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

5 Running title: Urban great tits take greater risk

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38

39 **Abstract**

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

59

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

62

63 **Introduction**

64 Urban areas differ from natural habitats in a number of ecological characteristics (Sol et al.,
65 2013; Seress & Liker, 2015), one of the most obvious being the high abundance of humans.
66 Wild animals usually perceive humans as threat, responding to their proximity with similar
67 behaviors that they show towards predators, for example with alarm calls and mobbing or
68 with avoidance such as flight or hiding (Blumstein, 2014; Frid & Dill, 2002; Geffroy et al.,
69 2015). Such anti-predatory behaviors may have an energetic cost and can also lead to missed
70 opportunities, because they are in trade-off with behaviors such as foraging and offspring
71 provisioning. Therefore, fleeing is only advantageous if not fleeing is even more costly (Lima,
72 1998; Frid & Dill, 2002; Coleman et al., 2008). Humans in cities seldom pose direct threat to
73 free-living animals like birds (Clucas & Marzluff, 2012), thus greater risk-taking (e.g. reduced
74 avoidance) towards humans can be advantageous in urban habitats. Reduced flight responses
75 have been observed in many urban animals (Samia et al., 2015), including birds (Vincze et al.,
76 2016; Myers & Hyman, 2016; Carrete & Tella, 2017; Møller et al., 2015), mammals (Uchida
77 et al., 2016; McCleery, 2009) and reptiles (McGowan et al., 2014; Lapiedra et al., 2017).

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

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

102 However, such a correlation between risk-taking towards humans and risk-taking
103 towards non-human predators may not be adaptive in cities, because greater risk-taking driven
104 by tolerance to humans may result in higher mortality by predators if predation pressure is
105 high (i.e. human-mediated behavioral spillover, Geffroy et al. 2015). In such circumstances,
106 urban animals may benefit from ‘breaking down’ the phenotypic correlation between risk-
107 taking behaviors and showing differential responses to different types of threat. The ability to
108 recognize distinct types of predators and respond in specific ways to them has been
109 demonstrated in a number of species (Greene & Meagher, 1998; Zuberbühler et al., 1997;
110 Zuberbühler, 2001; Suzuki, 2011; Suzuki, 2012; Pongrácz & Altbäcker, 2000). Birds appear
111 to be good at estimating the level of threat by different types of predators and adjusting the
112 intensity of their anti-predator behaviors to it (Edelaar & Wright, 2006; Templeton et al.,

113 2005; Curio et al., 1983). As humans in cities are seldom hostile toward birds (Clucas &
114 Marzluff, 2012), whereas non-human predators, particularly those specialized on birds,
115 represent a high level of danger, the ‘threat-specific risk-taking’ hypothesis predicts that urban
116 individuals take greater risk specifically towards humans while remaining vigilant towards
117 non-human predators that pose real danger to them. Animals can achieve this by individual
118 behavioral plasticity such as habituation and learning (Vincze et al., 2016; McCleery, 2009;
119 Weaver et al., 2018), but also by evolving predator discrimination (Carthey & Blumstein,
120 2018).

121 In our study, we aimed to contrast the general risk-taking hypothesis and the threat-
122 specific risk-taking hypothesis by comparing responses to humans and to a non-human
123 predator. What makes this challenging is that predictions of the threat-specific risk-taking
124 hypothesis depend on the level of predation pressure in urban habitats. A number of empirical
125 studies reported high predator abundance or high nest predation rates in urban compared to
126 non-urban habitats (Haskell et al., 2001; Jokimäki & Huhta, 2000) or stronger anti-predator
127 behavior in urban than in non-urban populations (Coleman et al., 2008; Bókony et al., 2012),
128 suggesting high predation pressure. In such conditions, urban animals are expected to be
129 tolerant of humans but not of non-human predators. However, other studies found low
130 abundance of predators or low predation risk (Møller & Ibáñez-Álamo, 2012; McCleery et al.,
131 2008) as well as weak anti-predator behaviors (McCleery, 2009) in urban habitats, suggesting
132 that the effect of urbanization on predation pressure can vary among species or localities, or
133 with other factors such as age (Seress et al., 2011). If predation pressure is low in cities, the
134 threat-specific risk-taking hypothesis predicts that urban animals should take greater risk
135 towards humans and predators alike. Although this latter prediction is identical to what the
136 general risk-taking hypothesis predicts, the underlying mechanisms are different. Thus, it is
137 possible to confront the two hypotheses if, beside comparing the average behavior of animals

138 between urban and non-urban habitats (Weaver et al., 2018), the correlation between
139 responses to humans and to non-human predators within habitats is also tested (Myers &
140 Hyman, 2016; Carrete & Tella, 2017). The general risk-taking hypothesis predicts that
141 individuals that take more risk towards humans will also take more risk towards predators
142 both across and within habitats. In contrast, the threat-specific risk-taking hypothesis predicts
143 the within-habitat ‘breakdown’ of this phenotypic correlation, because responses to humans
144 and predators should be adjusted independently from each other to the fine-scale variation of
145 danger in the microhabitat of each individual. Several species exhibit such urban breakdown
146 of correlation between risk-taking behaviors, e.g. between neophobia and exploration (Riyahi
147 et al., 2017) or between intraspecific aggression and risk-taking towards humans (Scales et al.,
148 2011). Two recent studies found that non-urban birds that were more tolerant of humans were
149 also more risk-taking in response to natural predators, while urban conspecifics did not show
150 such correlation (Carrete & Tella, 2017; Myers & Hyman, 2016), supporting the ‘threat-
151 specific risk-taking’ hypothesis. However, in both studies, risk-taking towards humans was
152 quantified via flight initiation distances (i.e. avoidance), whereas risk-taking towards
153 predators was quantified by mobbing behavior (i.e. aggression) elicited by a predator dummy
154 or by heterospecific alarm calls. Because urbanization may select for changes in aggressive
155 behaviors (Myers and Hyman 2016, Sprau and Dingemanse 2017), testing whether the
156 avoidance of non-human predators (i.e. a non-aggressive response) is related to avoidance of
157 humans within different habitats could make an important contribution to validating the
158 breakdown of phenotypic correlation and thereby understanding how animals adapt to urban
159 environments. The only study we know of that quantified responses to humans and to non-
160 human predators using similar behaviors along the urban-rural gradient did not report formal
161 tests of the breakdown of phenotypic correlation (Weaver et al., 2018).

162 Threat-specific behavior can also go beyond differentiating between humans and non-
163 human predators, as it may also be advantageous to discriminate between individual enemies
164 of the same species, such as individual humans. Although the majority of humans, especially
165 in cities, are neutral towards wild animals like birds in their environment (Clucas & Marzluff,
166 2012), some people still pose a threat to wildlife by hunting, pest control or various other
167 forms of repeated disturbance. Under such conditions, it pays off to recognize hostile humans
168 and show increased anti-predator behaviors towards these specific individuals (Nordell et al.,
169 2017; Levey et al., 2009; Lee et al., 2011) while tolerating other humans that represent lower
170 threat, avoiding the cost of flight from them. Accordingly, differential responses towards
171 more threatening and less threatening people have been found in a number of bird species
172 living in anthropogenic habitats, including corvids (Lee et al., 2011; Marzluff et al., 2010),
173 pigeons (Belguermi et al., 2011) and small passerines (Levey et al., 2009; Vincze et al.,
174 2015). However, no study to our knowledge has tested whether urban-dwelling individuals
175 are actually better at this discrimination than conspecifics living in non-urban habitats where
176 humans are seldom present (Vincze et al., 2015).

177 Our present study investigated the behavior of urban and non-urban great tits (*Parus*
178 *major*), asking four questions: 1) Do urban and forest birds differ in their responses to human
179 disturbance? 2) Do urban and forest birds differ in their responses to familiar hostile versus
180 unfamiliar humans? 3) Do urban and forest birds differ in their responses to one of their
181 principal natural predators, the Eurasian sparrowhawk (*Accipiter nisus*)? 4) Are the responses
182 to humans and responses to sparrowhawk correlated, across habitats and within either of the
183 two habitat types? We predicted reduced responses to humans and greater discrimination of
184 hostile and non-hostile humans by urban birds. We also predicted that, in case of general risk-
185 taking, we would find reduced responses to sparrowhawk in urban birds and also a positive
186 phenotypic correlation between the responses to different threats in both habitats. Conversely,

187 in case of threat-specific responses, we would find no such phenotypic correlation in urban
188 birds. Great tits inhabit both human settlements and forests, and often breed in artificial nest
189 boxes; therefore they provide an excellent study system to investigate these questions.

190

191 **Methods**

192 This study was conducted as part of a series of field experiments in April to July, 2013 in four
193 study sites in Hungary (Preiszner et al., 2017; Bókonyi et al., 2017). The two urban sites were
194 in the cities of Veszprém (47°05'17"N, 17°54'29"E) and Balatonfüred (46°57'30"N,
195 17°53'34"E); the former consisted of smaller parks, cemeteries and university campuses,
196 whereas the latter consisted of one larger (ca. 9 ha) park surrounded by an urban matrix with
197 residential areas and roads with heavy traffic, in cities with residential human population
198 density of 495.2 and 278.9 people/km², respectively (data from the Hungarian Central
199 Statistical Office). The two forest study sites were deciduous forests at Vilma-puszta
200 (47°05'06"N, 17°51'51"E), characterized by sessile oak (*Quercus robur*) and flowering ash
201 (*Fraxinus ornus*), and near Szentgál (47°06'39"N, 17°41'17"E), characterized by beech
202 (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*), surrounded by a rural matrix, both ca. 3
203 km away from the closest human settlement. At each site we monitored great tits breeding in
204 artificial nest boxes that were placed on trees. Throughout the breeding season, we checked
205 the nest boxes twice a week and recorded the number of eggs and/or nestlings at each visit. To
206 avoid inducing nest desertion, we never removed incubating females from their nests during
207 nest checks (Dubiec, 2011). When the nestlings were 5-9 days old (day 1 being the day when
208 the first nestling hatched), we captured one parent with a string-operated trap door on their
209 nest (described in detail in Seress et al. 2017); this trapping method does not harm the parents,
210 and has no significant effect on the survival and body condition of nestlings (Seress et al.,
211 2017). Upon capture, we ringed the birds with a unique combination of a metal ring and 3

212 plastic color rings and recorded their sex based on plumage characteristics, and released them
213 near their nest after a standard, 10-15 minutes long measurement routine. The color rings
214 ensured that we could distinguish the two parents on video recordings. To minimize stress, we
215 always trapped only one of the two parents before the tests, or neither of them in case of 15
216 pairs where one or both parents had already been ringed in previous years.

217 Between 8 and 16 days (mean \pm *SD*, urban birds: 12.15 \pm 1.69; forest birds: 13.17 \pm
218 1.38) of nestling age, we conducted two behavioral tests that quantified the birds' responses to
219 humans (questions 1, 2 and 4) and to a sparrowhawk (questions 3 and 4). These two tests took
220 place in randomized order, each on a different day (1 to 5 days apart from each other, mean \pm
221 *SD* = 1.78 \pm 1.16 days). Tests have been performed at varying time of the day, between 7:12
222 and 18:49 (mean \pm *SD* = 11:15 \pm 178 minutes). Both tests consisted of three main phases
223 (Figure 1): a 15 minutes long (mean \pm *SD* = 932 \pm 77 sec) pre-stimulus phase and two test
224 phases, each 20 minutes long (1224 \pm 52 sec and 1237 \pm 59 sec for the first and the second
225 test phase respectively). Both test phases were further divided into two equal-length periods:
226 the first with a stimulus present (stimulus period) and the second after removing the stimulus
227 (post-stimulus period, see below). The tests were recorded by a camera (GoPro Hero 2; 7 \times
228 5.5 \times 5 cm), which was concealed in a black plastic box that was 15 cm from the nest
229 entrance and was permanently attached to the nest box, installed before the breeding season so
230 birds were already familiar with its presence. In a former experiment we have validated that
231 this box hid the camera effectively, as further familiarization to the camera did not have any
232 effect on the birds' return latency after nest disturbance (Seress et al., 2017). Due to logistic
233 constraints as well as to avoid too much disturbance for ethical reasons, we kept the length of
234 each daily test \leq 1 hour, and we never conducted the two tests on the same day at the same
235 nest, and we conducted each test only once at each nest. While this approach did not allow us
236 to test within-individual repeatability and within-individual correlation of the two forms of

237 risk-taking behavior (as suggested by Dingemanse et al., 2010; Dingemanse et al., 2012), it
238 still allowed us to test the within-site and across-site phenotypic correlation of the two
239 responses (Myers & Hyman, 2016; Davidson et al., 2018; Scales et al., 2011; Bókony et al.,
240 2012; Riyahi et al., 2017).

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

245

246 ***Human disturbance test***

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

262 order of the two persons was randomized between the two test phases. Both persons
263 announced their arrival and their departure audibly to the camera, thereby the start and end of
264 each stimulus phase was identifiable from the video recordings.

265

266 *Sparrowhawk test*

267 The sparrowhawk test followed a protocol largely similar to the human disturbance test, with
268 a pre-stimulus phase and two test phases (Figure 1). Before checking the contents of the nest
269 box and starting the pre-stimulus phase, the experimenter placed a tripod below the nest box,
270 with the tripod's top ca. 3 m away from the entrance, which remained there until the end of
271 the test. We considered this distance to be short enough for the birds to perceive approaching
272 and entering the nest box in presence of the stimulus as risky (i.e. even though being inside
273 the nest box may be safe, approaching it when a predator is nearby is likely dangerous). The
274 experimenter left the proximity of the nest and only returned briefly at the start and end of
275 each stimulus period to place or remove the stimulus under the nest. The first test phase was a
276 'dove phase', during which a mounted collared dove (*Streptopelia decaocto*) was present on
277 the tripod for the 10 minutes of the stimulus period (608 ± 42 sec), whereas the second test
278 phase was a 'sparrowhawk phase' during which a mounted sparrowhawk was present on the
279 tripod for the 10 minutes of the stimulus period (611 ± 33 sec). Both stimuli were followed by
280 a 10-minute (627 ± 36 sec) post-stimulus period, during which no dummy was present on the
281 tripod. The order of the two stimuli was fixed, with the dove always preceding the
282 sparrowhawk. We decided on fixed order because we expected the sparrowhawk to be a lot
283 more threatening than the collared dove, and thus there would be strong carry-over effects in
284 the second phase if the sparrowhawk was presented first (Bell, 2013). We used sparrowhawk
285 as the predator stimulus because it preys primarily on small passerines, including great tits
286 (Newton & Marquiss, 1982; Götmark & Post, 1996; Zawadzka & Zawadzki, 2001) and also

287 frequently breed in both urban and non-urban habitats (Thornton et al., 2017). We used the
288 collared dove as control because it is a granivorous species (thus not perceived by tits as
289 potential predator or competitor) that is common in both urban and non-urban habitats in
290 Hungary, and is close in size to the sparrowhawk. We had two dove mounts and two
291 sparrowhawk mounts, which were randomly alternated between tests. At the start and end of
292 each stimulus period, the placement and the removal of the mount was announced audibly by
293 the experimenter.

294

295 *Data processing*

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

312 whereas in the sparrowhawk test we could use 40 males and 34 females from 43 nesting
313 attempts. We tested the correlation between the two responses for a subset of individuals
314 where both tests could be analyzed (33 males and 22 females from 36 nesting attempts).

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

330 A few (1 to 7; mean \pm *SD* = 2.93 \pm 1.56) days before the human disturbance and the
331 sparrowhawk tests, we conducted 3 other behavioral tests, described in detail in Preiszner et
332 al. (2017). These tests began with a 30-minute baseline observation period each, which we
333 used in our current analyses to quantify the birds' provisioning behavior when no threatening
334 stimulus (tripod, mount, or human) was present at the nest (apart from the very short presence
335 of the experimenter at the beginning of the test to install and start the camera). We calculated
336 a 'baseline return latency' from the 3 \times 30 minutes of these observations as each bird's

337 average return latency, i.e. the time elapsed until the first return into the nest box averaged
338 over the three observations (13%, 10% and 6% of birds did not return to the nest during the 30
339 minutes in the first, second and third baseline observations, respectively; these birds were
340 given a latency of 1800 sec). We used this baseline provisioning behavior because it was
341 estimated from a broader time range (90 minutes over several days) compared to the pre-
342 stimulus behavior (15 minutes right at the test start), thus it may more accurately represent
343 persistent characteristics such as territory quality in regards of food (Tremblay et al., 2005)
344 and intrinsic foraging abilities of the parents (Cole et al., 2012). By contrast, pre-stimulus
345 behavior may more accurately represent the immediate inner state of the parents.

346

347 *Statistical analyses*

348 All analyses were run in R (version 3.3.0; R Core Team 2016), using the ‘irr’ (Gamer et al.,
349 2012), ‘coxme’ (Therneau, 2012), ‘car’ (Fox et al., 2010), ‘MASS’ (Venables & Ripley,
350 2002) and ‘lsmeans’ (Lenth, 2016) packages. First, to validate that return latency is an
351 individually consistent variable, we tested the repeatability of return latencies by comparing
352 the pre-stimulus phases of the two tests using Spearman’s rank correlation and the intraclass
353 correlation coefficient (ICC; Nakagawa and Schielzeth 2010). These pre-stimulus latencies
354 are likely influenced by both the birds’ motivation to feed their offspring and their sensitivity
355 to short disturbance at the beginning of the test. Birds that did not enter the nest during one or
356 both pre-stimulus phases were excluded from the ICC analysis because this method requires
357 normally distributed residuals, which would be violated if we used the maximal values for
358 those latencies we could not measure. All data were used for the Spearman’s rank correlation.

359 To test our research questions, we built Cox’s proportional hazards models (henceforth
360 Cox models), with maximal latencies used as censored observations. For each question, we

361 ran a separate model and extracted pre-planned comparisons from the model's estimates as
362 follows. For our first 3 research questions, each model included a focal interaction, along with
363 a set of potentially confounding variables that may influence return latency, and bird ID
364 nested in pair ID as random factors. The focal interaction estimated the birds' mean behavior
365 (i.e. their log hazards ratio, expressing their chances of returning to the nest) in each phase at
366 each site. We then removed statistically non-significant confounding variables with $P > 0.1$
367 via stepwise backwards model selection, but never omitted our focal interaction. For factors
368 with more than two levels and their interactions, we calculated P-values with simultaneous
369 (type 2) analysis-of-deviance tests. This model-reduction procedure enhanced model fit
370 ($\Delta AIC > 6$) and reduced estimation uncertainty while retaining all important parameters with
371 estimates qualitatively similar to the full models (Supplementary Tables S1-4). The full
372 models including all considered confounding variables and the final models that contain only
373 the statistically significant ($P < 0.05$) and marginally non-significant ($0.05 < P < 0.1$)
374 confounding variables besides our focal interaction are presented in the supplementary
375 material (Supplementary Tables S1-4). From the estimates of the final models, we calculated
376 the birds' behavioral response, i.e. the difference between test phases, for each site. Finally,
377 we compared these behavioral responses between the two habitat types by calculating the
378 difference in response between the two forest sites versus the two urban sites (Figure 1). All
379 these differences were derived from the parameter estimates and errors estimated by each
380 model as linear contrasts of least-squares means (Lenth, 2016). We used this approach rather
381 than including habitat type as a fixed effect and site as a random effect because variance
382 estimations of random effects with few levels are unreliable (Piepho et al., 2003; Bolker et al.,
383 2008), whereas including both habitat type and site as fixed effect would have resulted in a
384 model with high collinearity between these two factors (Dormann et al., 2013). Note that pre-
385 planned comparisons are a powerful approach for testing *a priori* hypotheses (Ruxton &

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

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

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

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

406 In this model, we included site \times person as the focal interaction, where “person” was a 2-level
407 factor (familiar or unfamiliar). Response to hostile versus unfamiliar humans was calculated
408 as the difference between the unfamiliar and familiar person phases. The initial model also
409 included the following confounding variables: baseline return latency, pre-stimulus return

410 latency, trapping status, trapping status \times person interaction (to test whether trapped birds
411 were sensitized to the familiar hostile person specifically), number of nest checks, test order,
412 nest height from the ground, sex, number of nestlings, age of nestlings, calendar date and time
413 of day, as well as the phase \times site \times person interactions (“phase” in this case was a 2-level
414 factor, i.e. first or second test phase). By the latter interaction we aimed to test whether the
415 birds’ discrimination between persons depended on the order the people were presented, and
416 whether this order effect differed between sites.

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

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

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

425 To test our fourth question, we used a subset of birds ($N = 55$ birds from 36 nests) for which
426 we had data from both tests. We could not directly test the relationship between the response
427 to humans and the response to sparrowhawk with a Cox model, because we had censored
428 latencies in both variables (i.e. the only information we have on some birds is that they did not
429 return during the entire phase; such information can be adequately handled in the dependent
430 variable of Cox models but not in the predictor variables). Therefore, first we tested the
431 relationship between return latencies in the human disturbance test and in the sparrowhawk
432 phase of the sparrowhawk test with Spearman rank correlation. However, this analysis does
433 not take into account the control variables (i.e. behavior in the pre-stimulus phase of the

434 human disturbance test and in the dove phase) and pseudo-replication (i.e. two latencies for
435 each individual in the human disturbance test and two birds per nest). To handle these issues
436 in a more complex analysis, we estimated each bird's response to each stimulus as its residual
437 latency in the test phase relative to its latency in the respective control phase, as follows. We
438 expressed the birds' response to human disturbance (regardless whether the person was
439 familiar hostile or unfamiliar) by building a Cox model with return latency in the test phases
440 (two phases per bird) as dependent variable and pre-stimulus return latency as fixed effect
441 (covariate). This model contained no random factors because it was not used for significance
442 testing but for estimating the relationship between the individuals' behaviors in non-disturbed
443 and disturbed situations. We extracted the martingale residuals (Therneau et al., 1990) for
444 each bird in each test phase from this model (henceforth 'residual return speed'; note that
445 larger residuals belong to faster returns, i.e. shorter latencies). To similarly express the birds'
446 response to sparrowhawk, we built a Cox model with return latency in the sparrowhawk phase
447 as dependent variable and return latency in the dove phase as fixed effect (covariate), and then
448 extracted the martingale residuals (one for each bird) from this model. To test whether there
449 was a linear relationship between the responses elicited by the two types of threat across all
450 birds, we built a linear mixed-effects model with residual return speed in the human
451 disturbance test as the dependent variable (two data points per bird), residual return speed in
452 the sparrowhawk test as fixed effect (covariate), and bird ID nested in pair ID as random
453 factors. We tested whether the regression slope differed among sites using a similar model
454 that also included site as fixed factor and its interaction with the covariate. Additionally, we
455 included sex, trapping status, nest height, number of nestlings, age of nestlings, and phase
456 (first or second person) as fixed effects in our initial model, and removed them stepwise until
457 only statistically significant ($P < 0.05$) and marginally non-significant ($0.05 < P < 0.1$)
458 confounding variables remained. From the final model, we estimated the slope of regression

459 (i.e. relationship between the two responses) for each site; then we compared the two forest
460 slopes with the two urban slopes by calculating a single linear contrast (see Supplementary R
461 script) to test whether the relationship between the two responses differed between the two
462 habitat types.

463

464 **Results**

465 Return latencies in the pre-stimulus phase were significantly correlated between the human
466 disturbance test and the sparrowhawk test using all birds (Spearman's $\rho = 0.288$, $P = 0.032$, N
467 $= 55$). Among birds that returned to their nest in both pre-stimulus phases, we found fairly
468 high and significant repeatability between the two pre-stimulus phases ($ICC = 0.51$, $F_{30,31} =$
469 3.08 , $P = 0.001$, $N = 31$, Supplementary Figure S1). Both estimates indicate consistent
470 variation among individuals in their return latency after the brief disturbance of test start (i.e.
471 their risk-taking in a mildly risky situation).

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

473 Overall, the birds responded to the presence of humans, as they returned to the nest later in the
474 test phases than in the pre-stimulus phase (Supplementary Table S1, Figure 2A)., This
475 response was stronger in trapped birds than in non-trapped birds (linear contrast: $0.953 \pm$
476 0.346 , $z = 2.76$, $P = 0.006$; Supplementary Table S1, Table 2A). The difference between the
477 pre-stimulus and test phases (i.e. response to human disturbance) was significant for both
478 trapped and non-trapped birds in all sites except for Balatonfüred, the site with the lowest
479 sample size for this test, where it was marginally non-significant for the trapped and non-
480 significant for the non-trapped birds (Table 2A, Figure 2A).

481 Response to human disturbance was significantly greater in forest than in urban sites,
482 i.e. forest-dwelling birds increased their latencies in the test phases compared to the pre-

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

489

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

492 Return latencies did not differ significantly between the familiar hostile and unfamiliar
493 persons' phases in any of the four sites (Table 2B), and there was no significant difference
494 between urban and forest habitats in the response to hostile versus unfamiliar humans (Table
495 2B, Figure 2B). There was a marginally non-significant phase \times person interaction
496 (Supplementary Table S2), but none of the pairwise comparisons were significant following
497 FDR correction (Supplementary Table S6; Supplementary Figure S2). Trapped birds returned
498 later than non-trapped birds, but the trapping status \times person interaction was non-significant
499 (Supplementary Table S6).

500

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

502 Return latencies were longer in the sparrowhawk phase than in the dove phase in all four sites
503 (Table 2C, Figure 2C); these differences were statistically significant in Veszprém and
504 Szentgál (the city and forest site, respectively, with the largest sample size) (Table 2C).
505 Responses to sparrowhawk (i.e. contrasts between the two phases) tended to be greater in
506 forest than in urban habitats, i.e. forest birds delayed their return in the sparrowhawk phase

507 compared to the dove phase to a greater extent than urban birds did (Table 2C, Figure 2C). In
508 this test, one forest bird at Vilma-puszta was an outlier (Figure 2C) that did not return in the
509 dove phase; after removing this outlier the difference between forest and urban birds'
510 responses increased and became statistically significant (contrast \pm SE = 1.220 ± 0.550 ; $z =$
511 2.22 ; $P = 0.027$). Furthermore, only 3 out of 27 forest birds (11%) entered the nest while the
512 sparrowhawk dummy was present, whereas 43% of urban birds did so (χ^2 test: $\chi^2_1 = 6.515$, P
513 $= 0.011$; Table 1).

514

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

516 Across all birds we found a weak but significant correlation between the return latencies in
517 the human disturbance and the sparrowhawk tests (Spearman's $\rho = 0.233$, $P = 0.014$ $N = 55$.
518 individuals); however, when we controlled for "baseline behaviors" and pseudo-replication,
519 this correlation was no longer significant (regression slope: $b \pm SE = 0.12 \pm 0.14$, $t_{18} = 0.87$, P
520 $= 0.396$, $N = 55$ birds). Within each of the four study sites, the correlation between responses
521 to humans and responses to sparrowhawk was not significant either with simple Spearman
522 correlations (Szentgál: $\rho = -0.034$, $P = 0.860$; Vilma-puszta: $\rho = 0.165$, $P = 0.648$;
523 Balatonfüred: $\rho = 0.291$, $P = 0.275$; Veszprém: $\rho = 0.095$, $P = 0.494$; Figure 3A) or with the
524 mixed model of residuals (Table 3, Figure 3B). Importantly, the regression slopes did not
525 differ significantly between urban and forest sites (linear contrast: -0.248 ± 0.428 ; $t = -0.58$; P
526 $= 0.570$).

527 The other predictors of return latencies were also different between the two test
528 situations. Trapped birds returned later than non-trapped birds in the human disturbance test
529 (Supplementary Tables S1, S2, S4) but not in the sparrowhawk test (Supplementary Table
530 S3). Return latencies in the sparrowhawk test were longer at later times of the day, and
531 somewhat also later in the season (Supplementary Table S3), whereas birds with longer

532 latencies in the baseline observation also had longer latencies in the human disturbance test
533 (Supplementary Table S1). In both tests, birds with fewer nestlings returned later
534 (Supplementary Table S1, S2, S3).

535

536 **Discussion**

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

543

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

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

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

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

564 Whether a person was previously hostile or had no previous encounter with the birds had very
565 little if any effect on the great tits' behavior in the human disturbance test. This lack of
566 differentiation between the familiar hostile and unfamiliar person indicates that great tits
567 either did not recognize the people or perceived them as equally threatening. Although the
568 ability to recognize individual humans is often associated with particularly intelligent species
569 such as corvids (Marzluff et al., 2010; Lee et al., 2011), it has also been demonstrated in other
570 birds like passerines and pigeons (Levey et al., 2009; Vincze et al., 2015; Belguermi et al.,
571 2011). Great tits often perform well in learning and problem-solving tasks (Sasvári, 1979;
572 Preiszner et al., 2017), thus, if individual recognition of humans is part of a more general set
573 of cognitive abilities, great tits are likely to have the cognitive capacity for it. Instead, we
574 suggest that differentiating between humans might have little ecological relevance for both
575 urban and forest great tits, for two reasons. First, recognizing individual humans may be the
576 most relevant in habitats with low but non-negligible human population density (such as
577 farmlands) where repeated encounters with the same individual humans are likely (Vincze et
578 al., 2015). In forest habitats, encounters with humans are very uncommon, whereas in cities,
579 only few of the many people may be encountered repeatedly, at least in public areas like our
580 study sites. Second, as great tits are perceived as pleasant birds by the public, hostility

581 towards them is probably rare in both habitat types. Some species where the ability to
582 differentiate between hostile and non-hostile humans was demonstrated, such as pigeons
583 (Belguermi et al., 2011) and house sparrows (Vincze et al., 2015), have long evolutionary
584 history with humans who have often persecuted them as pests, thus recognizing hostile people
585 may be more beneficial for them.

586

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

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

600 Urban birds tended to show a weaker avoidance response to the sparrowhawk, i.e. they
601 were more likely to enter their nest while the raptor dummy was present, and they did not
602 increase their return latency compared to the dove phase as strongly as forest birds did. The
603 higher risk-taking of urban birds might be explained by sparrowhawk attacks being less
604 frequent in cities. For example, some censuses indicate that raptors like sparrowhawks are less

605 common in urban habitats (Møller & Ibáñez-Álamo, 2012), possibly because they are more
606 sensitive to human disturbance than smaller prey species (Møller, 2012). Furthermore, even
607 predators that are abundant in urban habitats can pose a lower level of threat to certain prey,
608 for example by shifting their diet in cities, preferring easier and/or more abundant prey
609 (Rodewald et al., 2011). Although we do not have data on great tit predation rates by
610 sparrowhawks at our study sites, our earlier research indirectly suggests that urban
611 sparrowhawks in our area might preferentially hunt for house sparrows (Bókony et al., 2012;
612 Seress et al., 2011). Alternatively, it is possible that the weaker avoidance response to
613 sparrowhawk is due to a human-mediated spillover effect, i.e. that urban birds became less
614 vigilant towards humans, and thereby their vigilance towards non-human predators also
615 decreased (Geffroy et al., 2015). We would expect such an effect if responses to humans and
616 to non-human predators are forced by common mechanisms into a phenotypic correlation, as
617 predicted by the general risk-taking hypothesis. This possibility is discussed next.

618

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

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

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

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

655 Interestingly, both earlier studies found that behaviors within the same domain (i.e. avoidance
656 versus aggression) remained correlated even in urban birds: there was a habitat-independent
657 correlation between avoidance of humans and avoidance of novel objects (Carrete & Tella,
658 2017), as well as between aggression towards predators and aggression towards conspecifics
659 (Myers & Hyman, 2016). Despite focusing on a single domain, however, we found no
660 phenotypic correlation in the risk-taking in great tits. Taken together, these findings suggest
661 that detecting the existence or breakdown of phenotypic correlations might depend on the way
662 behaviors are quantified (Davidson et al., 2018).

663 *Cautionary remarks*

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

670 First, we could not ensure that the birds were present at the nest at the start of the tests,
671 and we could not collect reliable data on when each individual detected the stimulus, because
672 great tits often move hidden in the foliage and also because observing the vicinity of the nest
673 during the test would have caused too much disturbance. Thus, the variation in the time when
674 the birds arrive to the proximity of the nest and see the stimulus for the first time can cause
675 additional variation in their latencies to enter the nest. This shortcoming has two
676 consequences. On the one hand, it might bias our assessment of risk-taking if birds in one
677 habitat type systematically arrive earlier, e.g. due to higher chick-feeding frequency.
678 However, our analyses controlled for such potential biases by including several co-variables
679 that account for differences in "baseline behavior" (i.e. over 3 days before the tests, in the pre-

680 stimulus phase right at the test start, and in the dove phase). On the other hand, individual
681 variation in first arrival and detection time may also introduce noise into our data, which
682 makes our analyses conservative (i.e. less powerful to detect existing effects). Thus, while we
683 found convincing evidence for habitat-dependent risk-taking towards both stimuli, it is
684 unclear whether our negative results (i.e. lack of differentiation between hostile and
685 unfamiliar humans; no correlation between risk-taking towards the two stimuli) mean that the
686 effects were non-existent or existent but not strong enough to be detected. Because our study
687 apparently had the power to detect strong effects like the higher tolerance of human
688 disturbance in urban birds (which has been demonstrated in many other studies), we can
689 conclude that it is unlikely that noise in our data would have masked a strong differentiation
690 between hostile and unfamiliar humans or a strong correlation between risk-taking towards
691 humans and sparrowhawk. By hearing alarm calls or seeing a bird appearing on camera, we
692 could confirm that at least one member of the pairs was present in 53% of the stimulus
693 periods the human disturbance test and 87% in the stimulus periods of the sparrowhawk test.
694 Furthermore, in the 30-minute baseline observations (314 observations of 105 individual
695 birds), 87% entered the nest before 25 minutes, and following the first time they entered, they
696 had a nest visit rate of 1.55 ± 1.32 per 10 minutes. This also suggests that, if the nest visit rate
697 did not drop extremely within a few days, the vast majority of birds were in the proximity of
698 their nests during the stimulus periods.

699 Second, we could not measure the responses of the two parent birds at each nest
700 independently from each other. Theoretically, the parents may have influenced each other's
701 behavior, e.g. the more cautious member of the pair could have observed its mate entering the
702 nest, which might have altered its own latency either by encouraging it (shorter latency) or by
703 decreasing the urgency to feed the nestlings (longer latency). However, in another
704 experimental study with the same great tit populations, we found very little evidence for such

705 effects (Seress et al., 2017). Both sexes increased their vigilance at the nest after being
706 captured by humans, but it did not influence the partner males' behavior and, although
707 increasing the partner females' vigilance to a small extent, it did not alter the chick-feeding
708 rates of the partner females (Seress et al., 2017). These findings suggest that, if the partners
709 affect each other's risk-taking at all, they tend to become more similar to each other (e.g. a
710 cautious male making his mate more cautious). This would result in a strong random effect of
711 pair identity, which we took into account in all our analyses. Thus, we believe that our
712 conclusions are not likely to be confounded by partner effects.

713

714 ***Conclusions***

715 Risk-taking towards humans and towards non-human predators are often considered to be
716 correlated. We found that although urban great tits took more risk both towards humans and
717 towards sparrowhawks than forest-dwelling great tits, the two behaviors did not correlate with
718 each other either across or within habitats, which suggests that the habitat-specific changes in
719 risk-taking behavior of great tits may not be driven by a general "syndrome" (phenotypic
720 correlation) in risk-taking. These results have several implications for the research on anti-
721 predator behavior. First, behavior towards humans may not necessarily be a reliable indicator
722 of overall anti-predator behavior (Seress & Liker, 2015). Several studies treat the two as
723 equivalents, generalizing responses to humans as an estimate of responses to any kind of
724 predator (Møller & Ibáñez-Álamo, 2012; Møller, 2012; Jiang & Møller, 2017; Møller et al.,
725 2013; Michelangeli et al., 2018). Our results suggest that responses to humans and to non-
726 human predators do not necessarily covary, thus we need to be careful with this kind of
727 interpretation. Second, our results show that measuring the same behavior on different levels
728 (i.e. populations versus individuals) can lead to different conclusions. If we compare the mean
729 behavior between habitats, we may come to the conclusion that responses to humans and

730 responses to sparrowhawk are strongly related to each other, as urban birds were more risk-
731 taking towards both stimuli. However, looking at correlations between the two responses
732 within populations can lead to the opposite conclusion, i.e. that there is no relationship
733 between responses to humans and responses to sparrowhawk. Thus, it is important to look at
734 behavioral variation on multiple levels (Dingemanse et al., 2010). Third, the contrast between
735 our results and other recent studies addressing the relationship between responses to humans
736 and to non-human predators (Myers & Hyman, 2016; Carrete & Tella, 2017) suggests that
737 estimating the same trait (e.g. risk-taking) from different forms of behavior (e.g. aggression
738 versus avoidance) might yield different results. Therefore, comprehensive studies
739 investigating several behavioral domains at the same time along the urbanization gradient will
740 be important for furthering our understanding of urban adaptations.

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

753

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971

972

973 **Table 1:** Percentage of birds that entered the nest while the stimulus was present (number of
 974 birds that entered and did not enter shown in brackets; the latter category includes those that
 975 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)

976

977 **Table 2:** Responses to various threats within the 4 study sites, and differences (linear
978 contrasts) of these responses between urban and non-urban sites. A: Responses to human
979 disturbance (i.e. linear contrasts between behavior in the pre-stimulus phase and the test
980 phases, estimated separately for trapped and non-trapped birds). B: Responses to familiar
981 versus unfamiliar humans (i.e. linear contrasts between behavior in the test phases with the
982 unfamiliar and familiar persons). C: Responses to sparrowhawk (i.e. linear contrasts between
983 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

984

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

991 ^b P-values of within-site comparisons were adjusted with the FDR method.

992 ^c Sample size: 86 individuals of 50 pairs.

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

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

1000 ^f Sample size: 74 individuals from 43 pairs.

1001 ^g Positive contrast indicates that urban birds responded less strongly to the sparrowhawk than
1002 forest birds, i.e. the difference between the return latencies in the dove and sparrowhawk
1003 phases was smaller for urban than for forest birds.

1004

1005 **Table 3.** Regression slopes from models with behavior in the human disturbance test as
1006 dependent variable and behavior in the sparrowhawk test as explanatory variable (testing the
1007 relationship between responses to humans and responses to sparrowhawk by great tits) with
1008 confidence intervals (95% CI); sample size: 55 individuals from 36 pairs.

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

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1010

1011

1012 **Figure legends**

1013 **Figure 1.** Schematic illustration of our test protocols and the statistical analysis process
1014 (sketches drawn by EV).

1015 **Figure 2.** Return latencies at the four sites in the pre-stimulus phase and the two test phases of
1016 the human disturbance test (A), in the familiar and unfamiliar person phases of the human
1017 disturbance test (B) and in the two test phases of the sparrowhawk test (C). Sample sizes
1018 (number of individual birds) at each site for the human disturbance test and sparrowhawk test,
1019 respectively, are provided in brackets. Boxplots show the median and the interquartile range,
1020 with the whiskers representing data within the $1.5 \times$ interquartile range.

1021 **Figure 3.** Correlations at the four sites between return latencies in seconds in the human
1022 disturbance test and the sparrowhawk test (A) and between responses to human disturbance
1023 and responses to sparrowhawk (residual return speed expressed as martingale residuals from
1024 Cox models, controlling for pre-test behavior; see Methods) (B). Sample sizes (number of
1025 individual birds) at each site are provided in brackets.