initiation distances from humans showed more intense mobbing behavior towards non-human predators, while the same correlation was absent in urban birds (Myers & Hyman, 2016; Carrete & Tella, 2017). These two studies notably differ from ours in that they assessed responses to humans through avoidance behavior (flight initiation distances) and responses to non-human predators through aggression (mobbing), whereas we assessed both behaviors through avoidance (i.e. delaying return to the nest box where the threat appeared).

Interestingly, both earlier studies found that behaviors within the same domain (i.e. avoidance versus aggression) remained correlated even in urban birds: there was a habitat-independent correlation between avoidance of humans and avoidance of novel objects (Carrete & Tella, 2017), as well as between aggression towards predators and aggression towards conspecifics (Myers & Hyman, 2016). Despite focusing on a single domain, however, we found no phenotypic correlation in the risk-taking in great tits. Taken together, these findings suggest that detecting the existence or breakdown of phenotypic correlations might depend on the way behaviors are quantified (Davidson et al., 2018).

Cautionary remarks

Our study was designed to assess the risk-taking of birds in urban and forest habitats in their natural environment, simulating ecologically realistic scenarios with as little disturbance as possible. Achieving this was not feasible without sacrificing certain aspects of measuring accuracy and precision which can be ensured by more controlled experimental setups usually applied in laboratory studies of behavior. Below we consider how these aspects of our study may affect the interpretation our results.

First, we could not ensure that the birds were present at the nest at the start of the tests, and we could not collect reliable data on when each individual detected the stimulus, because great tits often move hidden in the foliage and also because observing the vicinity of the nest during the test would have caused too much disturbance. Thus, the variation in the time when the birds arrive to the proximity of the nest and see the stimulus for the first time can cause additional variation in their latencies to enter the nest. This shortcoming has two consequences. On the one hand, it might bias our assessment of risk-taking if birds in one habitat type systematically arrive earlier, e.g. due to higher chick-feeding frequency. However, our analyses controlled for such potential biases by including several co-variables that account for differences in "baseline behavior" (i.e. over 3 days before the tests, in the pre-stimulus phase right at the test start, and in the dove phase). On the other hand, individual variation in first arrival and detection time may also introduce noise into our data, which makes our analyses conservative (i.e. less powerful to detect existing effects). Thus, while we found convincing evidence for habitat-dependent risk-taking towards both stimuli, it is unclear whether our negative results (i.e. lack of differentiation between hostile and unfamiliar humans; no correlation between risk-taking towards the two stimuli) mean that the effects were non-existent or existent but not strong enough to be detected. Because our study apparently had the power to detect strong effects like the higher tolerance of human disturbance in urban birds (which has been demonstrated in many other studies), we can conclude that it is unlikely that noise in our data would have masked a strong differentiation between hostile and unfamiliar humans or a strong correlation between risk-taking towards humans and sparrowhawk. By hearing alarm calls or seeing a bird appearing on camera, we could confirm that at least one member of the pairs was present in 53% of the stimulus periods the human disturbance test and 87% in the stimulus periods of the sparrowhawk test. Furthermore, in the 30-minute baseline observations (314 observations of 105 individual birds), 87% entered the nest before 25 minutes, and following the first time they entered, they had a nest visit rate of 1.55 ± 1.32 per 10 minutes. This also suggests that, if the nest visit rate did not drop extremely within a few days, the vast majority of birds were in the proximity of their nests during the stimulus periods.

Second, we could not measure the responses of the two parent birds at each nest independently from each other. Theoretically, the parents may have influenced each other's behavior, e.g. the more cautious member of the pair could have observed its mate entering the nest, which might have altered its own latency either by encouraging it (shorter latency) or by decreasing the urgency to feed the nestlings (longer latency). However, in another experimental study with the same great tit populations, we found very little evidence for such effects (Seress et al., 2017). Both sexes increased their vigilance at the nest after being captured by humans, but it did not influence the partner males' behavior and, although increasing the partner females' vigilance to a small extent, it did not alter the chick-feeding rates of the partner females (Seress et al., 2017). These findings suggest that, if the partners affect each other's risk-taking at all, they tend to become more similar to each other (e.g. a cautious male making his mate more cautious). This would result in a strong random effect of pair identity, which we took into account in all our analyses. Thus, we believe that our conclusions are not likely to be confounded by partner effects.

Conclusions

Risk-taking towards humans and towards non-human predators are often considered to be correlated. We found that although urban great tits took more risk both towards humans and towards sparrowhawks than forest-dwelling great tits, the two behaviors did not correlate with each other either across or within habitats, which suggests that the habitat-specific changes in risk-taking behavior of great tits may not be driven by a general "syndrome" (phenotypic correlation) in risk-taking. These results have several implications for the research on anti-predator behavior. First, behavior towards humans may not necessarily be a reliable indicator of overall anti-predator behavior (Seress & Liker, 2015). Several studies treat the two as equivalents, generalizing responses to humans as an estimate of responses to any kind of predator (Møller & Ibáñez-Álamo, 2012; Møller, 2012; Jiang & Møller, 2017; Møller et al., 2013; Michelangeli et al., 2018). Our results suggest that responses to humans and to non-human predators do not necessarily covary, thus we need to be careful with this kind of interpretation. Second, our results show that measuring the same behavior on different levels (i.e. populations versus individuals) can lead to different conclusions. If we compare the mean behavior between habitats, we may come to the conclusion that responses to humans and responses to sparrowhawk are strongly related to each other, as urban birds were more risk-taking towards both stimuli. However, looking at correlations between the two responses within populations can lead to the opposite conclusion, i.e. that there is no relationship between responses to humans and responses to sparrowhawk. Thus, it is important to look at behavioral variation on multiple levels (Dingemanse et al., 2010). Third, the contrast between our results and other recent studies addressing the relationship between responses to humans and to non-human predators (Myers & Hyman, 2016; Carrete & Tella, 2017) suggests that estimating the same trait (e.g. risk-taking) from different forms of behavior (e.g. aggression versus avoidance) might yield different results. Therefore, comprehensive studies investigating several behavioral domains at the same time along the urbanization gradient will be important for furthering our understanding of urban adaptations.

Finally, our results also have implications for wildlife conservation. It has been suggested that in habitats with high anthropogenic disturbance, animals are more susceptible to predation due to the human-mediated spillover effect (Geffroy et al., 2015). Our results do not support general risk-taking responses that may result in such a spillover, suggesting that at least some species like the great tit may not suffer increased mortality from predation by natural predators as a consequence of increased tolerance of humans. On the other hand, our birds did not adjust their behavior to the threat based on previous experience with individual people, suggesting that species historically not exposed to persecution or other selection pressures for the discrimination of persons might be vulnerable to human hostility even after a relatively long evolutionary past of co-existing with humans. Exploring how widespread threat-specific habitat differences are across species and populations, and what cognitive, ecological and evolutionary processes lead to them, is a deserving direction of future research.

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Table 1: Percentage of birds that entered the nest while the stimulus was present (number of birds that entered and did not enter shown in brackets; the latter category includes those that entered in the post-stimulus period and those that did not enter in the phase at all).

	Familiar human	Unfamiliar human	Any human	Sparrowhawk
Non-urban	0 % (0, 38)	0 % (0, 38)	0 % (0, 38)	11 % (3, 24)
Szentgál	0 % (0, 27)	0 % (0, 27)	0 % (0, 27)	9 % (2, 20)
Vilma-puszta	0 % (0, 11)	0 % (0, 11)	0 % (0, 11)	20 % (1, 4)
Urban	33 % (16, 32)	25 % (12, 36)	42 % (20, 28)	43 % (20, 27)
Balatonfüred	20 % (2, 8)	10 % (1, 9)	30 % (3, 7)	36 % (4, 7)
Veszprém	37 % (14, 24)	29 % (11, 27)	45 % (17, 21)	44 % (16, 20)

Table 2: Responses to various threats within the 4 study sites, and differences (linear contrasts) of these responses between urban and non-urban sites. A: Responses to human disturbance (i.e. linear contrasts between behavior in the pre-stimulus phase and the test phases, estimated separately for trapped and non-trapped birds). B: Responses to familiar versus unfamiliar humans (i.e. linear contrasts between behavior in the test phases with the unfamiliar and familiar persons). C: Responses to sparrowhawk (i.e. linear contrasts between the dove phase and the sparrowhawk phase).

	Contrast[a] ± SE	z	P[b]
A) Human disturbance[c]			
Szentgál (forest)			
Non-trapped	1.210 ± 0.336	3.59	<0.001
Trapped	2.074 ± 0.389	5.33	<0.001
Vilma-puszta (forest)			
Non-trapped	1.498 ± 0.491	3.05	0.003
Trapped	2.362 ± 0.488	4.83	<0.001
Balatonfüred (urban)			
Non-trapped	0.308 ± 0.559	0.55	0.581
Trapped	1.171 ± 0.618	1.89	0.066
Veszprém (urban)			
Non-trapped	0.932 ± 0.263	3.55	<0.001
Trapped	1.795 ± 0.352	5.10	<0.001
Non-urban vs. urban[d]	0.875 ± 0.401	2.18	0.029
B) Familiar vs unfamiliar person[c]			
Szentgál (forest)	-0.439 ± 0.378	-1.16	0.437
Vilma-puszta (forest)	0.420 ± 0.552	0.76	0.447
Balatonfüred (urban)	-0.646 ± 0.637	-1.01	0.437
Veszprém (urban)	-0.283 ± 0.289	-0.98	0.437
Non-urban vs. urban[e]	0.455 ± 0.477	0.95	0.340
C) Sparrowhawk[f]			
Szentgál (forest)	2.309 ± 0.514	4.49	<0.001
Vilma-puszta (forest)	1.171 ± 0.778	1.51	0.176
Balatonfüred (urban)	0.683 ± 0.530	1.29	0.199
Veszprém (urban)	0.841 ± 0.276	3.05	0.004
Non-urban vs. urban[g]	0.978 ± 0.552	1.77	0.076

[a] Contrasts are expressed as log hazard ratios in Cox models. Larger positive (or smaller negative) values indicate stronger responses to human disturbance, i.e. greater difference in return latency between the test phases and the pre-stimulus phase (A); shorter latencies in the unfamiliar person phase and/or longer latencies in the familiar person phase (B); or stronger responses to the sparrowhawk, i.e. greater differences in return latencies between the sparrowhawk phase and the dove phase (C).

[b] P-values of within-site comparisons were adjusted with the FDR method.

[c] Sample size: 86 individuals of 50 pairs.

[d] Positive contrast indicates that urban birds responded less strongly to humans than forest birds, i.e. the difference between the return latencies in the pre-stimulus phase and the test phases was smaller for urban than for forest birds.

[e] Positive contrast indicates that the difference between the response to the familiar person versus the unfamiliar person was more positive (or less negative) than in forest birds, i.e. urban birds had either longer latencies in the familiar person phase, or shorter latencies in the unfamiliar person phase.

[f] Sample size: 74 individuals from 43 pairs.

[g] Positive contrast indicates that urban birds responded less strongly to the sparrowhawk than forest birds, i.e. the difference between the return latencies in the dove and sparrowhawk phases was smaller for urban than for forest birds.

Table 3. Regression slopes from models with behavior in the human disturbance test as dependent variable and behavior in the sparrowhawk test as explanatory variable (testing the relationship between responses to humans and responses to sparrowhawk by great tits) with confidence intervals (95% CI); sample size: 55 individuals from 36 pairs.

Site	Slope ± SE	95% CI
Szentgál (forest)	-0.092 ± 0.308	-0.750 to 0.565
Vilma-puszta (forest)	-0.025 ± 0.590	-1.283 to 1.232
Balatonfüred (urban)	0.337 ± 0.509	-0.747 to 1.421
Veszprém (urban)	0.042 ± 0.179	-0.339 to 0.424

Figure legends

Figure 1. Schematic illustration of our test protocols and the statistical analysis process (sketches drawn by EV).

Figure 2. Return latencies at the four sites in the pre-stimulus phase and the two test phases of the human disturbance test (A), in the familiar and unfamiliar person phases of the human disturbance test (B) and in the two test phases of the sparrowhawk test (C). Sample sizes (number of individual birds) at each site for the human disturbance test and sparrowhawk test, respectively, are provided in brackets. Boxplots show the median and the interquartile range, with the whiskers representing data within the 1.5 × interquartile range.

Figure 3. Correlations at the four sites between return latencies in seconds in the human disturbance test and the sparrowhawk test (A) and between responses to human disturbance and responses to sparrowhawk (residual return speed expressed as martingale residuals from Cox models, controlling for pre-test behavior; see Methods) (B). Sample sizes (number of individual birds) at each site are provided in brackets.