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2 **Altitudinal differences in foraging decisions under predation risk in great**

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4

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21 **ABSTRACT**

22 Foraging decisions under risk of predation are crucial for survival as predation risk can  
23 contribute to a reduction of food intake over time leading to a trade-off between starvation  
24 and predation. Environmental variation can provoke changes in food accessibility or predation  
25 risk that will in turn affect foraging decisions. Specifically, less predictable or harsher  
26 environments, such as those found at high elevation, should lead to more risk-prone foraging  
27 in order to prevent risk of starvation, but empirical confirmation of this hypothesis is lacking. In  
28 the current study, we used video playbacks combined with an automatic feeder to measure  
29 continuous foraging choices between control and predator videos by wild great tits originating  
30 from high and low elevations and tested under controlled conditions. Great tits discriminated  
31 between two conditions representing differences in predation risk and visited the feeder less  
32 frequently when a predator was shown. Moreover, we found that birds from low elevation  
33 populations were more risk-averse and visited the feeder significantly less when a predator  
34 video playback was broadcasted compared to high elevation individuals. This elevation related  
35 contrast was also dependent on the season, body mass and fat reserves of individuals, and was  
36 more marked in females. Furthermore, adults visited the feeder less in the presence of a  
37 predator compared to yearlings. These results are consistent with predictions from life history  
38 theory and starvation-predation trade-off hypotheses and could have implications for  
39 individual movements and population dynamics in changing environments.

40

41 **KEYWORDS**

42 Behavioral plasticity, elevation, foraging, *Parus major*, predation risk, risk-taking behavior,  
43 video playback

44

## 45 INTRODUCTION

46 Foraging decisions in the wild are in part driven by a starvation-predation risk trade-off  
47 (Houston et al. 1997). While it is vital to find food to survive, the associated risk-taking due to  
48 exposure to predators can lead to lethal consequences (Lima and Dill 1990). Animals are  
49 expected to evolve strategies to limit such risks and models have predicted the existence of  
50 behavioral variations in response to changes in predation pressure (Lima and Bednekoff 1999).  
51 For example, birds limit the time spent at foraging patches when the perceived risk of  
52 predation increased (Krams 2000; Verdolin 2006; Villén-Pérez et al. 2013). They can also rely  
53 on indirect cues of predator presence to stop their foraging activity such as mobbing calls  
54 (Desrochers et al. 2002), alarm calls (Lind et al. 2005) or odors (Amo et al. 2008). By choosing  
55 more exposed foraging patches when hungry, individuals may be more exposed to predators  
56 (Hilton et al. 1999). Likewise, through a dilution effect, foraging in groups can reduce the risk  
57 of being predated while foraging (Hamilton 1971; Morse 1978). As a consequence, birds in  
58 large flocks are more risk-prone (i.e. are willing to take more risks) than solitary conspecifics  
59 (Dolby and Grubb 2000). These foraging decisions can have effects on reproductive success  
60 and fitness as well as consequences on population dynamics (Cresswell 2008).

61

62 Theory on foraging strategies predicts that the starvation-predation risk trade-off should be  
63 impacted by environmental variation (Cresswell et al. 2009). Foraging decisions of passerines  
64 in winter should aim to optimize fat reserves in order to avoid starvation in harsher conditions  
65 (e.g. shorter days, less and more unpredictable food; Lima 1986; Houston and McNamara  
66 1993). Therefore, individuals with higher metabolic rates (Mathot et al. 2015) or lower body  
67 mass (Rogers 1987) are more-risk prone, as their trade-offs tilt towards a higher risk of  
68 starvation (Pakanen et al. 2018). Similarly, individuals from different elevations face different  
69 foraging constraints as colder temperatures increase metabolic requirements and resource

70 availability is more uncertain and scarce as elevation increases (Körner 2007). At high  
71 elevation, passerines have different daily routines, with foraging peaks in early morning and  
72 late afternoon, compared to low elevation birds which prefer to forage during the middle of  
73 the day (Pitera et al. 2018). These differences were more marked in harsher periods such as  
74 winter, where birds needed to make greater investments in foraging to reach their optimal  
75 level of reserves to avoid starvation (Pitera et al. 2018). Foraging decisions are predicted to  
76 also depend on predation (McNamara et al. 1994). Predation risk might decrease with  
77 elevation in some cases (Sasvári and Hegyi 2011). For example, European sparrowhawk –a  
78 major songbird predator– abundance decreases with increased elevation (Newton et al. 1977;  
79 Newton et al. 1986). Reduced predator avoidance behaviors should arise at lower predation  
80 risk, a pattern confirmed in a meta-analysis pointing out that high elevation individuals show  
81 less intense predator avoidance behaviors on average (Stankowich and Blumstein 2005).  
82 However, not all studies show the same general pattern. In response to a threat, flight  
83 initiation distance in dark-eyed juncos (*Junco hyemalis*) from high elevation was greater than  
84 for low elevation individuals (Andrade and Blumstein 2020). Likewise, in a breeding context,  
85 latency of mountain chickadees (*Poecile gambeli*) to go back to their nest box after a predator  
86 presentation was longer in high elevation birds (Kozlovsky et al. 2015a). Results from these  
87 two studies do not match the prediction that birds from high elevation should show weaker  
88 anti-predator responses and suggest that the specific life-history contexts may influence risk-  
89 taking behavior. Indeed, parameters other than elevation may impact risk avoidance decisions,  
90 notably in a foraging context.

91

92 Apart from environmental variation, individuals may exhibit different risk-taking foraging  
93 behaviors depending on their individual attributes such as physiological state (McNamara and  
94 Houston 1990). Lighter individuals with fewer fat reserves may suffer faster from food

95 deprivation and thus might forage under higher predation risk to avoid starvation (Rogers  
96 1987). Moreover, females (Saitou 1979) and smaller or younger individuals (Hegner 1985;  
97 Sandell and Smith 1991) are usually subordinates and therefore are expected to have access to  
98 lower quality foraging habitats. As a consequence, these categories of individuals might have  
99 to forage in less optimal foraging patches with higher predation exposure thus taking more  
100 risks (Brown 1999; Brodin and Utku Urhan 2015). Furthermore, predator recognition and the  
101 ability to react properly to predators might require time to develop and not yet be fully  
102 operational in yearlings (Putman et al. 2015). Thus, anti-predator behavior could be age-  
103 dependent. Similarly, consistent behavioral variations among individuals, i.e. personality could  
104 impact foraging decisions (Sih et al. 2004). The fast-slow exploration continuum (Dingemanse  
105 et al. 2002) is thought to be closely related to optimal foraging decisions (Toscano et al. 2016).  
106 The link between exploration and foraging has been experimentally confirmed in different taxa  
107 under predation risk (Réale et al. 2007; Jones and Godin 2010; Dammhahn and Almeling 2012).  
108 In birds, the perception of predation risk is integrated differently by individuals based on their  
109 personality (Quinn and Cresswell 2005). Shy individuals appear to be more sensitive to the risk  
110 of predation while bolder individuals are more risk-prone in their foraging decisions (van Oers  
111 et al. 2004; Quinn et al. 2012; Coomes et al. 2022). However, the impact of personality on  
112 foraging decisions under predation risk has, to our knowledge, not yet been investigated  
113 across contrasting elevations.

114

115 In order to understand how elevation influences changes in the starvation-predation trade-off  
116 and associated risk-taking behavior, it is necessary to test individuals under controlled  
117 conditions (Kawecki and Ebert 2004). Bringing individuals into captivity allows standardization  
118 of recent exposure to predators, as well as controlling for food availability and energetic  
119 needs. In this study, we compared the foraging behavior of wild great tits (*Parus major*)

120 brought into captivity from high and low elevation populations expected to be facing different  
121 ecological and predation pressures. We used video playbacks to test behavioral responses to  
122 predator encounters, as birds are known to perceive information provided by videos as  
123 realistic information of risk of predation (Zoratto et al. 2014), and use them to make decisions  
124 and modify their behavior accordingly. We expected that birds would forage less during  
125 predator presentations compared to control stimuli. Then, we examined whether there were  
126 differences in responses towards predators in relation to the elevation of origin of the birds  
127 and if age, personality, fat reserves or sex influenced these responses.

128

129

## 130 **METHODS**

### 131 Study sites and species

132 We caught wild great tits (N=192) from 4 distinct populations in the French Pyrenees (Aubert,  
133 430 m asl., 42°57'51.4"N, 1°06'11.3"E; Montjoie, 445 m asl., 42°59'56.0"N, 1°10'09.3"E; Antras,  
134 891 m asl., 42°52'51.7"N, 0°56'44.4"E; Villargein, 898 m asl., 42°54'17.1"N, 1°02'48.0"E). These  
135 populations were at least 5 km apart and no movement between them has been detected  
136 since the beginning of our group's population monitoring in 2012. In previous work, we studied  
137 the variation of ecological factors along this elevational gradient including differences in winter  
138 mean temperature (from 8°C at 200 m asl. to -0.5°C at 2000 m asl. with a decrease of  
139 ~5°C/1000 m, Buisan et al. 2016), increased variance in temperature at higher elevation, and  
140 ensuing impacts on nesting density, the phenology of nesting behavior and fitness (see Bründl  
141 et al. 2019; Bründl et al. 2020). Likewise, there are significant differences in vegetation cover  
142 and parental behavior across the same gradient (Lejeune et al. 2019). Studies on birds from  
143 these populations have also shown contrasts in cognitive traits across this relatively modest

144 elevational shift (Cauchoix et al. 2017; Hermer et al. 2018; Hermer et al. 2021). Based on this  
145 previous work, we grouped our capture sites by referring to “high” (Antras and Villargein;  
146 mean 894 m asl.) and “low” (Aubert and Montjoie; mean 437 m asl.) populations. At each  
147 elevation, we thus had several replicates where elevation was the key difference among  
148 experimental groups.

149

150 To verify that overall predation risk varied across elevations, we quantified relative predator  
151 abundance using camera traps (Busnell Trophy Cam HD Essential E2<sup>®</sup>) set in front of custom  
152 made resin great tit models placed 1.5m from the ground across our elevational range (See  
153 supplementary materials for images, Figure S1). From February to August of 2016 and 2017,  
154 we conducted a total of 232 week-long monitoring sessions. We scored images for avian  
155 versus mammalian predators and found that overall predator abundance decreased from  
156 lower to higher elevations (Main effect: ANOVA,  $N=143$ ,  $F=6.53$ ,  $P=0.002$ ; 100-600m vs 600-  
157 1000m:  $T=2.32$ ,  $N=96$ ,  $Est.=1.92\pm 0.83$ ,  $P=0.058$ ; 100-600m vs 1000-1500m:  $T=3.47$ ,  $N=106$ ,  
158  $Est.=2.72\pm 0.79$ ,  $P=0.002$ ; 600-1000m vs 1000-1500m:  $T=0.95$ ,  $N=104$ ,  $Est.=0.81\pm 0.86$ ,  $P=0.612$ ;  
159 Figure 1). Mammal predators are known to attack small passerines on the ground, at feeders  
160 and in roosting boxes through fall and winter (Orell 1989), creating a world of fear experienced  
161 by great tits. Although sparrowhawks were absent from our images, previous studies on  
162 similar elevation gradients suggest that sparrowhawks show the same pattern as other  
163 predators (Newton et al. 1977; Newton et al. 1986).

164

165 Captures using mist nets took place in 8 batches (24 individuals per batch) between mid-  
166 October 2020 and mid-March 2022 during fall (10 October – 20 December) and winter (21  
167 December – 10 March). We marked each bird with a unique CRBPO (Centre de Recherche sur  
168 la Biologie des Populations d’Oiseaux, French bird ringing office) metal band and a colored

169 band containing a PIT-tag (Passive Integrated Transponders, IB Technology, UK) for detection  
170 with an RFID (Radio Frequency Identification) reader. We used plumage dimorphism to sex  
171 (male or female) and age (adult or yearling) birds (Svensson 1992). We quantified fat reserves  
172 by scoring fat deposited in the furculum using a 4-point scale (0: no visible fat; 1: base of  
173 tracheal pit obscured by fat but less than half full; 2: flat filling the tracheal pit but not bulging;  
174 3: fat filling tracheal pit, bulging and overlying pectoral muscle, modified from Gosler 1996).  
175 We also measured body mass at capture and at release using a digital scale (nearest 0.1g) and  
176 tarsus length (nearest 0.1mm) at capture as a proxy for body size.

177

#### 178 Housing and captivity schedule

179 Each aviary at the CNRS-SETE facilities (1 x 5 x 3 m, W x L x H) consisted of an indoor (1 x 1 m,  
180 W x L) and an outdoor (1 x 4 m, W x L) area (See supplementary materials for images, Figure  
181 S2). Birds were housed individually, we alternated cages by elevation so that neighbors came  
182 from different elevations, and one empty cage separated neighboring birds who nonetheless  
183 remained visually and acoustically connected to others in outdoor areas in order to minimize  
184 stress. Birds freely moved in their aviaries between the indoor and the outdoor areas. Cages  
185 were enriched with foliage for cover, an artificial tree, horizontal perches, a roosting box, and  
186 water. Birds were fed *ad libitum* with sunflower seeds and mealworms between video  
187 playback experiments. In each indoor area of the aviary, an automatic, RFID-based feeder,  
188 called the "OpenFeeder" (Cauchoix et al. 2022) provided sunflower seeds. Upon release in  
189 aviaries, an exploratory score was measured for each bird as the total number of movements  
190 (either flights or hops) completed during a 3 min period, following Dingemanse et al. 2002).  
191 This measure performed in a novel environment has been found repeatable in other  
192 populations of great tits (Dingemanse et al. 2012). Furthermore, the first measure of  
193 exploratory behavior in a novel environment is a good proxy for the personality of an

194 individual (Niemelä and Dingemanse 2018). The predation risk experiment was performed on  
195 the last day of captivity (day 29) at which point birds were used to feeding from the  
196 OpenFeeder and had experience with images projected on video screens for other  
197 experiments. Previous exposure to screens entailed projection of different numbers of  
198 congeners presented on the screens, but our experimental birds had never seen predators on  
199 the screens. All birds had experienced the same tests prior to the present experiment. Sample  
200 sizes of some batches were lower than the maximum of 24 as a result of technical errors (N=6),  
201 a lack of interaction with the OpenFeeder (N=3), or death during a cold snap in January 2021  
202 (N=1; final sample size: 182 birds rather than 192). After the predation risk experiment, we  
203 removed the RFID tag, inspected each bird to make sure it was in good condition, and released  
204 them at their respective capture sites.

205

## 206 Video playback broadcasting

207 Perceived risk of predation was simulated with video playbacks (Oliveira et al. 2000; Rieucan  
208 and Giraldeau 2009; Zoratto et al. 2014; Snijders et al. 2017; Smit and van Oers 2019) which  
209 are an effective tool to test several individuals at the same time whilst controlling the  
210 predation risk stimuli. The stimuli were extracted from YouTube videos showing either a  
211 blackbird (*Turdus merula*) for control stimuli or an Eurasian sparrowhawk (*Accipiter nisus*) for  
212 predation stimuli. Only sequences of birds perched and life size at full screen projection were  
213 kept. Sound was removed from videos to avoid potential influences of vocalizations. Each  
214 stimulus was created with OpenShot Video Editor software (OpenShot Studios, LLC.) and lasted  
215 30s to mimic a realistic encounter with a wild bird (see supplementary materials).

216 The video presentations were performed during a morning session from 9 am to noon and an  
217 afternoon session from 1 pm to 4 pm. Outside of these periods, no video was projected on the  
218 screen and birds had *ad libitum* access to food. During the two experimental sessions, the

219 OpenFeeder was the only source of food available. Every morning, aviaries were swept to  
220 remove potential food present on the ground. In each aviary a 22-inch computer monitor (Dell  
221 P2219H or P2217) placed next to an OpenFeeder in the indoor section was used to broadcast  
222 videos through a Raspberry Pi 3B+ (Raspberry Pi Foundation). Every 30s, the Raspberry Pi  
223 played a video randomly selected from 18 different recordings (9 sparrowhawk, 9 blackbird)  
224 such that each bird experienced an equal number of predator and control videos but in a  
225 different order. The large number of projections (720 total playbacks to each bird) ensured  
226 that each bird would see both control and predator stimuli when seeking food. Although video  
227 playbacks were broadcasted without interruption, birds freely decided when to forage and  
228 were only in close proximity with a video playback for a limited amount of time as birds come  
229 to the feeder, take a single seed, and eat it on a perch away from the feeder. All birds of a  
230 specific batch were tested simultaneously and could only see the computer screen of their  
231 own aviary. The RFID reader on the OpenFeeder recorded when the bird came to feed and  
232 during which video. If the bird arrived during the last 5s of a video, the current video stimulus  
233 was reread another time to avoid a shift in stimulus while the bird was feeding.

234

## 235 Data analysis

236 All analyses were performed using R software (R version 4.2.2, R Core Team 2022). Foraging  
237 behavior of each individual was quantified by pooling the number of visits to the OpenFeeder  
238 during the whole day of the experiment as feeding patterns did not shift throughout the day  
239 (i.e. we did not detect habituation to the setup; See supplementary materials). To examine  
240 differences in feeder visitation rates between predation and control contexts, we compared  
241 the relative number of visits for these two conditions within individuals using a repeated  
242 measures ANOVA with season and site of capture as explanatory co-variables. In order to  
243 confirm the result of this analysis, we performed a permutation test (*permuco* package,

244 Frossard and Renaud 2021) with 10 000 iterations following the same structure as the initial  
245 ANOVA (season and site of capture as fixed factors, bird identity nested in video playback as a  
246 random factor) and following the Kennedy method adjusted for exact permutation of repeated  
247 measures models (Kherad-Pajouh and Renaud 2015). To examine the effect of individual  
248 characteristics (age, sex, exploration, body mass, fat reserves and body size) on predator-  
249 context dependent foraging, we built generalized linear mixed models (GLMM, *lme4* package,  
250 Bates et al. 2014) with a binomial distribution and the relative number of visits to predation  
251 and control contexts as the response variable. We used the `cbind` function of the number of  
252 visits during sparrowhawk playback (“predator”) and number of visits during blackbird  
253 playbacks (“control”; 2 column matrix) to account for variation in total number of visits among  
254 individuals in the response variable. Individual characteristics (sex, age, elevation of origin,  
255 exploration score, body mass, fat reserves, tarsus length, season of experiment; see  
256 supplementary materials, Table S1 for metric means and Table S2 for sample sizes by category)  
257 were included as explanatory variables. Dominance may impact risk-prone foraging behavior  
258 more in harsher, high elevation populations so we added interaction effects between elevation  
259 and body mass, fat reserves, tarsus length, sex and age as these variables may impact  
260 dominance rank. We also included an interaction between elevation and season as we  
261 expected high elevation sites to increase in harshness more with season shifts relative to low  
262 elevation populations. Finally, we added an interaction between elevation and exploration  
263 score as previous work in a congener has shown elevational differences in exploration of a  
264 novel environment (Kozlovsky et al. 2015b). All numeric variables (exploration score, body  
265 mass, fat reserves, tarsus length) were centered on the mean and scaled by their standard  
266 deviation prior to integration in the model. Batch of capture was added as a random factor to  
267 control for variation due to series of capture and year effects. Results were similar when using  
268 body mass at capture or at release. Only the former is presented in the results (but see

269 supplementary materials for model with body mass at release, Table S3). Final models included  
270 all main effects, but only significant interactions (Faraway 2016). Post-hoc Tukey HSD tests  
271 (*emmeans* package, Lenth et al. 2022) were run to assess the significance of differences  
272 between levels. Model performance was checked graphically using the *DARHMa* package  
273 (Hartig 2022). We also checked for multi-collinearity among fixed effects using the  
274 *performance* package to estimate the Variance Inflation Factor (VIF) which was below 5 for all  
275 variables (Lüdecke et al. 2021). While analyses were based on relative number of visits, figures  
276 represent the proportion of visits for graphical simplicity. The significance level for P-values  
277 was set at 0.05 (two-tailed tests).

278

279

## 280 **RESULTS**

### 281 Impact of predation risk on foraging preferences

282 As expected, birds visited the feeder less when a predator (sparrowhawk) was presented on  
283 the screen compared to when a control bird (blackbird) was shown on the screen (rmANOVA,  
284  $F=4.50$ ,  $df=181$ ,  $P=0.035$ ; Permutation test, 10 000 iterations,  $P=0.033$ ; Figure 2).

285

### 286 Correlates of variation in risk-taking foraging strategies

287 The birds' decision to reduce foraging in predation contexts depended on elevation in  
288 interaction with four ecological or individual factors (Table 1). First of all, the pattern was  
289 season-dependent (Elevation x Season:  $Z=2.51$ ,  $Est.=0.24\pm0.10$ ,  $P=0.012$ ; Table 1). In fall, birds  
290 from high elevation visited the feeder significantly more during predator playbacks than their  
291 low elevation counterparts (post-hoc test:  $Z=5.42$ ,  $N=92$ ,  $Est.=1.46\pm0.10$ ,  $P<0.001$ ; Figure 3A)  
292 whereas a tendency was detected in winter (post-hoc test:  $Z=2.17$ ,  $N=90$ ,  $Est.=1.15\pm0.07$ ,

293 P=0.061; Figure 3A). Second, heavier birds visited the feeder less when a predator was present  
 294 (Elevation x Body mass:  $Z=-2.00$ ,  $Est.=-0.12\pm0.06$ ,  $P=0.046$ ) but this pattern was only significant  
 295 for birds from low elevation (post-hoc test:  $Z=-3.96$ ,  $N=90$ ,  $Est.=-0.16\pm0.04$ ,  $P<0.001$ ; Figure  
 296 3B). Third, birds from high elevation visited the feeder more during predator playbacks when  
 297 their fat reserves were higher (Elevation x Fat score:  $Z=-2.10$ ,  $Est.=-0.11\pm0.05$ ,  $P=0.036$ ; post-  
 298 hoc test:  $Z=2.34$ ,  $N=92$ ,  $Est.=0.09\pm0.04$ ,  $P=0.019$ ; Figure 3C) whereas feeder visits did not differ  
 299 between contexts in relation to fat scores for birds from low elevation (post-hoc test:  $Z=-0.47$ ,  
 300  $N=90$ ,  $Est.=-0.02\pm0.04$ ,  $P=0.636$ ; Figure 3C). Finally, female foraging preferences differed  
 301 depending on their elevation of origin (Elevation x Sex:  $Z=2.91$ ,  $Est.=0.32\pm0.11$ ,  $P=0.004$ ) with  
 302 females from high elevation visiting more often the feeder when a predator was present (post-  
 303 hoc test:  $Z=4.92$ ,  $N=79$ ,  $Est.=1.46\pm0.11$ ,  $P<0.001$ ; Figure 3D). Interestingly, males showed an  
 304 opposite trend in their foraging decisions across elevations (post-hoc test:  $Z=1.97$ ,  $N=93$ ,  
 305  $Est.=1.15\pm0.08$ ,  $P=0.097$ ; Figure 3D). Overall, when birds from high and low elevation differed  
 306 in the proportion of visits during predator playbacks, high elevation birds were more risk-  
 307 prone (Figure 3).

308

309

310 Table 1: The relative number of visits to the OpenFeeder during predator (vs. control) video  
 311 stimuli is influenced by a bird's elevation of origin and individual characteristics. A positive  
 312 value for the estimate means that the bird is more likely to visit the OpenFeeder during  
 313 predator playbacks. For each categorical variable, the reference level is presented in brackets.  
 314 Values in bold are significant at  $P<0.05$ .

Model	Estimate	SE	95% conf int	Z value	P value
(Intercept)	-0.09	0.14	-0.37; 0.19	-0.64	0.524
<b>Elevation (Low)</b>	<b>-0.50</b>	<b>0.09</b>	<b>-0.68; -0.33</b>	<b>-5.59</b>	<b>&lt; 0.001</b>
Body mass	-0.05	0.05	-0.14; 0.05	-0.99	0.321

Model	Estimate	SE	95% conf int	Z value	P value
<b>Fat reserves</b>	<b>0.09</b>	<b>0.04</b>	<b>0.01; 0.16</b>	<b>2.34</b>	<b>0.019</b>
Sex (Male)	-0.03	0.08	-0.19; 0.13	-0.35	0.724
Season (Winter)	0.01	0.19	-0.36; 0.37	0.04	0.969
Tarsus length	0.00	0.03	-0.06; 0.05	-0.16	0.873
<b>Age (Yearling)</b>	<b>0.18</b>	<b>0.05</b>	<b>0.08; 0.28</b>	<b>3.61</b>	<b>&lt; 0.001</b>
Exploration Score	-0.04	0.02	-0.09; 0	-1.80	0.071
<b>Elevation x Body mass</b>	<b>-0.12</b>	<b>0.06</b>	<b>-0.23; 0</b>	<b>-2.00</b>	<b>0.046</b>
<b>Elevation x Fat reserves</b>	<b>-0.11</b>	<b>0.05</b>	<b>-0.21; -0.01</b>	<b>-2.10</b>	<b>0.036</b>
<b>Elevation x Sex</b>	<b>0.24</b>	<b>0.11</b>	<b>0.02; 0.46</b>	<b>2.10</b>	<b>0.036</b>
<b>Elevation x Season</b>	<b>0.24</b>	<b>0.10</b>	<b>0.05; 0.43</b>	<b>2.51</b>	<b>0.012</b>

315

316

317

## 318 **DISCUSSION**

319 The trade-off between starvation and predation in foraging decisions should change with  
320 environmental conditions (Bonter et al. 2013), for example, when facing less predictable or  
321 harsher environments like those encountered at higher elevations (Körner 2007; Pitera et al.  
322 2018). To control for the short-term influence of various factors interacting with elevation on  
323 foraging decisions under the risk of predation (e.g. food availability or thermal conditions)  
324 birds in our experiment were tested under standardized, controlled conditions in temporary  
325 captivity. As expected, we found that birds from high elevation maintained higher foraging  
326 frequency at the feeder under increased perceived predation risk compared to birds  
327 originating from lower elevations (Figure 3). This difference between high and low elevation  
328 birds was partly dependent on other factors, like the season (Table 1) as it was only significant  
329 for birds tested in fall (Figure 3A). In winter, individuals from low elevation became more risk-  
330 prone, approaching the risk levels during feeding of high elevation conspecifics. This could be  
331 linked with an increase in the harshness of foraging conditions (food limitation) from fall to  
332 winter at low elevation, leading to a higher risk of starvation under wintering climatic

333 conditions (Bejer and Rudemo 1985; Perdeck et al. 2000). In contrast, high elevation  
334 populations may experience more consistent harsher conditions from fall to winter. If  
335 conditions are already harsh in fall, birds may not shift their foraging decisions, which could  
336 explain the lack of seasonal difference of foraging decisions in high elevation birds. Food intake  
337 is critical to survival through winter and may therefore be the major driver of foraging  
338 decisions in our system where birds were kept in safe conditions (Houston and McNamara  
339 1993). Likewise, predator abundance could also be one of the factors explaining elevation  
340 differences we detected as lower risks of predation at high elevation might lead to lower  
341 vigilance and a more risk-prone foraging strategy. In line with previous studies (Newton et al.  
342 1977; Newton et al. 1986), we found that the number of predators detected decreased with  
343 elevation leading to a more intense “landscape of fear” at low elevation (Figure 1). This could  
344 partly explain the more risk-prone foraging detected in high elevation birds.

345

346 Interestingly, birds were tested after 28 days spent under controlled conditions with the same  
347 food availability and predator risk conditions, yet differences in risk-prone foraging strategies  
348 persisted between high and low elevation. While captivity could influence behavior (Butler et  
349 al. 2006), if birds had mostly used recent information on predation risk to make foraging  
350 decisions, we should not have detected differences in behavior between high and low  
351 elevation birds. Indeed, this captive period with homogenized conditions could have  
352 attenuated differences in behavior between high and low elevation birds, implying that our  
353 results are conservative. Moreover, it seems likely that reactions to the video playback were  
354 weaker than would be during exposure to a real predator as video playbacks do not affect all  
355 sensory channels (e.g. no acoustic signals). Finally, birds came from a number of populations at  
356 each elevation suggesting that elevation or life history traits tightly linked to elevation *per se*  
357 rather than other peculiarities of the different populations are responsible for the differences

358 we detected. Recent experimental studies have shown that presented with a disturbance or a  
359 threat, high elevation dark-eyed juncos flew away from a further distance (Andrade and  
360 Blumstein 2020) and high elevation mountain chickadees took longer to come back to their  
361 nest box (Kozlovsky et al. 2015a). While these studies show results going in the opposite  
362 direction to ours, both were performed during the reproductive period when birds might be  
363 facing other life-history trade-offs (e.g. current vs future reproductive success). In contrast,  
364 individual survival is the key fitness criteria for birds in winter, thus reducing the number of  
365 likely trade-offs impacting foraging decisions. Differences between our results and recent  
366 studies highlights the importance of considering a variety of ecological factors and life-history  
367 trade-offs to understand risk sensitive foraging decisions.

368

369 Starvation risk is influenced by the reliability of access to food and being dominant generally  
370 provides such access (Ficken et al. 1990). In our study, we found that at low elevation, heavier  
371 birds were more risk-averse than lighter conspecifics (Figure 3B). This result agrees with  
372 previous studies where body mass and risky decisions are negatively related (Rogers 1987;  
373 Macleod et al. 2005). Interestingly, lighter birds from both elevations appeared to be similarly  
374 risk-prone. These individuals may be facing similar high constraints to meet their nutritional  
375 needs since dominant individuals are usually heavier and have better access to food by  
376 competitively excluding lighter birds from food sources (Hegner 1985; Laet 1985; Ficken et al.  
377 1990). Despite ample food availability during captivity, differences in foraging behavior related  
378 to mass at capture were apparent and similar to the relationship with mass at release (Table  
379 S3). Birds can also modulate their metabolic effort to deal with starvation (Broggi and Nilsson  
380 2023) which could reinforce the effects of weight we detected. In addition, fat reserves can  
381 influence foraging decisions as with more fat reserves available, an individual is less  
382 susceptible to face starvation risks (Houston and McNamara 1993). We found that for low

383 elevation birds, the level of fat reserves did not impact risk-taking during foraging (Figure 3C).  
384 In our controlled system, food access is relatively predictable and available *ad libitum* so birds  
385 may not need to rely strongly on fat reserves (Gosler 1996). However, we still found that high  
386 elevation birds presenting a higher level of fat reserves were more risk-prone in their foraging  
387 decisions (Figure 3C). As starvation risk decreases with more fat reserves, we would expect  
388 birds with higher fat reserves to be more risk-averse (McNamara and Houston 1990). We can  
389 speculate that with higher fat reserves, metabolic expenditure increased (Brodin 2001) and so  
390 birds from harsher conditions need to be more risk prone to meet increased foraging needs.  
391 Fat reserves and metabolic rates likely interact in complex ways and influence how risk taking  
392 during foraging shifts with environmental harshness.

393

394 We also showed that females – who are often subordinate to male great tits (Carrascal et al.  
395 1998) – are sensitive to environmental contrasts (Figure 3D). Since males have priority access  
396 to food, females need to develop alternative strategies to meet their foraging needs, such as  
397 better memorization (Brodin and Utku Urhan 2015). In harsher environments such as those  
398 found at high elevations where finding food is expected to be harder, adult males should be  
399 able to have priority access to food resources and thus should be more risk-averse than  
400 females (Lahti 1998). Finally, yearlings were more risk-prone regarding their foraging decisions,  
401 although we found no significant effect of elevation on their responses (Figure 4A). Juveniles  
402 often have less access to food as they are subordinates to adults (Sandell and Smith 1991) and  
403 occupy less optimal habitats. Thus, adopting risk-prone foraging strategies could be the "best  
404 of a bad job" solution for non-dominant individuals allowing them to reach their minimal food  
405 intake and fat reserves (Krams et al. 2010). Alternatively, in some mammal and bird species,  
406 yearlings do not consistently discriminate between a predator and a non-predator (Kullberg  
407 and Lind 2002) and predator recognition improves with age (Putman et al. 2015). Learning

408 allows individuals to adjust their behavior according to the local risks they face and thus limit  
409 the costs associated with excessive vigilance behaviors (Blanchard and Fritz 2007). Our  
410 experiment took place during the winter season where yearlings were about 6-9 months post  
411 hatch. Due to their younger age, these birds could have had fewer encounters with predators  
412 in their life to date than adults and thus might be less likely to consistently identify  
413 sparrowhawks as a potential threat. However, Kullberg and Lind (2002) showed that four  
414 months after fledging juvenile great tits were able to responded to a predator stimuli. It is  
415 possible that the reaction of yearlings towards sparrowhawks in our populations takes longer  
416 to develop than the one found by Kullberg and Lind (2002) and is thus driven by naivety  
417 towards predators. As an alternative, yearlings could be slower to react to a predator's  
418 appearance or disappearance on the screen. A fast response relies on a high level of behavioral  
419 plasticity (Dingemanse and Wolf 2013), which has been shown to be lower for young  
420 individuals (Bonamour et al. 2020). Our study provides further evidence that age plays a critical  
421 role in driving behavioral foraging plasticity and suggests a mechanism to explain lower  
422 survival of first year birds compared to older ones (Martin, 1995). Nestlings face high rates of  
423 predation after fledging (Naef-Daenzer et al. 2001), and risk-prone yearlings might face higher  
424 rates of predation thus becoming proportionally less present in populations. Albeit difficult to  
425 quantify, future studies should examine the factors that underlie the ontogeny of risk-taking in  
426 juveniles and their effects on their first year survival.

427

428 Personality has been identified as a key component of individual decisions (Mathot et al. 2012;  
429 Rojas-Ferrer et al. 2020) and could have an important impact on foraging. However, we found  
430 no clear impact of exploration score in a novel environment on foraging decisions (Figure 4B).  
431 Previous studies showed that fast explorers decreased their foraging activity more under  
432 predation risk (Abbey-Lee et al. 2016) and that they are more flexible in their reaction to

433 predation risk by switching food preferences (Coomes et al. 2022) or returning to feed faster  
434 following a stressful disturbance (van Oers et al. 2004; Quinn and Cresswell 2005). Moreover,  
435 high elevation birds were identified as being slower explorers compared to low elevation birds  
436 (Kozlovsky et al. 2014). We therefore expected fast explorers to be more risk averse, especially  
437 for birds from low elevation, but this was not the case. In our experiment, we did not measure  
438 the rapidity to react to a change in the predation risk but overall preferences in foraging  
439 decisions. Such decisions are known to also depend on dominance status (Quinn et al. 2012).  
440 Future studies should directly examine whether exploration behavior is really associated with  
441 risk-prone strategies, in interaction with dominance status, and linked to other fitness traits.

442

443 Overall, we found that foraging decisions under predation risk vary among elevations in  
444 association with individual characteristics, in accordance with starvation-predation trade-off  
445 theory. The differences in risk-taking during foraging we detected were still persistent despite  
446 the fact that birds spent 28 days under standardized conditions where all individuals had the  
447 same levels of food, competition, ambient temperature, and risk of predation. The contrast  
448 between adults and juveniles raises the question of how and when individuals learn the proper  
449 responses to be adopted. It would also be important to determine how long individuals retain  
450 information about predation risk in their habitat and use that information to modulate their  
451 foraging behavior. This question is not trivial as anthropogenic induced climate change is  
452 causing range shifts including movements towards higher elevations (Parmesan and Yohe  
453 2003; Campos-Cerqueira et al. 2017), which brings individuals adapted to their population of  
454 origin into areas with different risks and constraints. If such areas include a higher risk of  
455 predation, these "immigrant" birds may take more risks and suffer higher mortality. On the  
456 other hand, if individuals avoid risk-taking when moving to areas with lower risk, they may  
457 miss out foraging opportunities and not get enough food. Further experiments should examine

458 the mechanisms underlying risk-taking and whether there is a link between the ontogeny of  
459 risk-taking and the ability to move to new habitats. Such results would help us understand how  
460 individuals might cope with changing climates.

461

462

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469

470

## 471 **AUTHOR CONTRIBUTIONS**

472 TC, PH and ASC designed the study. TC collected, analyzed the data and wrote the first version  
473 of the manuscript. ASC and PH helped capture and house birds, provided input on analyzes,  
474 and corrected and improved the manuscript. All the authors gave final approval for  
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476

477

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488

489

## 490 **DATA AVAILABILITY STATEMENT**

491 Analyses reported in this article can be reproduced using the data provided by (Crouchet et al.  
492 XXXX).

493

494

## 495 **ANIMAL WELFARE NOTE**

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## 775 LIST OF FIGURES

776 Figure 1: Predator abundance distribution in great tit habitats. The predators, birds (dark  
777 orange) and mammals (green), were detected via camera traps along an elevation gradient in  
778 the Pyrenees split in three classes (100-600 m; 600-1000 m; 1000-1500 m). Letters above each  
779 bar denote significant differences in posthoc comparisons of altitudinal ranges.

780

781 Figure 2: Proportion of visits when a control (blackbird) or predator (sparrowhawk) was shown  
782 on the screen. Shown are the medians (black horizontal line), with the interquartile ranges  
783 (boxes) and distributions (violins) of the proportion of visits for each video playback category.

784

785 Figure 3: Proportion of visits during predator playbacks according to elevation of origin of focal  
786 birds (blue=high elevation and red=low elevation) according A) season of the experiment, B)  
787 body mass, C) fat reserves and D) sex of focal individual. Shown in colored dots are the  
788 predicted values from the model using the number of visits under predation or control  
789 contexts (cbind function). Regression lines with 95% confidence intervals (panel B and C) and  
790 mean predicted proportion of visits  $\pm$  SE from the model (panels A and D) are shown. N=182  
791 individuals.

792

793 Figure 4: Proportion of visits during predator playbacks according to age and exploration  
794 scores. Black dots show the predicted mean proportion of visits  $\pm$  SE from the model with the  
795 predicted median and quartiles shown in the boxes (panel A) and the regression line with 95%  
796 confidence intervals (panel B). Predicted values from the model using the number of visits  
797 under predation or control contexts (cbind function) are in colored dots (blue=high elevation,  
798 red=low elevation), with their distribution (violins in Panel A). N=176 individuals for Age and  
799 182 individuals for exploration score.

800

801 **LIST OF TABLES**

802 Table 1: The relative number of visits to the OpenFeeder during predator (vs. control) video  
803 stimuli is influenced by a bird's elevation of origin and individual characteristics. A positive  
804 value for the estimate means that the bird is more likely to visit the OpenFeeder during  
805 predator playbacks. For each categorical variable, the reference level is presented in brackets.  
806 Values in bold are significant at  $P < 0.05$ .