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# Repeatable parental risk taking across manipulated levels of predation threat: no individual variation in plasticity

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Individuals respond adaptively to their environment. Yet, they may differ in their responses even when confronted with the same environmental challenge. Several complementary conceptual frameworks suggest that within populations among-individual variation in life history strategies aligns not only with individuals' propensities to take risks across different situations but also with their sensitivity to variation in environmental cues. Risk-prone individuals, suggested to invest more in current reproduction at the cost of their future reproductive prospects, are predicted to be less sensitive to environmental variation than risk-averse individuals. We tested this prediction in a population of breeding blue tits, *Cyanistes caeruleus*, by confronting them with different levels of predation threat at their nests and recording their latency to resume brood provisioning after the removal of the predator stimulus. We presented taxidermic woodpecker, *Dendrocopos major* (a common brood predator) and sparrowhawk, *Accipiter nisus* (a common adult predator) mounts at each nest, respectively representing low and high levels of threat to adult blue tits. As a nonpredator control stimulus, we presented a blackbird, *Turdus merula*, mount. We found that on average parents took longer to resume provisioning after presentation of a sparrowhawk than a woodpecker or blackbird. Furthermore, individual latency responses across all threat levels taken together were repeatable. However, despite the population level plastic adjustment to the level of predation threat, we found no evidence for among-individual variation in plasticity. Instead, individual differences in responses were roughly maintained across all levels of threat. While our findings show that individuals differ in their level of risk taking, in the high-stakes and ecologically relevant context of predation risk during parental care, commonly held expectations about among-individual variation in behavioural plasticity were not met.

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Individuals continually adjust their behaviour to the temporal and spatial variation in their environment. Yet, there is plenty of evidence that individuals within populations consistently differ in their behavioural responses even when confronted with the same environmental challenges (Bell et al., 2009; Réale et al., 2007; Sih et al., 2004). While this suggests constraints on unlimited behavioural plasticity (DeWitt et al., 1998; Kappeler et al., 2013), plasticity itself can also vary among individuals (Kontiaainen et al., 2009; Stamps, 2016; Westneat et al., 2011). For example, in wild great tits, *Parus major*, individual males differ not only in the mean level but also in the plasticity of their territorial aggressiveness (Arya-Ajoy & Dingemanse, 2017). Importantly, variation in behavioural plasticity may be heritable (Arya-Ajoy & Dingemanse, 2017;

Dingemanse et al., 2012) and can have fitness consequences (Han & Brooks, 2014; Houslay & Wilson, 2017). While among-individual variation in the mean expression of behaviours has been well documented across a plethora of contexts (reviewed by Bell et al., 2009; Garamszegi et al., 2013; Réale et al., 2010), the quantification of individual variation in behavioural plasticity, particularly in the wild, has received far less empirical attention (but see e.g. Class & Brommer, 2016; Hertel et al., 2020; Kontiaainen et al., 2009; Stamps & Biro, 2016; Westneat et al., 2015).

Several conceptual frameworks explaining the emergence and persistence of individual behavioural variation within populations also take the fact that individuals may vary in their plasticity into account. Early work rooted primarily in laboratory studies on feral mice and rats posits that individuals differ in behavioural (and neurophysiological) 'coping styles' along a reactive–proactive axis in response to environmental challenges (Koolhaas et al., 1999, 2010). According to this coping-style concept, reactive individuals

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adapt flexibly to variation in the environment and are generally cautious whereas proactive individuals are rigid in their behaviour, often forming routines (Koolhaas et al., 1999, 2010). Proactive individuals also tend to take greater risks, for example in the face of predation (Dingemanse & Réale, 2005; Koolhaas et al., 1999, 2010; Quinn et al., 2012). Complementing these ideas, behavioural, physiological and life history traits are suggested to covary among individuals that broadly differ in their so-called 'pace of life' along a continuum (Dammhahn et al., 2018; Réale et al., 2010; Wolf et al., 2007). Risk-prone individuals on the 'fast' end of the continuum are hypothesized to increase investment in current reproduction, whereas risk-averse 'slow' individuals safeguard their survival to invest in future reproduction (Réale et al., 2010). Fitness payoffs for 'fast' and 'slow' individuals purportedly differ depending on fluctuating population densities (Mouchet et al., 2021; Nicolaus et al., 2016). This pace-of-life syndrome framework has been extended to accommodate the additional hypothesis that risk-prone individuals are behaviourally less flexible than risk-averse individuals (Milles et al., 2022; Snell-Rood, 2013; Wright et al., 2019). Along similar lines, a speed–accuracy trade-off is invoked as a mechanistic link between the 'fast–slow' pace-of-life axis and variation in so-called individual 'cognitive styles' (Sih & Del Giudice, 2012). Finally, game-theoretical work shows behaviourally responsive and unresponsive individuals can coexist within populations as a mixed evolutionarily stable strategy (ESS) under the assumption that the fitness payoff to being responsive is negatively frequency dependent (Wolf et al., 2008; see also Dubois, 2019; Gomez-Mestre & Jovani, 2013). In parallel with such conceptual proliferation (see also Dingemanse & Wolf, 2010), there has also been advancement in the statistical approaches with which behavioural variation at different hierarchical levels (e.g. within and among individuals) can be analysed (Araya-Ajoy et al., 2015; Dingemanse & Dochtermann, 2013; Dingemanse et al., 2010; Housley et al., 2018; O'Dea et al., 2022; for details on our statistical approach see below). Despite development on both conceptual and methodological fronts, few studies have quantified among-individual variation in behavioural plasticity in response to ecologically relevant cues in the wild (but see e.g. Araya-Ajoy & Dingemanse, 2017; Couchoux et al., 2021; Dammhahn et al., 2022; Hall & Chalfoun, 2019; Mathot et al., 2011; Niemelä et al., 2021).

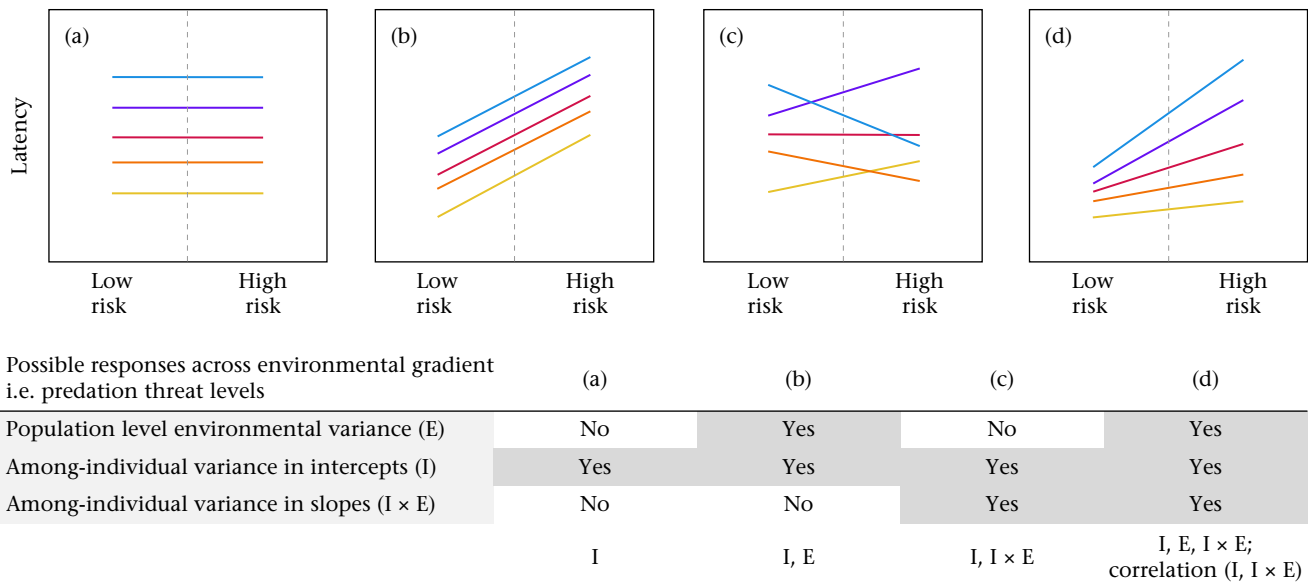
The phase of breeding in which parents care for young presents a unique opportunity to study individual variation in behavioural plasticity in a natural setting (Lucass et al., 2016; Royle et al., 2014; Westneat et al., 2011). Provisioning parents often face the conflict of whether to feed soliciting young or respond cautiously to an ambient threat of predation (Lima, 2009). The trade-offs for parental decisions in such circumstances are subject to a host of ecological conditions, and adaptive adjustment to these may have important fitness consequences (Dale et al., 1996; Ghalambor & Martin, 2001; Lima, 2009). Across varying levels of perceived predation threat, individuals may differ in their relative investments in current versus future reproduction and thereby in their propensity to take risks to provision their young (Dale et al., 1996; Lima, 2009). Moreover, individuals may differ in their responsiveness to varying levels of predation risk and hence in their plastic adjustment to the level of threat (Eggers et al., 2005). The study of plastic responses to predators within the context of parental care has already been put to good use in cross-species and cross-population comparisons (reviewed by Martin & Briskie, 2009 and Ibáñez-Álamo et al., 2015). There is now ample evidence for population level behavioural plasticity in response to predators at the nest, but few studies have implemented this paradigm to investigate within-population variation in individual plasticity (Royle et al., 2014; but see Betini & Norris, 2012; Thys et al., 2019).

In this study, we manipulated levels of perceived predation risk at the nests of breeding blue tits, *Cyanistes caeruleus*. Capitalizing

on a well-established assaying paradigm, we assessed individual differences in response to varying levels of risk to test for among-individual variation in behavioural plasticity. We measured the latencies of individual parents to resume brood provisioning (following Salazar et al., 2021) after presenting taxidermic mounts of a great spotted woodpecker, *Dendrocopos major*, and a Eurasian sparrowhawk, *Accipiter nisus*, representing different levels of predation risk to the adults. Both these species are found at our study site (S. M. Salazar, personal observation) and while woodpeckers pose a greater threat to blue tit nestlings as common nest predators (Curio et al., 1983; Stenning, 2018), sparrowhawks are known to predate heavily on both fledglings and adults (e.g. Adriaensen et al., 1998; Dhondt et al., 1998; Tinbergen, 1946; Vedder et al., 2014). As a nonpredator control stimulus, we presented a blackbird, *Turdus merula*, taxidermic mount at the nest. Blackbirds are also found in abundance at the field site (S. M. Salazar, personal observation). Each type of predator was presented twice at every nest to estimate both within-predator and overall repeatability.

We aimed at estimating individual variation in the plastic adjustment towards the manipulated levels of predation risk. We expected that at the population level latency measures would be shortest in response to a blackbird, longer in response to a woodpecker and longest in response to a sparrowhawk, matching the relative level of risk posed to adult blue tits. Our previous work has shown that individuals differ in their average level of risk taking (Salazar et al., 2021). In line with the conceptual frameworks described above we predicted that risk-prone individuals would be insensitive to the level of threat posed, whereas risk-averse individuals may be more sensitive to the differences in the type of predators and adjust their responses accordingly. Thus, our specific research questions were as follows. (1) Do breeding blue tits adjust their responses to different levels of predation threat at the nest and are individual responses repeatable across and within threat levels? (2) Do individuals also differ in their plasticity to respond to threat? (3) If individuals differ in their plasticity, then are the more plastic individuals also more risk averse?

We used two complementary statistical techniques to test for individual variation in plasticity (similar to the approach used in Housley et al., 2018 and Schmoll et al., 2020): first, a (behavioural) reaction-norm approach that models variation in the intercepts and slopes of individual behavioural phenotypes across an environmental gradient (Dingemanse et al., 2010; Nussey et al., 2007), and second, a character-state approach that treats responses measured in different contexts as separate response variables (Housley & Wilson, 2017; Mitchell & Housley, 2021). Within the behavioural reaction-norm approach so-called random regressions can be employed to estimate the (co)variance(s) of individual intercepts and slopes of behavioural phenotypes across an environmental gradient (commonly termed an individual-by-environment interaction, i.e. 'I × E'), but also across categorically different contexts (Brommer, 2013a; Dingemanse et al., 2010; Nussey et al., 2007). For an illustration of the reaction-norm approach in line with predictions of this study see Fig. 1. This approach is useful in simultaneously modelling individual mean level variation (as variation in intercepts: I) and plasticity (as variation in slopes) of behavioural phenotypes (I × E), as well as the covariance (correlation) between the two (Dingemanse et al., 2010). Using a multivariate modelling approach on the other hand, the character-state approach treats responses measured in different contexts as separate response variables, each with their independent fixed effects model structure (Brommer, 2013a; Via et al., 1995). The individual (co)variances between each of the response variables can be estimated in the same model (Housley & Wilson, 2017; Mitchell & Housley, 2021). Accordingly, deviation from a perfect, positive among-individual correlation between character states signals the presence of



**Figure 1.** A set of possible outcomes of our predation threat level manipulation illustrated using the behavioural reaction norm approach. Lines with different colours represent individuals' reaction norms of the latency to resume brood provisioning across levels of predation risk. In all cases here (a–d) we assume that individuals vary in the elevation of their individual intercepts across levels of threat (i.e. 'I', measured at the theoretical average level of threat; shown as a vertical dashed line). (b, d) Plastic adjustment to the manipulated levels of threat may occur at the level of the population (seen as an overall response to the environment, 'E'). (c, d) Individuals may also vary in the slopes of their reaction norms resulting in an individual-by-environment interaction ( $I \times E$ ). (d) In line with predictions of several conceptual frameworks, intercept elevation and slope may covary positively reflecting that risk-averse individuals are more plastic in their behaviour. Note that in line with our behavioural assay, shorter latencies reflect greater risk-taking responses, whereas longer latencies reflect lower risk taking. For a comprehensive illustration of variation at different hierarchical levels within a population see Figure 2 of Nussey et al. (2007).

individual variation in plasticity, an absence of plasticity variance being the null hypothesis.

## METHODS

### General Field Procedures

We conducted this study on a nestbox-breeding population of blue tits during the spring of 2019. The study site, on the de Vosbergen estate in the Netherlands (53°08'N, 06°35'E), held 200 nestboxes in 2019 designed specifically to accommodate breeding blue tits (26 mm entrance hole diameter). The nestboxes are mounted onto trees at roughly 2 m from the ground and are accessed using ladders. We conducted regular checks to monitor the start of breeding and establish lay date at each nest. Ten days after clutch completion, daily checks were conducted to establish the hatch date at the nest (for details on recording of the lay date and clutch size see Salazar et al., 2021). We also closely monitored brood sizes until nestlings fledged. We caught adult breeders when their broods were 7–9 days old (day 0 = hatching of the first egg, i.e. hatching date). Birds were caught with a spring-trap inside the nestbox while provisioning their broods. We fitted all breeders with a standard aluminium ring of the Dutch ringing station (Vogeltrekstation: <https://vogeltrekstation.nl/>) if not already present from previous captures, along with an RFID-equipped ring (2.3 mm EM4102 PIT tag, Eccel Technology Ltd., Groby, U.K.) which allowed us to record provisioning visits of an individual (see details below). The birds' sex (presence or absence of a brood patch; present in females only), age (first-year breeder or older; following Svensson, 1992) and standard morphological measures (tarsus length, third primary feather length and body mass) were recorded as part of the long-term population monitoring (following Korsten et al., 2006). We procured a small blood sample (around 10  $\mu$ l) by brachial venepuncture from all adults caught and from 15-day-old nestlings. DNA extracted from these blood samples was used for

microsatellite-based parentage analysis (as in de Jong et al., 2017) as part of a different study, but also to identify and discard risk-taking responses by polygynous males (following Salazar et al., 2021; see below for details).

### Measuring Responses to Manipulated Risk Levels

We conducted predator trials by simulating threat at the nest to measure the parents' latencies to resume brood provisioning as a measure of risk taking (following Salazar et al., 2021). At each nest, we presented taxidermic mounts of a woodpecker and a sparrowhawk of which the sparrowhawk represented a higher level of risk to adults. As a nonpredator control, we presented a blackbird at the nest (see Fig. 2 for a picture of the predator trial set-up). We set up RFID loggers at each nestbox (for details see Salazar et al., 2021), which allowed us to automatically record every entry and exit of provisioning birds (fitted with RFID rings, see above) as well as the latency to resume provisioning after presentation of a predator at the nest. The RFID loggers were programmed to run between 0600 and 2000 on days when brood ages were 10, 11 and 12 days at a respective nest. Over these 3 days we conducted two woodpecker, two sparrowhawk and two blackbird trials at every nest. One predator trial was conducted in the morning (between 0800 and 1100 hours) and one in the afternoon (between 1400 and 1700 hours) per nest. We thus aimed to carry out a total of six predator trials at every nest. The order of the predator type presented (i.e. blackbird, woodpecker or sparrowhawk) at each nest was randomized for the first three trials and this order was repeated for the next three trials (see Table 1 as an example). In doing so, each predator type was presented once in the morning and once in the afternoon and the presentation of the same predator type would only be repeated after a minimum of 1 day. Mounts of each predator type were randomly assigned to a given trial from a pool of three specimens each and no mount was presented more than once



**Figure 2.** Set-up of the (a) blackbird, (b) woodpecker and (c) sparrowhawk predator trials in which taxidermic mounts were placed atop a nestbox for 10 min during parental provisioning of blue tits. In (c) the RFID-equipped dummy nestbox is shown adjacent to that of the focal nestbox. A circular antenna around the entrance of the focal nestbox was used to read the RFID PIT tag of a provisioning parent and thus obtain its latency response.

at a given nest. An online random integer set-generator ([random.org/integer-sets](http://random.org/integer-sets)) was used for all randomizations.

Predator trials were carried out in a manner identical to those of an earlier study conducted in the spring of 2018 (Salazar et al., 2021). In short, a taxidermic mount was placed on the nestbox by an observer who left the area for the duration of the 10 min trial and returned to collect the mount at the end of the trial. If an adult blue tit was found inside the nestbox prior to the start of the trial, it was gently flushed out by the observer. The RFID set-up automatically measured the latency (s) of individual blue tit parents to resume provisioning their nestlings after the 10 min predator presentation (see Fig. 2). If individuals returned to feed before the end of the trial, we measured the latencies as negative values with the end of the 10 min trial taken as the zero mark. Additionally, from 1 h prior to the start of each predator trial, for each member of a breeding pair we calculated the mean time between consecutive provisioning events (hereon, the intervisit interval; see Salazar et al., 2021 for details on the calculation of intervisit intervals

from the RFID data). Taxidermic mounts were concealed during transport in the field.

In all, we conducted 377 predator trials at 64 nests. From these, we excluded individuals' latency responses for the following reasons. (1) At eight nests, males were not successfully trapped, ringed and RFID-tagged, and therefore we could not confirm their contributions to brood provisioning. Hence, we dropped all latency data from these nests (24 trials at eight nests). (2) Following Salazar et al. (2021), latency data collected at 16 nests were dropped altogether (94 trials at 16 nests) because the males were identified to be polygynous from the RFID data (for criteria applied see supplement of Salazar et al., 2021) or paternity analysis (following criteria in Vedder et al., 2011). Provisioning behaviour of polygynous males and their female partners is known to differ from regular biparental provisioning patterns (Schlicht & Kempenaers, 2021; see supplement of Salazar et al., 2021). (3) In 42 trials (conducted at 10 nests), provisioning by either member of the focal breeding pair before the predator presentation could not be

**Table 1**

An example of the order of predator type presented in consecutive predator trials conducted at two different nestboxes

Nestbox ID	Trial day	Time of day	Brood age (days)	Trial number	Predator type
A	Day 1	Morning	10	1	Woodpecker
		Afternoon		2	Sparrowhawk
	Day 2	Morning	11	3	Blackbird
		Afternoon		4	Woodpecker
	Day 3	Morning	12	5	Sparrowhawk
		Afternoon		6	Blackbird
B	Day 1	Morning	10	1	Blackbird
		Afternoon		2	Woodpecker
	Day 2	Morning	11	3	Sparrowhawk
		Afternoon		4	Blackbird
	Day 3	Morning	12	5	Woodpecker
		Afternoon		6	Sparrowhawk

Taxidermic mounts of either a woodpecker, sparrowhawk or blackbird were presented in morning and afternoon predator trials, when broods were 10, 11 and 12 days old. The order of the type of predator presented at a nestbox was randomized for the first three trials and this order was repeated for the next three trials such that for each predator type we conducted a morning and an afternoon trial.

confirmed based on the RFID data (five males, five females), possibly due to a long halt in provisioning or failure of the RFID tag. For these trials, we dropped all latency data (42 trials at 10 nests, with five nests dropping out entirely). (4) We excluded the data from seven predator trials at two nests (with one nest dropping out entirely) because of brood predation events prior to the start of these trials. (5) Twenty-four responses of individuals (14 females and six males from 16 nests) that were flushed out of the nestbox prior to the start of the trial (10 blackbird, seven woodpecker and seven sparrowhawk trials) were excluded as this procedure is known to affect provisioning latency (Davidson et al., 2018). (6) In one sparrowhawk trial (afternoon) a male did not resume provisioning until the next afternoon (i.e. prior to the start of the next afternoon trial). This was considered as an outlying response, and it was excluded. Our final sample size was 345 latency responses (121 woodpecker, 113 sparrowhawk and 111 blackbird) from a total of 34 males and 34 females measured in 186 predator trials conducted at 34 nests. We retained data of all individuals for which at least one latency measure was obtained (following Martin et al., 2011).

### Statistical Analysis

In brief, our statistical approach broadly comprised two main steps, the details of which can be found below. First, we estimated the repeatability of latency measures across and within levels of predation threat. In this step, we also investigated other sources of variation in latency and tested for overall differences in responses towards the blackbird, woodpecker and sparrowhawk. Second, using two complementary statistical techniques we investigated individual variation in plasticity. One technique was to model behavioural reaction norms: in three separate models, we compared the latency responses to the three levels of threat, taken two at a time (i.e. responses to blackbird versus woodpecker, blackbird versus sparrowhawk and woodpecker versus sparrowhawk). The other technique was to model character states: using this method we considered the latency measures in the blackbird, woodpecker and sparrowhawk predator trials as separate character states. In a single trivariate mixed model we estimated individual correlations between the three response variables along with the within-threat level repeatability. A high positive among-individual correlation of responses across predation threat levels denotes low among-individual variation in plasticity.

### Estimating repeatability of latency responses

In a first step we estimated the overall repeatability of latency by pooling latency responses across all predator trials (i.e. blackbird, woodpecker and sparrowhawk) in a single univariate mixed model. In this model, we included individual ID and breeding pair ID as random variables. We also estimated pairwise mean differences between blackbird, woodpecker and sparrowhawk trial latencies from this model. To estimate the repeatability of latency measures for a specific predator type, we ran separate univariate mixed-effects models for responses towards each predator type. In these models, we aimed to include individual ID, breeding pair ID and mount ID as random variables. However, the predator-specific models could not simultaneously estimate the effects of breeding pair ID and individual ID. Therefore, to estimate the proportion of variance explained by breeding pair ID we ran two separate sets of models: one including individual ID and mount ID and the other including breeding pair ID and mount ID (see Tables A1–A4).

Following Salazar et al. (2021) we controlled for a set of biologically relevant and study-design-specific variables as fixed effects in all models: sex and age (first-year breeder or older) of the bird, the number of nestlings in its brood (continuous variable), the hatching date of its brood (continuous variable), the age of the

brood in days (as a factor with three levels; 10, 11 or 12 days old), the time of day at which the trial was conducted (morning or afternoon), and the intervisit interval as measured prior to the trial (continuous variable). Additionally, we controlled for the effect of repeated measure sequence (first or second) of the same predator type as this is known to be an important variable in repeated measure designs (Dingemans et al., 2012). However, since it was not possible to simultaneously estimate the effects of brood age and of repeated measure sequence in the predator-specific models we ran two sets of models in which one or the other fixed effect was included (see Tables A1–A4).

### Individual variation in plasticity

To estimate individual variation in reaction norms using random regression (random intercept and random slope) models, we quantified variation in latency reaction norm slopes (and intercepts) from three univariate random-regression models. Based on our specific hypotheses, we modelled latency measures as a function of the level of predation threat (type of predator presented). We hypothesized that the level of threat posed would be in the order blackbird < woodpecker < sparrowhawk. Specifically, responses towards blackbird versus woodpecker, blackbird versus sparrowhawk and woodpecker versus sparrowhawk were run as three separate models in which individuals were allowed to vary in the elevation (intercept) and slope of their reaction norms, across the two predator types. For each of the three models, coding of the predator levels (initially 0 and 1) was mean centred. This procedure centres the (categorical) predictor variables to 0, at which the intercept variances (and hence also the intercept slope covariances) are measured (as illustrated in Fig. 1; Schielzeth, 2010). In each of three reaction norm models, we aimed also to include breeding pair ID as a random variable but were unable to simultaneously estimate the effects of breeding pair ID and individual ID. Therefore, to estimate the proportion of variance explained by breeding pair ID we ran two separate sets of models: one including only individual ID and the other including only breeding pair ID, estimating their respective variation in intercepts, variation in slopes and the correlation of intercepts and slopes (see Tables A5 and A6). Accounting for random slopes has the additional benefit of appropriately estimating uncertainty in the population level slope (Schielzeth & Forstmeier, 2009). Fixed effects found to be important in explaining variation in latency responses from the previous step (see Estimating repeatability of latency responses above) were included in each of these models.

To estimate among-individual correlations across character states, we fitted a trivariate mixed model. Latency responses in the blackbird, woodpecker and sparrowhawk predator trials were fitted simultaneously as separate response variables (character states). In this model, we estimated the among-individual variance for each of the three response variables as well as the among-individual covariances (correlations). Across-state within-individual covariances were constrained to zero by design (Dingemans & Doehrmann, 2013). We also estimated the among-breeding pair variance for the three response variables simultaneously (i.e. among-breeding pair variances were constrained to be equal across the response variables). The model was specified to estimate correlations rather than covariances as these are more stably estimable (Butler et al., 2009). This specification also allowed us to directly test whether individual correlations between character states differed significantly from 1 by comparing the initial model with identical models wherein the focal among-individual correlation was fixed at 1 (Dingemans et al., 2010; Mitchell & Houslay, 2021; for details on significance testing see below). Fixed effects found to be important in explaining variation in latency responses from the

previous step (see [Estimating repeatability of latency responses](#) above) were included in each of these models.

#### General modelling procedures

Statistical analyses were carried out using the R software (version 4.0.5, [R Core Team, 2021](#)). All models were fitted with a Gaussian error distribution using the ASReml R package (version 4.1.0, [Butler et al., 2020](#)). For the pairwise comparisons between blackbird, sparrowhawk and woodpecker latencies, we used the asremlPlus package ([Brien, 2021](#)). Significance estimates of the fixed effects were inferred from conditional Wald  $F$  tests. From the univariate models we calculated repeatability by dividing the among-individual variance by the total (phenotypic) variance. For the trivariate model we calculated repeatability for a given predation threat level, i.e. the response variable, by dividing the among-individual variance by the sum of the among-individual, among-breeding pair and residual variance for that specific response variable. Significance estimates for the individual random effects from all univariate models were inferred from likelihood ratio tests comparing nested models and using the chi-square distribution. The test statistic was calculated as twice the difference in log-likelihoods between the nested models and the degrees of freedom were taken as the difference in the number of their (co)variance parameters estimated. Similar likelihood ratio tests were used to infer significance estimates of the among-individual correlations in the character state model. Accordingly, the trivariate model was compared with subsequent models wherein the correlation of interest was fixed at +1 ([Dingemans et al., 2010](#); [Mitchell & Houslay, 2021](#)). Alpha was set to 0.05 for all analyses. We mean-centred all continuous fixed variables, aiding in interpretation of their respective model coefficients ([Schielzeth, 2010](#)). Homogeneity of variances and normality of residuals were visually assessed by plotting model residuals versus fitted values and with quantile–quantile ('QQ') plots.

#### Ethical Note

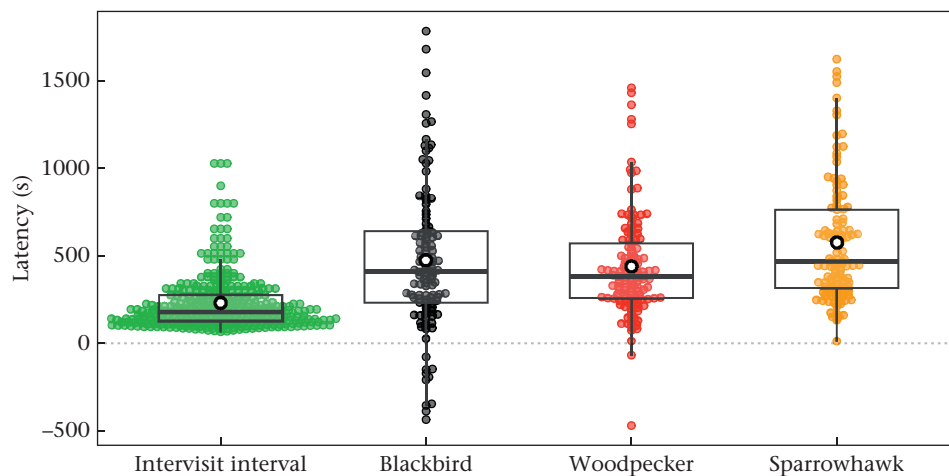
This study was approved by the Dutch Competent Authority (CCD; licence no. AVD1050020184968). The procedures involving handling of animals were carried out following Dutch and institutional guidelines for the care and use of animals. Trapping and ringing of birds were carried out under the supervision of persons licensed by the Dutch ringing authority (Vogeltrekstation). We conducted predator trials at a point of development when nestlings

have sufficiently developed feathers to thermoregulate independently of their parents. The 10 min duration of the predator trials was decided based on known provisioning rates in our study population ([Salazar et al., 2021](#)), with the intent of maximizing the probability that both members of a pair would encounter the stimulus while still minimizing interruption of nestling provisioning. Our randomization procedure also prevented breeding birds (and their nestlings) from being exposed consecutively to the high-risk treatment level (and to long feeding interruptions). Additionally, we set apart morning and afternoon predator trial time slots such that nestlings received sufficient feeds (1) prior to the predator trials in the morning, (2) between two trials conducted on the same day, and (3) before the onset of adult roosting in the evening. In the single case where a male did not resume provisioning after a morning predator trial until the next day, the female continued to provision despite the absence of the male. To minimize potential disturbance during breeding, all nestboxes in our study area are fitted year-round with dummy RFID antennas which are replaced with functional antennas during the 3-day RFID data collection.

## RESULTS

### Fixed Effects on Latency Responses

Latency measures in response to blackbird (median 408 s; range –436 to 1784 s), woodpecker (median 382 s; range –470 to 1460 s) and sparrowhawk (median 469 s; range 13–1624 s) showed considerable variation and were on average substantially longer than regular intervisit intervals in the absence of a predator trial ([Fig. 3](#)). In 10 blackbird and two woodpecker trials, birds resumed provisioning before the predator exposure ended (taken as negative values). No such responses occurred in the sparrowhawk trials, as birds never resumed provisioning while the sparrowhawk mounts were still present at the nestbox. We found the sparrowhawk latency responses (predicted mean = 560 s) to be 1.2 times (20%) greater than responses to a blackbird (predicted mean = 466 s) and 1.3 times (30%) greater than responses to a woodpecker (predicted mean = 436 s; sparrowhawk versus blackbird:  $\beta = 94 \text{ s} \pm 43 \text{ SE}$ ,  $P < 0.05$ ; sparrowhawk versus woodpecker:  $\beta = 124 \text{ s} \pm 42 \text{ SE}$ ,  $P < 0.01$ ; see [Table 2](#)). Latencies in response to a blackbird and to a woodpecker showed no overall difference (woodpecker versus blackbird:  $\beta = -31 \text{ s} \pm 42 \text{ SE}$ ,  $P = 0.45$ ; [Table 2](#)).



**Figure 3.** Risk-taking responses of breeding blue tits measured as the latency (s) to resume brood provisioning after 10 min presentations of blackbird, woodpecker or sparrowhawk taxidermic mounts at their nests. Box plots show the median, first and third quartiles and whiskers indicate values within 1.5 times the interquartile range; large circles represent mean latency/intervisit interval values.

**Table 2**

Sources of variation in the latency responses of blue tits towards a blackbird, a woodpecker and a sparrowhawk taxidermic mount modelled together

		Latency
		$N_{\text{resp}} = 345, N_{\text{ind}} = 68$
<b>Fixed effects</b>		
Intercept (s)		475.26 (57.08)
Predator (ref: blackbird)		Woodpecker: -30.62 (41.99) Sparrowhawk: 93.79 (42.84)*
Age (ref: first-year breeder)		-23.38 (56.87)
Sex (ref: female)		98.99 (53.78) <sup>†</sup>
Brood size		-10.88 (14.95)
Hatch date		13.17 (7.55)
Brood age (ref: 10 days)		11 days: -30.22 (51.06) 12 days: 16.72 (74.89)
Sequence (ref: first trial)		-69.50 (62.34)
Time of day (ref: morning)		13.98 (39.08)
Intervisit interval (s)		0.30 (0.14)*
<b>Random effects</b>		
		Variance (SE)
Individual ID		22757.06 (10952.71)**
Breeding pair ID		2226.16 (8148.39)
Residual		100105.81 (8628.17)
<b>Variance proportions</b>		
Individual ID		0.18 (0.08)
Breeding pair ID		0.02 (0.07)

Predictor variables tested were (1) the type of predator (blackbird, woodpecker or sparrowhawk), (2) age of the bird (factor with two levels: first-year breeder or older), (3) the sex of the bird, (4) the number of nestlings in its nest, i.e. its brood size (continuous variable), (5) the hatch date of its brood (continuous variable) (6) age of the brood on the day of the predator trial (three-level factor: 10, 11 and 12 days old), (7) the repeated measure sequence (two-level factor), (8) the time of day when the trial was conducted (two-level factor: morning or afternoon), (9) intervisit interval (s; continuous variable). Blue tit ID and breeding pair ID ( $N = 34$ ) were included as random variables. For test statistics and significance estimates see Table A7.  $N_{\text{resp}}$  and  $N_{\text{ind}}$  are, respectively, the number of latency responses obtained and number of individuals sampled.

<sup>†</sup> $P < 0.10$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ .

Across levels of threat, latency increased with increasing intervisit interval measured prior to the predator trial (Tables 2 and A7), but this effect was minor. No other fixed predictors significantly explained variation in overall latency (Tables 2 and A7). However, predator-specific analyses showed evidence that the sex of a bird, the date of hatching of its brood, the sequence of the repeated measures and its intervisit interval influenced the latency to resume provisioning with one or more of the predator types (Tables 3 and A1–A4). Specifically, individuals showed reduced

latencies in the second repeated presentation of a sparrowhawk and males had markedly longer latencies than females in the woodpecker predator trials. These potentially important fixed effects were retained in the reaction norm and character state models (see below and Table 4). In a separate analysis the type of predator presented in the morning trials was not found to influence the latency in the afternoon trial (Table A8).

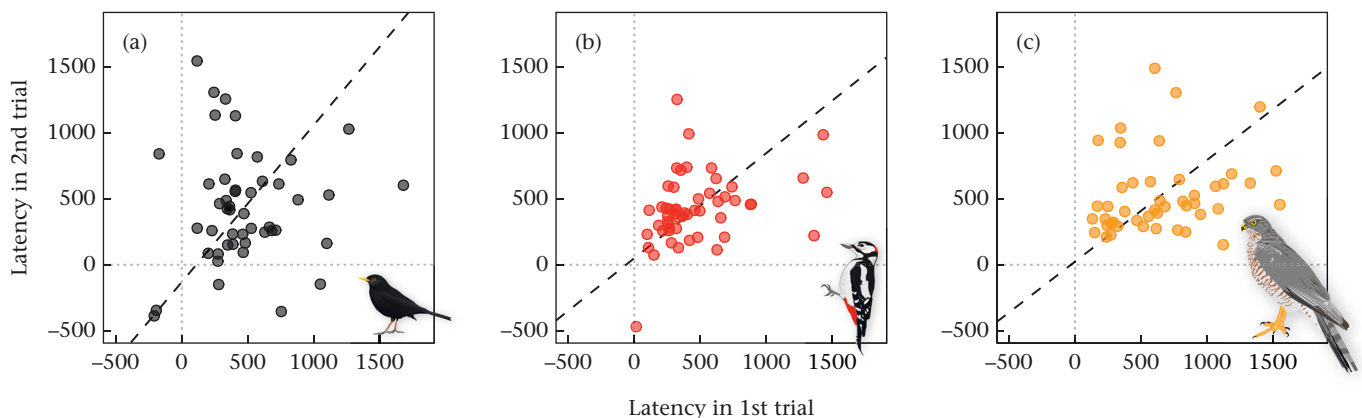
#### Among-individual Variation in Mean Level of Latency Responses

The latency to resume provisioning across the different levels of predation threat was found to be repeatable within individuals ( $R = 0.18 \pm 0.08$  SE), while breeding pair ID explained little additional variance ( $R = 0.02 \pm 0.07$ ; Table 2). Latencies in the woodpecker trials and to a lesser extent in the sparrowhawk trials were repeatable (woodpecker:  $R = 0.31 \pm 0.13$  SE; sparrowhawk:  $R = 0.12 \pm 0.15$  SE; Fig. 4, Table 3). Repeatability of latency responses in the blackbird trials, however, was low ( $R = 0.04 \pm 0.15$  SE; Fig. 4, Table 3). Repeatability estimates remained similar when simplifying the fixed-effects structure of each model to include only age and sex of an individual (see Tables A9 and A10). Only when we excluded the random effect of individual ID did the breeding pair ID explain a considerable proportion of variation in the sparrowhawk predator trials (19–20%; see Tables A3, A4) and in the woodpecker–sparrowhawk reaction norm model (12%; see Table A6). Identity of the woodpecker and sparrowhawk mounts explained little variation in latency (both  $<0.01\%$ ;  $P = 0.99$ ; see Tables 3 and A1–A4). However, in the blackbird trials mount identity explained a significant proportion of variation in latency (10%,  $P = 0.05$ ; see Tables 3 and A1–A4).

#### Among-individual Variation in Latency Response Plasticity

##### Reaction norm approach

In the reaction norm models we found similar pairwise mean latency differences between predator levels (see Table 4, Fig. 5) as in the model described above pooling all latency values (Fig. 4, Table 2) representing population level plasticity ('E'). Additionally, in agreement with the previous models we found considerable variation in the intercepts of individual latency reaction norms (i.e. 'I'; Table 4, Fig. 5), from the blackbird–woodpecker (18% variance explained) and woodpecker–sparrowhawk (21% variance explained), but not so much for the blackbird–sparrowhawk model (5% variance explained). However, these models, which estimate among-individual variation both in slopes ('I × E') and in intercepts along with their covariance, explained negligible additional



**Figure 4.** Scatterplots illustrating the repeatability of latency responses in response to a specific level of predation threat. Latency was measured as the time (s) to resume brood provisioning after a 10 min presentation of a simulated predation threat at the nest. Latencies are shown for the second versus the first (a) blackbird, (b) woodpecker and (c) sparrowhawk trials. Dotted lines represent the standardized major axis lines for the second versus the first repeated measure.



**Table 3**  
Sources of variation in the latency responses of blue tits towards a blackbird, a woodpecker or a sparrowhawk taxidermic mount each modelled separately

	Blackbird	Woodpecker	Sparrowhawk
	$N_{\text{resp}} = 111, N_{\text{ind}} = 63$	$N_{\text{resp}} = 121, N_{\text{ind}} = 68$	$N_{\text{resp}} = 113, N_{\text{ind}} = 67$
<b>Fixed effects</b>			
Intercept (s)	Coefficient (SE) 455.19 (121.67)	Coefficient (SE) 356.11 (58.67)	Coefficient (SE) 666.60 (71.06)
Age (ref: first-year breeder)	22.10 (88.04)	-42.81 (66.96)	-71.98 (71.22)
Sex (ref: female)	76.43 (85.11)	166.90 (66.04)*	46.34 (69.51)
Brood size	6.19 (23.07)	-7.02 (17.05)	-33.24 (18.57) †
Hatch date	24.06 (11.92)*	3.88 (8.97)	14.21 (8.80)
Sequence (ref: first trial)	-21.44 (80.68)	-16.13 (46.98)	-133.72 (64.01)*
Time of day (ref: morning)	-29.23 (83.51)	-36.30 (47.78)	-63.39 (64.00)
Brood age <sup>1</sup>			
Intervisit interval (s)	0.43 (0.26)†	0.20 (0.19)	0.32 (0.20)
<b>Random effects</b>			
Individual ID	Variance (SE) 7377.87 (27846.13)	Variance (SE) 27108.20 (12980.11)*	Variance (SE) 12469.29 (16522.66)
Mount ID	18184.86 (23259.75)†	<0.01	<0.01
Residual	161325.71 (34650.27)	61067.91 (11971.54)	96396.92 (19664.54)
<b>Variance proportions</b>			
Individual ID	0.04 (0.15)	0.31 (0.13)	0.12 (0.15)
Mount ID	0.10 (0.12)	<0.001	<0.001

Predictor variables tested in each model were (1) age of the bird (two-level factor: first-year breeder or older), (2) the sex of the bird, (3) the number of nestlings in its nest, i.e. its brood size (continuous variable), (4) the hatch date of its brood (continuous variable), (5) the repeated measure sequence (two-level factor), (6) the time at which the trial was conducted (factor with two levels: morning or afternoon), (7) intervisit interval (s; continuous variable). Blue tit ID and taxidermic mount ID ( $N = 3$ ) were included as random variables in each model. For test statistics and significance estimates see Table A1.  $N_{\text{resp}}$  and  $N_{\text{ind}}$  are, respectively, the number of latency responses obtained and number of individuals sampled.

† $P < 0.10$ ; \* $P < 0.05$ .

<sup>1</sup> Models could not simultaneously estimate the effects of brood age and sequence of repeated measures. For estimates of brood age see Tables A2 and A4.

**Table 4**  
Reaction norm model outputs in which latency responses of blue tits towards the three different taxidermic mounts were taken two at a time in separate models

	Blackbird—Woodpecker	Blackbird—Sparrowhawk	Woodpecker—Sparrowhawk
	$N_{\text{resp}} = 232, N_{\text{ind}} = 68$ Coefficient (SE)	$N_{\text{resp}} = 224, N_{\text{ind}} = 68$ Coefficient (SE)	$N_{\text{resp}} = 234, N_{\text{ind}} = 68$ Coefficient (SE)
<b>Fixed effects</b>			
Intercept (s)	403.05 (46.29)	526.10 (47.14)	480.67 (42.20)
Predator	-29.88 (43.28)	98.73 (47.56)*	125.12 (35.77)**
Sex (ref: Female)	125.49 (58.86)*	63.64 (59.18)	100.92 (55.31)†
Hatch date	11.09 (8.03)	18.84 (7.69)*	13.62 (7.24)†
Sequence (ref: first trial)	-28.12 (43.51)	-72.40 (47.72)	-65.86 (36.21)†
Intervisit interval (s)	0.29 (0.17)†	0.41 (0.17)*	0.27 (0.15)†
<b>Random effects</b>			
Intercept variance (SE)	22745.41 (10484.46)†	16526.49 (10575.54)	26619.53 (8871.65)**
Slope variance (SE)	<0.001	<0.001	<0.001
Intercept-slope covariance (SE)	-0.15 (0.03)	-0.13 (0.04)	0.16 (0.03)
Residual (SE)	106612.50 (11901.21)	124774.90 (14167.42)	73165.53 (8088.96)
<b>Variance proportions</b>			
Among-individual intercepts	0.18 (0.07)	0.12 (0.07)	0.26 (0.07)
Among-individual slopes	<0.001	<0.001	<0.001

Predictor variables included were those found to be important when modelling latency measures together and in predator-specific models (see Tables 1 and 2, respectively). Blue tit ID was included as a random variable in each model. For test statistics and significance estimates see Table A5.  $N_{\text{resp}}$  and  $N_{\text{ind}}$  are, respectively, the number of latency responses obtained and number of individuals sampled.

† $P < 0.10$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ .

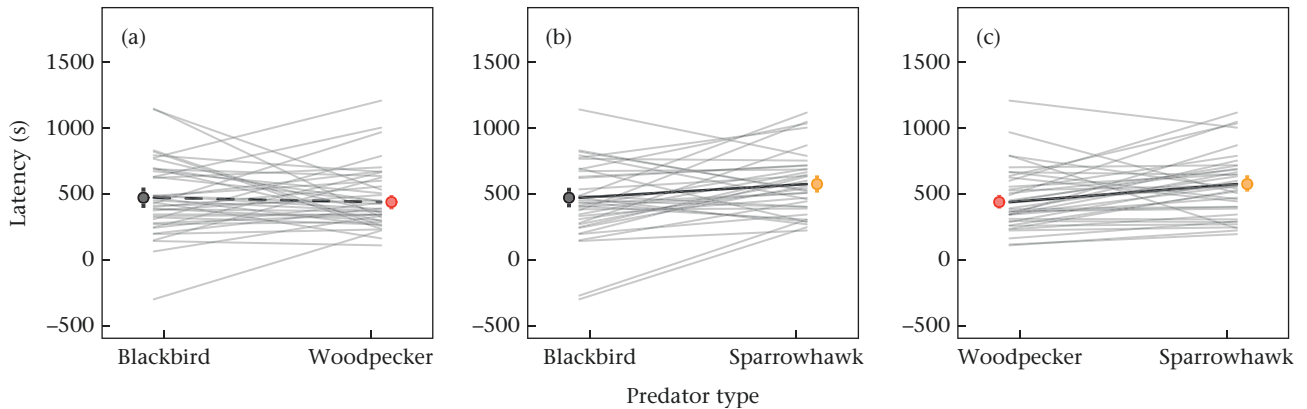
variation in latency when compared with random intercept-only models (Fig. 5, Table 4).

#### Character-state approach

We found strong positive among-individual correlations between latency responses to each of the three predator types. None of the correlations differed significantly from 1 (i.e. a perfect correlation: Fig. A1, Table 5). Repeatability estimates for latency responses of individuals derived from the trivariate model were comparable to those from the univariate models (see Tables 2, 3 and 5). Variance explained by breeding pair ID could only be estimated across all response variables simultaneously.

## DISCUSSION

To test predictions of several complementary conceptual frameworks in the wild, we manipulated levels of perceived predation threat at the nests of breeding blue tits. We investigated individual variation in the plastic adjustment to predators during parental care provisioning. Individual parents showed repeatable differences in their latency to resume brood provisioning within and across levels of threat. Although birds plastically adjusted their responses to the manipulated threat levels at the population level, we found no evidence that individuals differed in their plasticity. This refutes the prediction that risk-averse individuals are more flexible.



**Figure 5.** An illustration of individual reaction norms across the different levels of predation threat: (a) blackbird—woodpecker, (b) blackbird—sparrowhawk and (c) woodpecker—sparrowhawk. Lines represent reaction norms connecting individuals' means across repeated measures in response to a given threat level. Note that reaction norms are not shown in cases for which repeated measures for an individual were not obtained. The population-specific means of the latency responses to the blackbird, woodpecker and sparrowhawk presentations are shown as points. Error bars around the points show the 95% bootstrapped confidence intervals of the mean latency for each predator type. Solid lines indicate significant population level differences in latencies and the dashed line a nonsignificant difference.

**Table 5**

Character state model output in which the latency responses to the three different taxidermic mounts were modelled simultaneously as multiple response variables

	Blackbird	Woodpecker	Sparrowhawk
	$N_{\text{resp}} = 111, N_{\text{ind}} = 63$	$N_{\text{resp}} = 121, N_{\text{ind}} = 68$	$N_{\text{resp}} = 113, N_{\text{ind}} = 67$
<b>Fixed effects</b>	Coefficient (SE)	Coefficient (SE)	Coefficient (SE)
Intercept (s)	436.76 (71.16)	371.87 (48.98)	607.32 (55.46)
Sex (ref: female)	92.22 (85.63)	154.33 (63.16)*	31.77 (69.63)
Hatch date	18.16 (11.87)	6.60 (8.77)	20.06 (8.86)*
Sequence (ref: first trial)	−32.79 (75.84)	−26.71 (43.73)	−125.75 (56.07)*
Intervisit interval (s)	0.46 (0.25) <sup>†</sup>	0.16 (0.18)	0.31 (0.19)
<b>Random effects</b>	Variance (SE)	Variance (SE)	Variance (SE)
Individual ID	24705.18 (1957.30)	31940.96 (14215.74)	23101.91 (1612.40)
Breeding pair ID	1254.80 (8429)	1254.80 (8429)	1254.80 (8429)
Residual	159614.60 (24475.11)	56670.45 (10233.44)	89095.59 (14354.62)
<b>Variance proportions</b>			
Individual ID	0.11 (0.08)	0.35 (0.13)	0.21 (0.13)
Breeding pair ID	0.007 (0.044)	0.015 (0.090)	0.012 (0.071)
	Among-individual covariance (SE)	Among-individual correlation (SE)	
Blackbird—Woodpecker	24084.48 (12893.04)	0.99 <sup>1</sup>	
Blackbird—Sparrowhawk	20940.32 (13059.77)	0.99 <sup>1</sup>	
Woodpecker—Sparrowhawk	26932.39 (12005.97)	0.99 <sup>1</sup>	

Predictor variables included were those found to be important when modelling latency measures together and in predator-specific models (see Tables 1 and 2, respectively). Blue tit ID was included as a random variable for each response variable. Breeding pair ID ( $N = 34$ ) was estimated once across all response variables. For test statistics and significance estimates see Table A11.  $N_{\text{resp}}$  and  $N_{\text{ind}}$  are, respectively, the number of latency responses obtained and number of individuals sampled.

<sup>†</sup> $P < 0.10$ , \* $P < 0.05$ .

<sup>1</sup> Standard errors were inestimable as estimates were fixed to the boundary.

### Population Level Effects

At the population level, we detected plastic adjustment of latency responses to the level of predation threat. Our sparrowhawk presentation provoked a stronger response (longer latencies) than a blackbird or woodpecker presentation. In line with our expectation and with our earlier findings (Salazar et al., 2021), individuals recognized differences in the predator mounts and showed seemingly adaptive adjustment of their behaviour based on the prevailing level of threat. By itself, this finding is not surprising as threat-sensitive responses to predators are a well-established finding in birds (e.g. Curio et al., 1983; Lima, 2009; Mahr et al., 2014; Suzuki, 2011) and other taxa (e.g. Helfman, 1989; Lima & Dill, 1990). Notably, we observed these differences despite the brief presence of a human at the nestbox at the start and end of each trial. Through our earlier study we established that although human presence at the nest provokes a threat response, birds

quickly resume provisioning once relieved from the human disturbance, in contrast to their response towards sparrowhawk exposure (Salazar et al., 2021; see similar result obtained by Mutzel et al., 2019). This finding also goes against the possibility that population level latency differences in the current study may be merely due to size differences of the different predation threat stimuli (mounts).

Contrary to our expectation, we found no population mean difference between the latencies towards a blackbird and woodpecker. We presented the blackbird as a nonthreat control stimulus intended to serve as an absence of predation threat treatment level. An earlier study comparing the responses of breeding great tits towards taxidermic woodpecker and blackbird mounts found a clear difference in latency responses (Mutzel et al., 2019). Notably, Mutzel et al. (2019) presented the mounts on a pole 2 m from the nestbox, whereas by placing the models directly on the nestbox we may have presented blue tit parents with a different type of cue.

Apparently, a blackbird mount placed directly on the nestbox elicited on average similarly strong responses as a woodpecker.

Interestingly, it appeared that the presentations of blackbird mounts resulted in a larger spread in latencies than presentations of woodpeckers and sparrowhawks. While in blackbird trials several individuals started provisioning before the mount was removed, this never happened in sparrowhawk trials and only twice in a woodpecker trial. At the same time, some latencies in response to a blackbird were even longer than the strongest responses to the woodpecker and sparrowhawk presentations (see Fig. 3). In contrast to the woodpecker and sparrowhawk mounts, which present unambiguous threats of predation, a blackbird directly on a nestbox may present an ecologically ambiguous cue, potentially causing the larger variability of the latency measures. Across taxa such patterns are typically observed in response to novel object presentations or tests of so-called 'boldness' or neophobia (Feyten et al., 2019; Greggor et al., 2015; Mutzel et al., 2013; see also meta-analysis by Takola et al., 2021). Indeed, exposure to novel environments has been suggested to release cryptic individual (genetic) variation (Schlichting, 2008). While overall the sparrowhawk presentations elicited the strongest latency responses, we also found a clear sequence effect. Individual latencies were reduced in the second sparrowhawk presentation (see Fig. 4c, Table 3, comparable to sequence effects described in e.g. Dingemanse et al., 2012). This likely effect of habituation (for example through learned irrelevance; Greggor et al., 2019) appeared strongest for the individuals with relatively long latencies in the first sparrowhawk trial (see Fig. 4c), which could have reduced the individual repeatability estimate obtained for the sparrowhawk trials.

In addition to predator type, we found a few other biological variables were related to the observed latencies. First, we found that individuals provisioning at higher rates (shorter intervisit intervals) prior to the predator trials had shorter latencies (see Table 2) and we controlled for this effect in our analyses. Yet, we found evidence for among-individual variation in latencies (see below for further discussion), which indicates that observed individual differences in latency responses are not a mere reflection of variation in provision rates. Additionally, we found that males had a slight tendency to resume provisioning later than females, and this was most pronounced in the woodpecker trials (see Table 3). Such a sex difference in responses to predation threat at the nest has been previously observed (e.g. Fernández et al., 2015; van den Bemt et al., 2021; Krenhardt et al., 2021) and attributed to differences in the economics of parental investment for each sex (Fromhage & Jennions, 2016). Finally, in the sparrowhawk trials we found individuals with larger broods resumed provisioning sooner (see Table 3). This observation could be interpreted as consistent with larger broods having a higher reproductive value shifting the balance of the costs and benefits of predation threat-induced interruptions of parental care (Clark, 1994; Ghalambor & Martin, 2001).

#### *Repeatability of Risk Taking During Provisioning*

We found that individuals differed consistently in their risk-taking responses across predation threat levels. This result agrees with our earlier finding (Salazar et al., 2021) and those of other studies using a similar set-up (Davidson et al., 2018; Mutzel et al., 2013, 2019), offering further support to the idea that individuals within the same population differ in how they cope with environmental challenges. Risk taking towards predators within the context of parental care may thus be an important dimension of within-population behavioural variation in the wild. Whether these risk-taking propensities are also related to how individuals resolve life history trade-offs as predicted by the pace-of-life-

syndrome hypothesis is still an open question. However, to date there is only weak support for within-population covariation of risk-taking behaviours with life history and physiological traits as predicted by the pace-of-life-syndrome hypothesis (meta-analysis by Royauté et al., 2018).

In our previous study, we recorded male blue tit latencies to one human and one sparrowhawk predator trial and obtained an across-predator repeatability of  $R \pm SE = 0.51 \pm 0.13$  (Salazar et al., 2021). This estimate was considerably higher than the overall repeatability estimate from the current study (which included both males and females;  $R \pm SE = 0.18 \pm 0.08$ ; see Table 2). However, a direct comparison of these estimates is hindered by the fact that in our previous study, due to a positive distributional skew, we log-transformed the latency measures prior to analysis. Moreover, our current study design differs substantially from the previous one, to match our specific research aims. Since we aimed at estimating predator-specific repeatability and plasticity across different predation threat levels we presented each of our three mount types (blackbird, woodpecker and sparrowhawk) twice at each nest. However, repeated presentations of the same mount type, particularly the sparrowhawk, showed a habituation effect (see Table 3). This may have lowered both the sparrowhawk-specific and the overall repeatability estimates. While latency responses to a woodpecker were clearly repeatable, those towards the blackbird showed surprisingly low repeatability. As discussed above, responses to the blackbird stimulus may differ qualitatively from regular responses to predation threat (i.e. to woodpeckers and sparrowhawks). In general, we found repeatability estimates to be higher when pooling responses (either of all mount types, see Table 2, or responses to pairs of mount types from the reaction norm models, see Table 4) than to those from threat level-specific models. This indicates that responses of the same individuals were overall more similar across levels of threat (after controlling for mean threat level effects as a fixed effect) compared to those within predation threat levels. We imagine this to be the result of the presence of stronger habituation effects when presenting the same stimulus (mount type) compared to different types of stimuli. Habituation itself may vary among individuals as a form of behavioural plasticity (e.g. Dingemanse et al., 2012; Vincze et al., 2021), which in turn can lower repeatability (but see Martin & Réale, 2008).

As indicated by the overall low variance explained by breeding pair ID (see Tables A3, A4 and A6), members of a pair showed hardly any synchrony in their latency responses to predation threat (except when the individual ID effect was excluded from the model in the case of the sparrowhawk predator trials; see Table A4). Overall, our results therefore suggest that risk-taking differences are intrinsic to individuals and apparently largely uninfluenced by the shared (social and nonsocial) environment of breeding partners. These intrinsic individual differences may be related to genetic differences or differences in past experiences (permanent environmental effects; see Nussey et al., 2007). As in our previous study, the identity of taxidermic mounts was unimportant in explaining variation in latency measures, except in blackbird predator trials. One of our three blackbird taxidermic mounts was affixed to a base resembling a rock while the other two were secured to a small section of wood. This may possibly explain the observed variation (which was also evident from visual inspection, data not shown). We cannot exclude that other minor, unobvious differences in mount character may also have contributed to differences in responses to the different blackbird mounts.

#### *Individual Level Plasticity*

Within a short timespan during parental care provisioning (twice per day, over 3 days) we manipulated levels of predation

threat at the nests of breeding blue tits and found no evidence that individuals differed in how strongly they adjust their responses to varying levels of threat. Instead, our results reveal that individuals all adjusted to risk in a similar fashion despite individual differences in their average responses across manipulated threat levels (in line with Fig. 1b).

In terms of our statistical approaches, rank differences in latency responses were roughly conserved across all threat levels in the reaction norm approach indicating no detectable individual variation in plasticity (Brommer, 2013b). Correspondingly, among-individual correlations of latencies in response to the different predator types (character states) were positive and did not differ significantly from 1. Admittedly, both of our adopted statistical approaches are data-hungry techniques that are not ideally suited for a sample size such as ours (Dingemanse & Dochtermann, 2013; Martin et al., 2011). However, merely plotting the raw data shows that (average) reaction norms along the predation threat level gradient (particularly between the most relevant predator treatments: i.e. woodpecker versus sparrowhawk) are largely parallel substantiating our results of no individual slope variation (Fig. 5, see also Fig. A2 for an illustration using reaction norms from the model predictions). Furthermore, because of uniform reaction norm intercept differences we are not faced with the question of where best to measure variance in individual intercepts (i.e. repeatability; Brommer, 2013b; Nussey et al., 2007; Schielzeth & Nakagawa, 2022). The presence of individual reaction norm slope variance would distort our interpretation of repeatability as among-individual variation in intercepts would vary across the gradient of the covariate (in our case, across predation threat levels; see Schielzeth & Nakagawa, 2022).

A key question that arises from our finding that individuals do not differ in their plasticity is: are certain contexts or temporal scales, particularly those related to variation in predation threat, more (or less) likely to expose individual variation in behavioural plasticity? In a study on great tits, Thys et al. (2019) provoked females with a taxidermic woodpecker presentation at the entrance hole of their nestboxes during egg laying and incubation. They found no among-female variation in the plasticity of hissing behaviour (a form of nest defence), over the nesting cycle. Other studies on great tits have indeed detected individual variation in plasticity to the risk of predation (Coomes et al., 2021; Quinn & Cresswell, 2005; Quinn et al., 2012), although these have been carried out in the context of foraging and outside the breeding season. Across breeding events, among-individual variation in nest defence plasticity towards a (human) predator has also been reported in several long-lived bird species (Betini & Norris, 2012; de Jong et al., 2020; Kontiainen et al., 2009; Moring et al., 2022). Finally, laboratory studies on species of fish and amphibians detected little if any variation in individual plasticity across levels of predation threat (Fürstbauer et al., 2015; Houslay et al., 2018; Kim, 2016; Urszán et al., 2018; but see Jolles et al., 2019).

Our results suggest that responses to different kinds of predators probably have the same biological underpinnings, as implied by the strong among-individual correlation in responses across predators and a corresponding lack of individual plasticity variation. Individual variation in plasticity is likely to be manifested when mechanisms maintaining or depleting variation act partly independently across (the ends of) the environmental gradient along which behaviour is measured. If the population's response is fixed at any one end of an environmental gradient (i.e. individuals show little variation in their responses), among-individual variation in plasticity may simply result from individual intercept differences at the other end forming a 'fanning-in/out' pattern of reaction norms (O'Dea et al., 2022). This is particularly plausible in

the case of habituation effects, which lead to fanning-in of reaction norms.

## Conclusions

Taken together our findings suggest that in the context of predation threat perceived during parental care provisioning, individuals differ at the level of their mean propensity to take risks and not in their plasticity to varying levels of threat. Parent birds demonstrated similar flexibility in their responses to short-term manipulation of predation threat but individual differences in risk taking were retained across threat levels. The absence of individual plasticity variation rules out the commonly held expectation that risk-averse individuals are more responsive to cues of environmental variation. While our results concur with widespread empirical findings of among-individual mean behavioural variation, they also question the generality of common assumptions about within-population differences in behavioural flexibility.

## Author Contributions

**S.M.S.:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – Original draft preparation, review & editing. **K.H.:** Investigation, Methodology, Writing – Review. **J.K.:** Project administration, Resources, Writing – Review & editing. **P.K.:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – Review & editing.

## Data Availability

Data and R code used in the analyses are uploaded as [Supplementary material](#).

## Declaration of Interest

None.

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## Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.anbehav.2022.12.003>.

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## Appendix

**Table A1**

Sources of variation in the latency responses of blue tits towards a blackbird, a woodpecker or a sparrowhawk taxidermic mount each modelled separately

		Wald $F/\chi^2$	df	P
<b>Blackbird</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	455.19 (121.67)			
Age (ref: first-year breeder)	22.10 (88.04)	0.063	1, 51.1	0.80
Sex (ref: female)	76.43 (85.11)	0.807	1, 50.0	0.37
Brood size	6.19 (23.07)	0.072	1, 50.7	0.79
Hatch date	24.06 (11.92)	4.075	1, 61.1	0.048
Sequence	–21.44 (80.68)	0.071	1, 52.7	0.79
Time of day (ref: morning)	–29.23 (83.51)	0.122	1, 59.4	0.73
Intervisit interval (s)	0.43 (0.26)	2.697	1, 76.5	0.104
Random effects	Variance (SE)			
Individual ID	7377.87 (27846.13)	0.060	1	0.81
Mount ID	18184 (23259.75)	3.717	1	0.054
Residual	161325.71 (34650.27)			
Variance proportions				
Individual ID	0.04 (0.15)			
Mount ID	0.10 (0.12)			
<b>Woodpecker</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	356.11 (58.67)			
Age (ref: first-year breeder)	–42.81 (66.96)	0.409	1, 60.1	0.53
Sex (ref: female)	166.90 (66.04)	6.387	1, 62.3	0.015
Brood size	–7.02 (17.05)	0.169	1, 60.6	0.68
Hatch date	3.88 (8.97)	0.187	1, 69.5	0.67
Sequence	–16.13 (46.98)	0.118	1, 58.6	0.73
Time of day (ref: morning)	–36.30 (47.78)	0.577	1, 65.5	0.45
Intervisit interval (s)	0.20 (0.19)	1.052	1, 95.1	0.31
Random effects	Variance (SE)			
Individual ID	27108.20 (12980.11)	4.841	1	0.028
Mount ID	<0.01	<0.001	1	0.99
Residual	61067.91 (11971.54)			
Variance proportions				
Individual ID	0.31 (0.13)			
Mount ID	<0.001			
<b>Sparrowhawk</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	666.60 (71.06)			
Age (ref: first-year breeder)	–71.98 (71.22)	1.021	1, 57.6	0.32
Sex (ref: female)	46.34 (69.51)	0.444	1, 60.4	0.51
Brood size	–33.24 (18.57)	3.206	1, 63.2	0.078
Hatch date	14.21 (8.80)	2.607	1, 52.8	0.112
Sequence	–133.72 (64.01)	4.364	1, 58.3	0.041
Time of day (ref: morning)	–63.39 (64.00)	0.981	1, 61.8	0.33
Intervisit interval (s)	00.32 (0.20)	2.526	1, 94.5	0.115
Random effects	Variance (SE)			
Individual ID	12469.29 (16522.66)	0.604	1	0.44
Mount ID	<0.01	<0.001	1	0.99
Residual	96396.92 (19664.54)			
Variance proportions				
Individual ID	0.12 (0.15)			
Mount ID	<0.001			

Wald  $F$  values are given for fixed effects and  $\chi^2$  values for random effects. Predictor variables tested in each model were (1) age of the bird (two-level factor: first-year breeder or older), (2) the sex of the bird, (3) the number of nestlings in its nest, i.e. its brood size (continuous variable), (4) the hatch date of its brood (continuous variable), (5) the repeated measure sequence (two-level factor), (6) the age of its brood on the day of predator trial (three-level factor: 10, 11 and 12 days old), (7) the time at which the trial was conducted (factor with two levels: morning or afternoon), (8) pretrial intervisit interval (s; continuous variable). Blue tit ID (blackbird:  $N = 63$ ; woodpecker:  $N = 68$ ; sparrowhawk:  $N = 67$ ) and taxidermic mount ID ( $N = 3$ ) were included as random variables in the blackbird, woodpecker and sparrowhawk models, respectively.

**Table A2**

Sources of variation in the latency responses of blue tits towards a blackbird, a woodpecker or a sparrowhawk taxidermic mount each modelled separately

		Wald $F/\chi^2$	<i>df</i>	<i>P</i>
<b>Blackbird</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	440.88 (131.51)			
Age (ref: first-year breeder)	31.17 (88.52)	0.124	1, 52.4	0.73
Sex (ref: female)	76.04 (83.57)	0.828	1, 29.2	0.37
Brood size	11.32 (23.08)	0.241	1, 26.7	0.63
Hatch date	22.55 (11.83)	3.633	1, 31.4	0.066
Brood age (ref: 10 days)	11 days: -77.60 (94.16) 12 days: 68.04 (103.83)	1.126	2, 72.2	0.33
Time of day (ref: morning)	11.31 (81.20)	0.019	1, 58.3	0.89
Intervisit interval (s)	0.46 (0.26)	3.194	1, 64.9	0.079
Random effects	Variance (SE)			
Individual ID	3258.77 (27557.52)	0.105	1	0.75
Mount ID	21805.10 (26887.82)	2.115	1	0.03
Residual	162879.66 (35122.10)			
Variance proportions				
Individual ID	0.02 (0.15)			
Mount ID	0.12 (0.13)			
<b>Woodpecker</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	370.55 (60.96)			
Age (ref: first-year breeder)	-40.78 (67.52)	0.365	1, 59.2	0.55
Sex (ref: female)	166.95 (66.54)	6.296	1, 61.3	0.014
Brood size	-7.02 (17.18)	0.167	1, 59.6	0.68
Hatch date	4.58 (9.06)	0.256	1, 68.9	0.62
Brood age (ref: 10 days)	-42.33 (58.37) -31.63 (59.95)	0.292	2, 76.0	0.75
Time of day (ref: morning)	-38.44 (47.74)	0.648	1, 64.1	0.42
Intervisit interval (s)	0.21 (0.20)	1.141	1, 96.5	0.29
Random effects	Variance (SE)			
Individual ID	28301.19 (13317.20)	4.887	1	0.027
Mount ID	<0.001	<0.001	1	0.99
Residual	60621.27 (12048.35)			
Variance proportions				
Individual ID	0.32 (0.13)			
Mount ID	<0.001			
<b>Sparrowhawk</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	624.71 (72.67)			
Age (ref: first-year breeder)	-66.17 (72.66)	0.829	1, 56.1	0.37
Sex (ref: female)	44.00 (77.01)	0.384	1, 58.9	0.54
Brood size	-31.74 (19.18)	2.739	1, 64.4	0.10
Hatch date	14.94 (8.98)	2.766	1, 51.2	0.10
Brood age (ref: 10 days)	-63.98 (75.20) -73.01 (75.59)	0.570	2, 80.3	0.57
Time of day (ref: morning)	13.66 (60.77)	0.051	1, 60.7	0.82
Intervisit interval (s)	0.33 (0.21)	2.621	1, 93.2	0.11
Random effects	Variance (SE)			
Individual ID	13106.46 (17667.17)	0.563	1	0.45
Mount ID	0.013	<0.001	1	0.99
Residual	100154.30 (20806.80)			
Variance proportions				
Individual ID	0.12 (0.15)			
Mount ID	<0.001			

Wald  $F$  values are given for fixed effects and  $\chi^2$  values for random effects. Predictor variables tested in each model were (1) age of the bird (two-level factor: first-year breeder or older), (2) the sex of the bird, (3) the number of nestlings in its nest, i.e. its brood size (continuous variable), (4) the hatch date of its brood (continuous variable), (5) the age of its brood on the day of predator trial (three-level factor: 10, 11 and 12 days old), (6) the time at which the trial was conducted (factor with two levels: morning or afternoon), (7) pretrial intervisit interval (s; continuous variable). Blue tit ID (blackbird:  $N = 63$ ; woodpecker:  $N = 68$ ; sparrowhawk:  $N = 67$ ) and taxidermic mount ID ( $N = 3$ ) were included as random variables in the blackbird, woodpecker and sparrowhawk models, respectively.



**Table A3**

Sources of variation in the latency responses of blue tits towards a blackbird, a woodpecker or a sparrowhawk taxidermic mount each modelled separately

		Wald $F/\chi^2$	df	P
<b>Blackbird</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	452.47 (121.60)			
Age (ref: first-year breeder)	21.65 (87.36)	0.062	1, 70.5	0.80
Sex (ref: female)	77.93 (82.92)	0.883	1, 83.9	0.35
Brood size	6.50 (23.24)	0.078	1, 26.9	0.78
Hatch date	23.92 (12.01)	3.967	1, 31.8	0.055
Sequence	-20.14 (81.53)	0.061	1, 82.8	0.81
Time of day (ref: morning)	-27.05 (84.32)	0.103	1, 88.7	0.75
Intervisit interval (s)	0.44 (0.26)	2.912	1,101.2	0.091
Random effects	Variance (SE)			
Breeding pair ID	3460.96 (15843.75)	0.050	1	0.82
Mount ID	18143.63 (23316.29)	3.639	1	0.056
Residual	164257.10 (27181.32)			
Variance proportions				
Breeding pair ID	0.02 (0.08)			
Mount ID	0.10 (0.11)			
<b>Woodpecker</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	350.46 (58.74)			
Age (ref: first-year breeder)	-29.82 (61.14)	0.238	1, 77.5	0.63
Sex (ref: female)	163.98 (57.72)	8.070	1, 96.3	0.005
Brood size	-6.35 (16.24)	0.153	1, 29.3	0.70
Hatch date	3.39 (8.67)	0.153	1, 35.5	0.70
Sequence	-8.82 (53.94)	0.027	1, 92.0	0.87
Time of day (ref: morning)	38.32 (54.17)	0.500	1,103.7	0.48
Intervisit interval (s)	0.22 (0.18)	1.472	1,111.9	0.23
Random effects	Variance (SE)			
Breeding pair ID	4968.93 (8145.14)	0.429	1	0.51
Mount ID	<0.01	<0.001	1	1
Residual	82729.24 (12830.13)			
Variance proportions				
Breeding pair ID	0.06 (0.09)			
Mount ID	<0.001			
<b>Sparrowhawk</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	624.88 (73.04)			
Age (ref: first-year breeder)	-58.87 (74.33)	0.627	1, 85.3	0.43
Sex (ref: female)	54.30 (62.53)	0.754	1, 85.4	0.39
Brood size	-31.01 (22.20)	1.951	1, 31.9	0.17
Hatch date	14.86 (10.68)	1.936	1, 26.3	0.18
Sequence				
Time of day (ref: morning)	-11.81 (59.01)	0.040	1, 88.0	0.84
Intervisit interval (s)	0.41 (0.20)	4.300	1,101.0	0.041
Random effects	Variance (SE)			
Breeding pair ID	20517.82 (13238.87)	3.809	1	0.051
Mount ID	564.74 (3571.54)	0.029	1	0.86
Residual	89010.49 (14814.75)			
Variance proportions				
Breeding pair ID	0.19 (0.11)			
Mount ID	0.005 (0.03)			

Wald  $F$  values are given for fixed effects and  $\chi^2$  values for random effects. Predictor variables tested in each model were (1) age of the bird (two-level factor: first-year breeder or older), (2) the sex of the bird, (3) the number of nestlings in its nest, i.e. its brood size (continuous variable), (4) the hatch date of its brood (continuous variable), (5) the repeated measure sequence (two-level factor), (6) the time at which the trial was conducted (factor with two levels: morning or afternoon), (7) pretrial intervisit interval (s; continuous variable). Breeding pair ID (blackbird:  $N = 32$ ; woodpecker:  $N = 34$ ; sparrowhawk:  $N = 34$ ) and taxidermic mount ID ( $N = 3$ ) were included as random variables in the blackbird, woodpecker and sparrowhawk models, respectively.

**Table A4**

Sources of variation in the latency responses of blue tits towards a blackbird, a woodpecker or a sparrowhawk taxidermic mount each modelled separately

		Wald $F/\chi^2$	df	P
<b>Blackbird</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	439.06 (131.47)			
Age (ref: first-year breeder)	31.20 (88.07)	0.126	1, 73.6	0.73
Sex (ref: female)	76.77 (82.76)	0.860	1, 83.3	0.36
Brood size	11.58 (23.04)	0.253	1, 26.8	0.62
Hatch date	22.44 (11.82)	3.605	1, 31.4	0.067
Brood age (ref: 10 days)	11 days: -76.88 (94.56) 12 days: 69.67 (104.24)	1.127	2,100.1	0.33
Time of day (ref: morning)	-10.48 (81.63)	0.017	1, 88.0	0.90
Intervisit interval (s)	0.47 (0.26)	3.292	1,100.4	0.073
Random effects	Variance (SE)			
Breeding pair ID	997.37 (15365.16)	0.004	1	0.95
Mount ID	21798.67 (26925.80)	4.669	1	0.03
Residual	165132.08 (27264)			
Variance proportions				
Breeding pair ID	0.12 (0.13)			
Mount ID	0.01 (0.08)			
<b>Woodpecker</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	361.24 (61.09)			
Age (ref: first-year breeder)	-29.40 (61.42)	0.229	1, 75.6	0.63
Sex (ref: female)	163.99 (57.91)	8.020	1, 94.9	<0.01
Brood size	-6.30 (16.32)	0.149	1, 28.1	0.70
Hatch date	3.56 (8.74)	0.166	1, 34.1	0.69
Brood age (ref: 10 days)	-20.68 (65.27) -33.45 (66.98)	0.131	2,111.6	0.88
Time of day (ref: morning)	-42.18 (54.36)	0.602	1,101.9	0.44
Intervisit interval (s)	0.23 (0.19)	1.446	1,110.0	0.23
Random effects	Variance (SE)			
Breeding pair ID	5060.06 (8444.33)	0.400	1	0.53
Mount ID	0.0023	<0.001	1	1
Residual	83246.88 (13027.99)			
Variance proportions				
Breeding pair ID	0.06 (0.09)			
Mount ID	<0.001			
<b>Sparrowhawk</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	624.88 (73.04)			
Age (ref: first-year breeder)	-58.87 (74.33)	0.627	1, 85.3	0.43
Sex (ref: female)	54.30 (62.53)	0.754	1, 85.4	0.39
Brood size	-31.01 (22.20)	1.951	1, 31.9	0.17
Hatch date	14.86 (10.68)	1.936	1, 26.3	0.18
Brood age (ref: 10 days)	-75.50 (75.85) -96.83 (75.75)	0.911	2,100.4	0.41
Time of day (ref: morning)	-11.81 (59.01)	0.040	1, 88.0	0.84
Intervisit interval (s)	0.41 (0.20)	4.300	1,101.0	0.041
Random effects	Variance (SE)			
Breeding pair ID	23270.48 (14132.43)	4.434	1	0.035
Mount ID	0.016	<0.001	1	0.99
Residual	91198.37 (14922.97)			
Variance proportions				
Breeding pair ID	0.20 (0.10)			
Mount ID	<0.001			

Wald  $F$  values are given for fixed effects and  $\chi^2$  values for random effects. Predictor variables tested in each model were (1) age of the bird (two-level factor: first-year breeder or older), (2) the sex of the bird, (3) the number of nestlings in its nest, i.e. its brood size (continuous variable), (4) the hatch date of its brood (continuous variable), (5) the age of its brood on the day of predator trial (three-level factor: 10, 11 and 12 days old), (6) the time at which the trial was conducted (factor with two levels: morning or afternoon), (7) pretrial intervisit interval (s; continuous variable). Blue tit ID (blackbird:  $N = 63$ ; woodpecker:  $N = 68$ ; sparrowhawk:  $N = 67$ ) and taxidermic mount ID ( $N = 3$ ) were included as random variables in the blackbird, woodpecker and sparrowhawk models, respectively.

**Table A5**

Reaction norm model outputs in which latency responses of blue tits towards the three different taxidermic mounts were taken two at a time in separate models

		Wald $F/\chi^2$	df	<i>P</i>
<b>Blackbird—Woodpecker</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	403.05 (46.29)			
Predator	−29.88 (43.28)	0.477	1, 167.8	0.49
Sex (ref: female)	125.49 (58.86)	4.546	1, 62.2	0.037
Hatch date	11.09 (8.03)	1.905	1, 69.0	0.17
Sequence	−28.12 (43.51)	0.418	1, 172.3	0.52
Intervisit interval (s)	0.29 (0.17)	3.024	1, 159.1	0.084
Random effects				
Intercept variance (SE)	22745.41 (10484.46)	6.481	3	0.09
Slope variance (SE)	<0.001	<0.001	2	0.99
Intercept-slope covariance (SE)	−0.15 (0.03)			
Residual (SE)	106612.50 (11901.21)			
Variance proportions				
Among-individual intercepts	0.18 (0.07)			
Among-individual slopes	<0.001			
<b>Blackbird—Sparrowhawk</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	526.10 (47.14)			
Predator	98.73 (47.56)	4.310	1, 166.0	0.039
Sex (ref: female)	63.64 (59.18)	1.160	1, 63.0	0.29
Hatch date	18.84 (7.69)	6.010	1, 60.7	0.017
Sequence	−72.40 (47.72)	2.300	1, 167.6	0.13
Intervisit interval (s)	0.41 (0.17)	6.030	1, 152.2	0.015
Random effects				
Intercept variance (SE)	16526.49 (10575.54)	3.012	3	0.37
Slope variance (SE)	<0.001	<0.001	2	0.99
Intercept-slope covariance (SE)	−0.13 (0.04)			
Residual (SE)	124774.90 (14167.42)			
Variance proportions				
Among-individual intercepts	0.12 (0.07)			
Among-individual slopes	<0.001			
<b>Woodpecker—Sparrowhawk</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	480.67 (42.20)			
Predator	125.12 (35.77)	12.24	1, 169.0	<0.001
Sex (ref: female)	100.92 (55.31)	3.33	1, 66.8	0.072
Hatch date	13.62 (7.24)	3.54	1, 64.4	0.064
Sequence	−65.86 (36.21)	3.31	1, 176.5	0.071
Intervisit interval (s)	0.27 (0.15)	3.33	1, 167.9	0.070
Random effects				
Intercept variance (SE)	26619.53 (8871.65)	16.476	3	<0.001
Slope variance (SE)	<0.001	<0.001	2	0.99
Intercept-slope covariance (SE)	0.16 (0.03)			
Residual (SE)	73165.53 (8088.96)			
Variance proportions				
Among-individual intercepts	0.26 (0.07)			
Among-individual slopes	<0.001			

Wald  $F$  values are given for fixed effects and  $\chi^2$  values for random effects. Predictor variables included were those found to be important when modelling latency measures together and in predator-specific models (see [Tables 1 and 2](#), respectively). Blue tit ID ( $N = 68$ ) was included as a random variable in each model.

**Table A6**

Breeding-pair level reaction-norm model outputs in which latency responses of blue tits towards the three different taxidermic mounts were taken two at a time in separate models

		Wald $F/\chi^2$	<i>df</i>	<i>P</i>
<b>Blackbird—Woodpecker</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	399.93 (42.44)			
Predator	−25.33 (46.22)	0.300	1, 200.9	0.58
Sex (ref: female)	129.64 (48.08)	7.272	1, 204.5	0.008
Hatch date	10.68 (7.55)	2.000	1, 35.6	0.17
Sequence	−25.53 (46.34)	0.304	1, 204.1	0.58
Intervisit interval (s)	0.35 (0.15)	5.159	1, 219.6	0.024
Random effects				
Intercept variance (SE)	5541.66 (6247.04)	0.99	3	0.80
Slope variance (SE)	<0.001	<0.001	2	0.99
Intercept-slope covariance (SE)	−0.08 (0.04)			
Residual (SE)	122666.80 (12447.73)			
Variance proportions				
Among-pair intercepts	0.04 (0.05)			
Among-pair slopes	<0.001			
<b>Blackbird—Sparrowhawk</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	519.28 (46.04)			
Predator	100.24 (48.83)	4.214	1, 29.5	0.049
Sex (ref: female)	71.16 (50.23)	2.007	1, 169.0	0.16
Hatch date	19.21 (8.20)	5.490	1, 30.3	0.026
Sequence	−69.07 (48.49)	2.028	1, 175.7	0.16
Intervisit interval (s)	0.45 (0.16)	5.490	1, 209.4	0.005
Random effects				
Intercept variance (SE)	11945.52 (8182.72)	3.689	3	0.30
Slope variance (SE)	1607.00 (21404.15)	0.140	2	0.93
Intercept-slope covariance (SE)	−3167.64 (8743.21)			
Residual (SE)	124774.90 (14167.42)			
Variance proportions				
Among-pair intercepts	0.08 (0.06)			
Among-pair slopes	0.01 (0.15)			
<b>Woodpecker—Sparrowhawk</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	474.58 (39.19)			
Predator	124.13 (38.51)	12.24	1, 169.0	<0.001
Sex (ref: female)	107.85 (40.42)	3.33	1, 66.8	0.072
Hatch date	13.38 (7.57)	3.54	1, 64.4	0.064
Sequence	−60.40 (38.93)	3.31	1, 176.5	0.071
Intervisit interval (s)	0.35 (0.14)	3.33	1, 167.9	0.070
Random effects				
Intercept variance (SE)	13876.86 (6742.05)	9.375	3	0.025
Slope variance (SE)	<0.001	<0.001	2	0.99
Intercept-slope covariance (SE)	0.12 (0.03)			
Residual (SE)	85362.67 (8612.53)			
Variance proportions				
Among-pair intercepts	0.14 (0.06)			
Among-pair slopes	<0.001			

Wald  $F$  values are given for fixed effects and  $\chi^2$  values for random effects. Predictor variables included were those found to be important when modelling latency measures together and in predator-specific models (see [Tables 1 and 2](#) in the main text, respectively). Breeding pair ID ( $N = 34$ ) was included as a random variable in each model.

**Table A7**

Sources of variation in the latency responses of blue tits towards a blackbird, a woodpecker and a sparrowhawk taxidermic mount modelled together

		Wald $F/\chi^2$	df	P
<b>Fixed effects</b>				
	Coefficient (SE)			
Intercept (s)	475.26 (57.08)			
Predator (ref: blackbird)	Woodpecker: -30.62 (41.99) Sparrowhawk: 93.78 (42.84)	4.76	2, 276.2	<0.01
Age (ref: first-year breeder)	-23.38 (56.87)	0.17	1, 56.4	0.68
Sex (ref: female)	98.99 (53.78)	3.39	1, 36.2	0.074
Brood size	-10.88 (14.95)	0.53	1, 30.8	0.47
Hatch date	13.17 (7.55)	3.04	1, 30.6	0.091
Brood age (ref: 10 days)	11 days: -30.22 (51.06) 12 days: 16.72 (74.89)	0.58	2, 284.3	0.55
Sequence	-69.50 (62.34)	1.24	1, 284.9	0.27
Time of day (ref: morning)	13.98 (39.08)	0.13	1, 279.1	0.72
Intervisit interval (s)	0.30 (0.14)	4.68	1, 202.2	0.032
<b>Random effects</b>				
	Variance (SE)			
Individual ID	22757.06 (10952.71)	9.677	1	<0.01
Breeding pair ID	2226.16 (8148.39)	0.076	1	0.78
Residual	100105.81 (8628.17)			
<b>Variance proportions</b>				
Individual ID	0.18 (0.08)			
Breeding pair ID	0.02 (0.07)			

Wald  $F$  values are given for fixed effects and  $\chi^2$  values for random effects. Predictor variables tested were (1) the type of predator (blackbird, woodpecker or sparrowhawk), (2) age of the bird (factor with two levels: first-year breeder or older), (3) the sex of the bird, (4) the number of nestlings in its nest, i.e. its brood size (continuous variable), (5) the hatch date of its brood (continuous variable), (6) age of the brood on the day of the predator trial (three-level factor: 10, 11 and 12 days old), (7) the repeated measure sequence (two-level factor), (8) the time of day when the trial was conducted (two-level factor: morning or afternoon), (9) intervisit interval (s; continuous variable). (10) Blue tit ID ( $N = 68$ ) and breeding pair ID ( $N = 34$ ) were included as random variables.

**Table A8**

Summary of the linear mixed-effects model investigating the effect of the type of predator trial (blackbird, woodpecker or sparrowhawk) conducted in the morning on the latency to resume provisioning in the afternoon predator trial

		Wald $F/\chi^2$	df	P
<b>Fixed effects</b>				
	Coefficient (SE)			
Intercept (s)	539.15 (82.05)			
Morning predator (ref: blackbird)	Woodpecker: -38.85 (71.50) Sparrowhawk: -66.59 (72.63)	0.430	2, 113	0.65
Afternoon predator (ref: blackbird)	Woodpecker: -95.22 (74.01) Sparrowhawk: 70.06 (73.90)	2.697	2, 113	0.071
<b>Random effects</b>				
	Variance (SE)			
Individual ID	31922.29 (17963.30)	5.387	1	0.020
Breeding pair ID	6648.71 (13555.22)	0.250	1	0.62
Residual	98055.91 (13752.26)			

Wald  $F$  values are given for fixed effects and  $\chi^2$  values for random effects. In addition to the type of predator in the morning we controlled for the type of predator used in the focal (afternoon) trials. Blue tit ID ( $N = 68$ ) and breeding pair ID ( $N = 34$ ) were included as random variables.

**Table A9**

Summary of the simplified linear mixed-effects model investigating sources of variation in the latency responses of blue tits towards a blackbird, a woodpecker and a sparrowhawk taxidermic mount modelled together

		Wald $F/\chi^2$	df	P
<b>Fixed effects</b>				
	Coefficient (SE)			
Intercept (s)	447.28 (48.28)			
Predator (ref: blackbird)	Woodpecker: -34.18 (41.89) Sparrowhawk: 95.78 (42.72)	5.149	2, 281.1	<0.01
Age (ref: first-year breeder)	-28.14 (59.40)	0.224	1, 59.7	0.64
Sex ref: female	73.10 (53.39)	1.742	1, 34.8	0.196
<b>Random effects</b>				
	Variance (SE)			
Individual ID	28376.38 (12199.95)	14.271	1	<0.01
Breeding pair ID	1922.63 (8933.66)	0.047	1	0.82
Residual	100125.38 (8549.59)			
<b>Variance proportions</b>				
Individual ID	0.22 (0.09)			
Breeding pair ID	0.01 (0.07)			

Wald  $F$  values are given for fixed effects and  $\chi^2$  values for random effects. Predictor variables tested were (1) the type of predator (blackbird, woodpecker or sparrowhawk), (2) age of the bird (factor with two levels: first-year breeder or older) and (3) the sex of the bird. Blue tit ID ( $N = 68$ ) and breeding pair ID ( $N = 34$ ) were included as random variables.

**Table A10**

Summary of the simplified linear mixed-effects models investigating sources of variation in the latency responses of blue tits towards a blackbird, a woodpecker or a sparrowhawk taxidermic mount each modelled separately

		Wald $F/\chi^2$	$df$	$P$
<b>Blackbird</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	442.54 (90.08)			
Age (ref: first-year breeder)	34.01 (91.61)	0.138	1, 54.0	0.71
Sex (ref: female)	Male: 43.15 (85.96)	0.252	1, 51.7	0.62
Random effects	Variance (SE)			
Individual ID	20013.9 (28344.95)	0.414	1	0.52
Mount ID	12359.4 (16990.01)	2.115	1	0.11
Residual	155057.7 (32797.60)			
Variance proportions				
Individual ID	0.11 (0.15)			
Mount ID	0.07 (0.08)			
<b>Woodpecker</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	375.41 (45.48)			
Age (ref: first-year breeder)	-31.53 (64.76)	0.237	1, 63.7	0.63
Sex (ref: female)	143.88 (61.97)	5.390	1, 63.9	0.023
Random effects	Variance (SE)			
Individual ID	26206.14 (12339.96)	5.038	1	0.025
Mount ID	23.65 (1793.101)	<0.001	1	0.99
Residual	60069.84 (11586.01)			
Variance proportions				
Individual ID	0.30 (0.13)			
Mount ID	<0.001			
<b>Sparrowhawk</b>				
Fixed effects	Coefficient (SE)			
Intercept (s)	589.58 (52.53)			
Age (ref: first-year breeder)	-80.61 (75.70)	1.134	1, 61.3	0.29
Sex (ref: female)	23.02 (71.60)	0.103	1, 60.6	0.75
Random effects	Variance (SE)			
Individual ID	20655.51 (18203.16)	1.342	1	0.25
Mount ID	0.006	<0.001	1	0.99
Residual	100797.70 (20319.55)			
Variance proportions				
Individual ID	0.17 (0.14)			
Mount ID	<0.001			

Wald  $F$  values are given for fixed effects and  $\chi^2$  values for random effects. Predictor variables tested were (1) the type of predator (blackbird, woodpecker or sparrowhawk), (2) age of the bird (factor with two levels: first-year breeder or older) and (3) the sex of the bird. Blue tit ID (blackbird:  $N = 63$ ; woodpecker:  $N = 68$ ; sparrowhawk:  $N = 67$ ) and taxidermic mount ID ( $N = 3$ ) were included as random variables in the blackbird, woodpecker and sparrowhawk models, respectively.

**Table A11**

Character-state model output in which the latency responses to the three different taxidermic mounts were modelled simultaneously as multiple response variables

		Wald $F/\chi^2$	$df$	$P$
<b>Fixed effects</b>				
Blackbird	Coefficient (SE)			
Intercept (s)	436.76 (71.16)			
Sex (ref: female)	92.22 (85.63)	1.160	1, 69.2	0.29
Hatch date	18.16 (11.87)	2.343	1, 71.3	0.13
Sequence (ref: first trial)	-32.79 (75.84)	0.187	1, 94.2	0.67
Intervisit interval (s)	0.46 (0.25)	3.439	1, 107.6	0.066
Woodpecker				
Intercept (s)	371.87 (48.98)			
Sex (ref: female)	154.33 (63.16)	5.970	1, 49.9	0.018
Hatch date	6.60 (8.77)	0.566	1, 44.4	0.45
Sequence (ref: first trial)	-26.71 (43.73)	0.373	1, 70.4	0.54
Intervisit interval (s)	0.16 (0.18)	0.823	1, 110.5	0.37
Sparrowhawk				
Intercept (s)	607.32 (55.46)			
Sex (ref: female)	31.77 (69.63)	0.208	1, 47.5	0.65
Hatch date	20.06 (8.86)	5.123	1, 49.9	0.028
Sequence (ref: first trial)	-125.75 (56.07)	5.030	1, 86.2	0.027
Intervisit interval (s)	0.31 (0.19)	2.515	1, 106.6	0.116

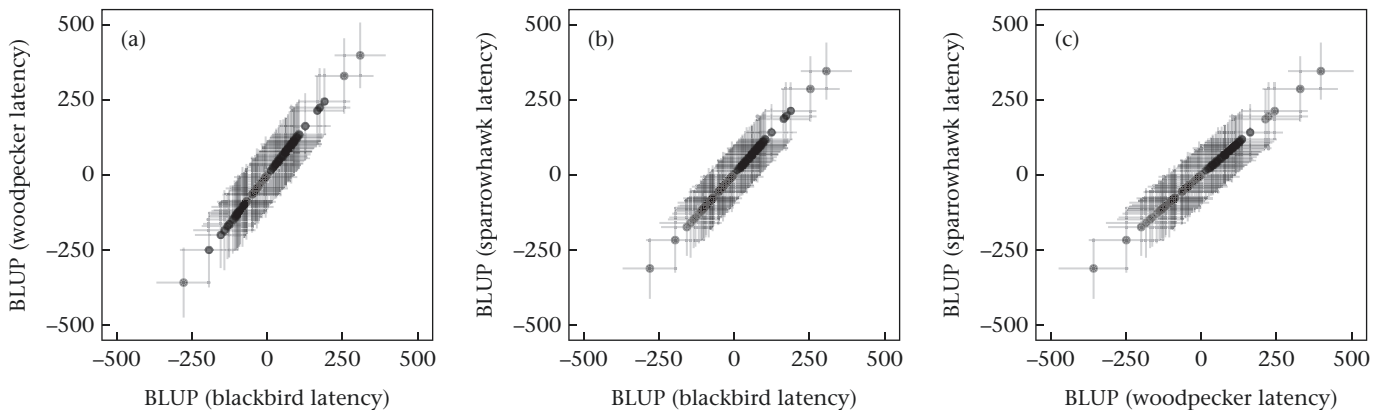
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**Table A11** (continued)

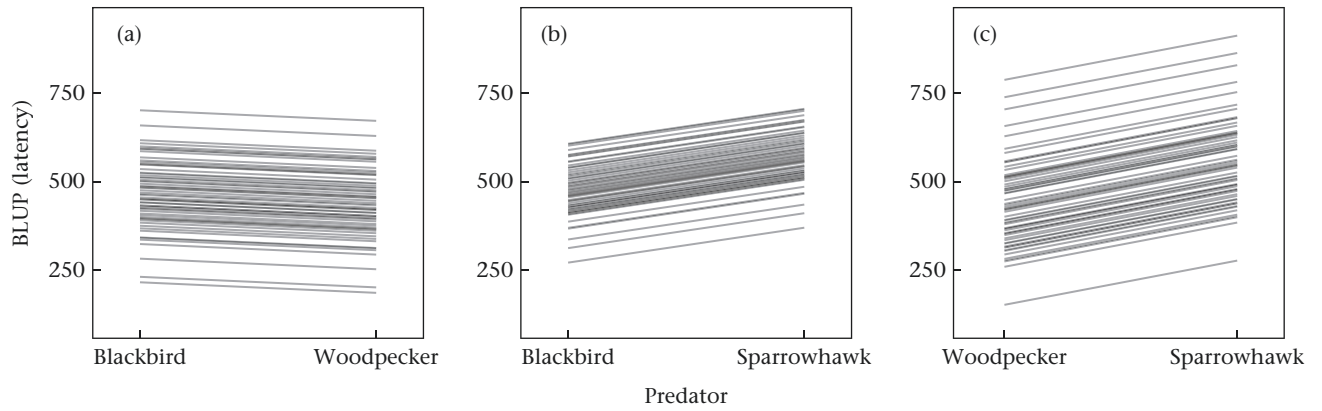
		Wald $F/\chi^2$	df	P
<b>Random effects</b>				
Breeding pair ID	Variance (SE)			
Individual ID (blackbird)	1293.92 (7894)			
Individual ID (woodpecker)	18765.42 (16609.13)			
Individual ID (sparrowhawk)	31027.63 (13646.23)			
Residual (blackbird)	23427.85 (15772.53)			
Residual (woodpecker)	157633.80 (23281.30)			
Residual (sparrowhawk)	55251.58 (9764.58)			
	86180.66 (13696.60)			
<b>Variance proportions</b>				
Pair ID (blackbird)	0.007 (0.044)			
Pair ID (woodpecker)	0.015 (0.090)			
Pair ID (sparrowhawk)	0.012 (0.071)			
Individual ID (blackbird)	0.11 (0.09)			
Individual ID (woodpecker)	0.35 (0.13)			
Individual ID (sparrowhawk)	0.21 (0.13)			
<b>Among-individual correlation</b>				
Blackbird—Woodpecker	0.99 <sup>1</sup>	0.009	1	0.93
Blackbird—Sparrowhawk	0.99 <sup>1</sup>	0.003	1	0.96
Woodpecker—Sparrowhawk	0.99 <sup>1</sup>	0.056	1	0.81
<b>Among-individual covariance</b>				
Blackbird—Woodpecker	20940.32 (13059.77)			
Blackbird—Sparrowhawk	26932.39 (12005.97)			
Woodpecker—Sparrowhawk	157633.80 (23281.30)			

Wald  $F$  values are given for fixed effects and  $\chi^2$  values for random effects. Predictor variables included were those found to be important when modelling latency measures together and in predator-specific models (see [Tables 1 and 2](#) in the main text, respectively). Blue tit ID (blackbird:  $N = 63$ ; woodpecker:  $N = 68$ ; sparrowhawk:  $N = 67$ ) were included as random variables for each response variable, respectively. Breeding pair ID ( $N = 34$ ) was estimated once across all response variables. Shown are estimates of the fixed variables and of the variances of random variables along with their respective proportions.  $P$  values of the individual correlations were inferred from log-likelihood ratio tests comparing models in which the correlation tested was fixed at +1.

<sup>1</sup> Standard errors were inestimable as estimates were fixed to the boundary.



**Figure A1.** Within-individual correlations across the different predation threat levels, illustrated using BLUPs (best linear unbiased predictors) of latency values. Individuals' BLUPs were extracted from a trivariate model wherein latency responses towards a blackbird, woodpecker and sparrowhawk were respectively taken as separate response variables (see [Table 5](#) in main text). Plotted are the BLUPs for individuals' (a) woodpecker versus blackbird, (b) sparrowhawk versus blackbird and (c) sparrowhawk versus woodpecker latency responses. Each point represents an individual and error bars represent standard errors of the predicted values.



**Figure A2.** Individual reaction norms across the (a) blackbird—woodpecker, (b) blackbird—sparrowhawk and (c) woodpecker—sparrowhawk threat levels, illustrated using BLUPs (best linear unbiased predictors) of latency values extracted from random-regression models (see [Table A8](#)).