

1 **Integration of multimodal cues does not alter mean but reduces variance in avian responses**
2 **to predators: a systematic review and meta-analysis**

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38 **Abstract**

39 Despite a wealth of studies documenting prey responses to perceived predation risk,
40 researchers have only recently begun to consider how prey integrate information from multiple
41 cues in their assessment of risk. We conduct a systematic review and meta-analysis of studies
42 that experimentally manipulated perceived predation risk in birds and evaluate support for
43 three alternative models of cue integration: redundancy/equivalence, enhancement, and
44 antagonism. One key insight from our analysis is that the current theory, generally applied to
45 study cue integration in animals, is incomplete. These theories specify the effects of increasing
46 information level on mean, but not variance, in responses. In contrast, we show that providing
47 multiple complementary cues of predation risk simultaneously does not affect mean response,
48 but rather, reduces variance in responses across studies. We propose this may arise via
49 maximum-likelihood estimation (MLE) integration. Although the MLE framework has been
50 applied to study cue integration in humans, to date, it has not been applied to studies of cue
51 integration in non-human animals. We highlight the broad applicability of MLE integration for
52 information integration problems and propose avenues for future work. Our meta-analysis
53 illustrates how explicit consideration of variance in responses can yield important biological
54 insights.

55 **Introduction**

56 A wealth of research demonstrates that prey can use a range of cue types when assessing
57 predation risk (Lima & Dill 1990) and numerous studies have shown that animals respond more
58 strongly to cues indicating higher average risk. For example, animals have a stronger response
59 to more lethal predator types (Greene & Meagher 1998; Blumstein 1999; Aliza Le *et al.* 2001;
60 Templeton *et al.* 2005) and to predators exhibiting more dangerous behaviours/postures
61 (Mathot *et al.* 2009; Kyle & Freeberg 2016; Kyle 2020). Theory predicts that the information
62 quality of a cue (i.e., certainty about current predation risk conferred by a given cue) should
63 also affect the magnitude of response (McClinn & Stephens 2006; Stephens & Dunlap 2009;
64 Munoz & Blumstein 2012). All else being equal, cues indicating a given level of predation risk
65 with high certainty should elicit stronger responses compared to cues indicating the same level
66 of predation risk with lower certainty (McClinn & Stephens 2006; Stephens & Dunlap 2009;
67 Munoz & Blumstein 2012), though empirical tests of this prediction are lacking (but see
68 Arteaga-Torres *et al.* 2020).

69 More recently, researchers have begun to address how prey integrate information from
70 multiple cues in their assessment of risk (McClinn & Stephens 2006; Munoz & Blumstein 2012;
71 Munoz & Blumstein 2019; Arteaga-Torres *et al.* 2020). Patterns of multimodal cue integration
72 can broadly be grouped into three types of integration: redundancy/equivalence,
73 enhancement, and antagonism (Munoz & Blumstein 2012). The expected outcome of
74 multimodal cue integration depends on the level of uncertainty associated with each cue on its
75 own relative to the uncertainty that results from the combined cues. Equivalence (or
76 redundancy) describes the scenario in which the response elicited by either cue on its own is

77 the same as the response elicited by two cues combined (Munoz & Blumstein 2012). If the
78 unimodal cues differ in the response they elicit, for example, because one provides greater
79 certainty about current risk, then we would expect the two cues combined to elicit the same
80 response as the higher certainty unimodal cue, in which case, the response might be described
81 as 'redundant' (Figure 1a). Equivalence (or redundancy) is expected when the addition of a
82 second cue provides no greater certainty about the current level of threat than the high
83 certainty cue on its own, nor does it change the estimated risk (Munoz & Blumstein 2012).
84 Alternatively, combined cues may result in enhancement, whereby the response to the
85 combined cues is greater than the response to either cue on its own (Figure 1b). This is
86 expected when two cues together indicate a higher likelihood than either cue on its own
87 (Munoz & Blumstein 2012). Finally, multiple cues can combine to produce antagonistic effects,
88 whereby the response to the combined cues are less than the response to the higher certainty
89 cue on its own or even lower than both cues (Figure 1c). This is expected to occur when the
90 combination of cues increases the certainty that predation risk is low relative to either cue on
91 their own (Munoz & Blumstein 2012).

92 Here, we conduct a systematic review and meta-analysis of studies that experimentally
93 manipulate perceived predation risk in birds with unimodal or multimodal cues of predation to
94 test predictions from the uncertainty reduction framework described above. We restrict our
95 review to birds because their anti-predator responses have been studied extensively, providing
96 a large number of studies with relatively comparable experimental designs. We use these
97 studies to test two predictions from the uncertainty reduction framework. First, we test the
98 prediction that anti-predator responses to unimodal cues of current predation risk increase

99 with increasing cue certainty (McClinn & Stephens 2006; Stephens & Dunlap 2009; Munoz &
100 Blumstein 2012; Arteaga-Torres *et al.* 2020). The three most common cue modalities used in
101 experimental manipulations of perceived risk in avian studies are visual (e.g., predator mounts),
102 acoustic (e.g., mobbing calls) and chemical (e.g., olfactory predator cues). Visual cues of
103 predation provide high certainty information that the predator is present and may also provide
104 postural or behavioural cues as to the predator's current state (Mathot *et al.* 2009; Kyle &
105 Freeberg 2016; Kyle 2020). Mobbing calls are uncertain because they can be given as false
106 alarms (Munn 1986; Møller 1988). However, when produced honestly, mobbing calls may
107 convey information about the level of threat the predator poses (Templeton *et al.* 2005), and
108 also convey that the threat is currently being attended to (Arteaga-Torres *et al.* 2020). An
109 olfactory predator cue provides information that a predator has been present in an area, but
110 not whether it is currently in the area or if it is, in what state (e.g., hungry or sated) (Kats & Dill
111 1998). Thus, we assumed that visual cues (e.g., predator mounts) provide greater certainty
112 compared to acoustic cues (e.g., mobbing calls), which provide greater certainty compared to
113 chemical cues (e.g., predator odour). Following this assumption, for unimodal cues, we
114 predicted that antipredator responses would be greatest in response to visual cues,
115 intermediate in response to acoustic cues, and lowest in response to chemical cues.

116 Second, we evaluated support for specific forms of cue integration. We predicted redundancy
117 between visual and chemical cues because adding a chemical cue should not provide any
118 further reduction in uncertainty regarding current predation risk compared to the direct
119 observation of a predator alone (Figure 1a). We predicted enhancement between acoustic cues
120 and chemical cues. On their own, acoustic and chemical cues each provide uncertain

121 information about whether a predator is present. Thus, receiving both cues simultaneously
122 should increase the certainty that a predator is currently present, resulting in an elevated
123 response (Figure 1b). Finally, we predicted antagonistic integration between visual and acoustic
124 cues. On their own, visual cues provide greater certainty that a predator is currently present
125 compared to mobbing calls for the reasons outlined above. However, acoustic cues such as
126 mobbing calls presented in combination with visual cues could lower perceived risk compared
127 to the visual cue alone by providing information that the threat is already being attended to, by
128 increasing real or perceived group size and thereby providing dilution of risk (e.g., Foster &
129 Treherne 1981), or both (Figure 1c).

130

131 **Methods**

132 ***(1) Literature search and inclusion/exclusion criteria***

133 We followed the steps outline in the Preferred Reporting Items for Systematic Review and
134 Meta—Analysis (PRISMA) protocol (Moher *et al.* 2009) for our meta-analysis as recommended
135 by Nakagawa and Poulin (2012). We additionally verified the reporting of our study items using
136 the PRISMA-EcoEvo guidelines outlined in O'Dea *et al.* (2021); see Supporting Information SI1.
137 We performed our literature search in the online databases Web of Science (All databases) and
138 Scopus accessed through the University of Alberta libraries subscription. We had search terms
139 related to predation, experiments, and taxa. The predation-related search terms used were:
140 “predat* risk” OR “pred* danger” OR “perceived predat*” OR “perceived risk”. The experiment-
141 related search terms were “experiment*” OR “manipulat*” OR playback* OR treatment*.

142 Because our meta-analysis was restricted to birds, we used the additional taxa-related search
143 terms: “bird*” OR “aves”. We searched for articles using these terms in the ‘Topic’ field. Articles
144 had to include at least one of the search terms from each of the three topic strings.

145 JDAT, NK and KJM conducted the initial scoping review, developed search terms, and defined
146 inclusion/exclusion criteria. The final literature search was conducted on February 18th, 2022.
147 Our search criteria produced a total of 814 unique references (Figure 2). As a first step, we
148 screened these references by title and abstract to assess their relevance to the meta-analysis.
149 Title and abstracts were screened by four observers (RAM, SS, DMH and KJM) independently
150 using Rayyan (Ouzzani *et al.* 2016). Any disagreements were resolved through joint discussion.
151 This resulted in a total of 171 articles for which the full text was read by JDAT or KJM. To be
152 included in the meta-analysis, studies had to fulfil each of the following criteria:

153 1) The study had to present an experimental manipulation of perceived predation risk.
154 Manipulations of perceived risk included experimentally providing cues of predator
155 presence (olfactory, visual or auditory cues), social cues of predation risk (e.g., mobbing
156 calls or alarm calls), or any combination of the above. For acoustic cues, we only
157 considered vocalizations made by known predators or vocalizations made by the focal
158 species (e.g., mobbing or alarm calls). We did not include studies that aimed to test
159 whether a cue was recognized by birds (e.g., presentation of novel predator or
160 evaluation of social learning about predation risk). We did not consider the presence of
161 human observers alone as an experimental manipulation of perceived predation.
162 Similarly, we did not consider mobbing or alarm calls produced in response to humans
163 as a relevant manipulation of perceived predation risk. We included studies that

164 manipulated perceived predation risk using live predators as long as the
165 presence/absence of the predator was determined experimentally (e.g., caged predator,
166 or presented via falconer).

167 Studies that manipulated predation risk without providing cues related to the presence
168 of actual predators were not included. For example, we excluded studies that
169 manipulated the size of the nest box entrance so that some were accessible by
170 predators and others were not, or studies that manipulated landscape features (e.g.,
171 distance to obstructive cover, distance to protective cover) that alter the ability to
172 detect and/or evade predators. We also did not include studies that manipulated
173 predation risk using predator removals or exclusions, as these did not report the
174 predator cues (type, frequency) that were encountered in the control groups (i.e., non-
175 removal plots or outside exclusions).

176 2) The study had to provide data on behaviour, life history, or physiology/morphology as a
177 function of manipulated perceived risk. The full list of traits included in the meta-
178 analysis and their definitions is provided in Supporting Information SI2.

179 3) The study had to allow for the calculation of effect size for a behavioural, life history or
180 physiological variable in response to a manipulation of perceived predation risk as
181 described in (1). The study had to include a control for the manipulation, such as data
182 on the response variable prior to the experiment in the same set of individuals (Before-
183 After-Control-Impact (BACI) or within-subject design), or contrasts between sets of
184 individuals exposed to the manipulation and individual not exposed to the manipulation
185 (among-subject design). Studies that only contrasted different manipulations of

186 perceived risk (e.g., response to visual cue versus response to acoustic cue) were not
187 included. We excluded any estimates for which there were less than $N = 3$ individuals in
188 a given treatment group because the standard deviation (SD) could not be estimated
189 well with small sample sizes (see below calculation details).

190 4) The study had to be conducted on birds and present species-specific results. Studies
191 that presented mixed-species responses (e.g., the average response of a mixed-species
192 flock) were not included in the meta-analysis.

193 5) We initially considered any behavioural, life history, or physiological trait if the study
194 fulfilled the four criteria listed above. However, following full-text screening of all
195 articles, we removed studies/estimates if there were not at least $N = 3$ studies that
196 provided extractable data for that response variable.

197 These selection criteria resulted in a total of 114 papers that were appropriate for inclusion in
198 our meta-analysis (indicated with asterisks in the References section). Studies that were
199 deemed not to fulfill these selection criteria ($N = 58$) upon reading the full text are listed in
200 Supporting Information S13, along with the reason for their exclusion. We additionally included
201 $N = 1$ article not captured by the search criteria but known to the authors to be relevant, and N
202 $= 1$ article that was rejected based on title/abstract but which was known by the authors to
203 include relevant data, resulting in a total of 116 articles from which we extracted estimates. The
204 full PRISMA flow chart is provided in Figure 2.

205 ***(2) Data coding and calculation of effect sizes***

206 For each estimate extracted, we noted the following variables: 1) the year the study was
207 published to allow us to investigate the time lag effects of published effect sizes (see
208 **Publication bias**, below), 2) the species name of the focal organism to allow us to control for
209 phylogeny in the meta-regression, 3) whether the experimental manipulation of perceived
210 predation risk involved cues of a single predator species (and if so, the predator species name)
211 or multiple predator species, 4) the guild of predator(s): bird, mammal, fish, reptile, not
212 specified, or multiple guilds, 5) whether the predator was a predator of adult birds (A), nests
213 (including eggs and nestlings, N), or both (B), 6) the setting of the study: field, lab, semi-natural
214 (e.g., wild-caught birds held in outdoor aviary), 7) the treatment: A = Acoustic, O = Olfactory, V
215 = Visual, or any combination of the above), 8) the season (breeding, non-breeding), 9) the type
216 of comparison: among = among individuals, cohort comparisons; within = within-subject
217 comparison such as before/after, 10) treatment duration, expressed as number of days.
218 Treatments conducted within a single day were coded as the proportion of the day that the
219 treatment lasted, assuming a 12hr daylength, 11) control type: blank = no experimental control
220 (e.g., before-after study design), NonPred = non predator control, disturbance = control for the
221 disturbance associated with the treatment or non-biological components of treatment such as
222 presence of a speaker, 12) sex of focal individuals: male, female, both (includes studies that
223 explicitly stated both sexes were included, as well as studies which made no explicit mention of
224 sex of focal subjects), 13) age of focal individuals when treatment was applied: A = adults, N =
225 nestlings, J = Juveniles, E = eggs.

226 We collected relevant sample statistics (e.g., mean, median, sample size, standard deviation,
227 standard error, quantile range, etc.) for responses to control and treatments from each study or

228 its associated data repository. When the relevant data were presented in figures, we extracted
229 the data using WebPlotDigitizer 4.1 (Rohatgi 2018). and transformed relevant study results into
230 a standardized effect size (SMD, or often referred to as Hedge's *g*). Effect sizes and variances
231 cannot be calculated when proportion responses include either 0 or 1 (e.g., proportion of nests
232 abandoned). Thus, we replace 0 proportion responses with 0.025, and 1 proportion responses
233 with 0.975 following Fox and Weisberg (2019). We used Hedge's *g* as our standardized effect
234 size because we were interested in the effect of categorical variables (predation risk treatment)
235 on behaviour, life-history and physiology, and this effect size removes bias for small sample
236 sizes that occur when using other effects sizes such as Cohen's *d*.

237

238 **(3) Meta-analysis and meta regression analysis**

239 We conducted all statistical analyses including exploratory data analyses in the program R
240 version 4.2.3 (R Development Core Team 2023). We calculated standardised effect sizes and
241 their sampling variance using a custom function that converted SMD (Hedge's *g*) calculated via
242 the effect size calculator at the Campbell Collaboration website (see Supplementary
243 Information SI4: <https://itchyshin.github.io/multimodality/#custom-functions>). Using these, we
244 constructed (phylogenetic) multi-level meta-analytic models (Nakagawa & Santos 2012); we
245 used the *rma.mv* function in the R-package *metafor* (Viechtbauer 2010) along with the R-
246 package MuMIn for multi-model inference (Bartoń 2012). The meta-analytic models were to
247 ascertain that, overall, birds responded to treatments compared to control conditions.
248 Initially, our meta-analytic model had five random effects that were considered *a priori* to be
249 potentially important sources of variation and non-independence in estimated effect sizes.

250 These were: (i) the phylogenetic effect of species, (ii) species identity (a non-phylogenetic
251 component of species), (iii) group (i.e., a unique set of individuals to account for the fact that
252 the same individual could be used to estimate multiple effect sizes), (iv) study ID (i.e., a unique
253 study identifier to account for non-independence between estimates derived from the same
254 study population), and (v) observation id (i.e., an effect size-level random effect equivalent to
255 residual term in a normal linear model). We obtained the avian phylogenetic tree from Jetz *et*
256 *al.* (2012). To account for phylogenetic uncertainty, we used 50 posterior samples of the avian
257 phylogenetic tree and merged results using Rubin’s rules according to Nakagawa and De
258 Villemereuil (2018). Because phylogeny played a little role in this analysis, we report results
259 from one tree in Results below (see also Supporting Information SI4;
260 <https://itchyshin.github.io/multimodality/#meta-analysis>).

261 These random effects did not account for all non-independence among sampling variances (i.e.,
262 correlations due to the same individuals being used to obtain more than one effect size)
263 (Nakagawa *et al.* 2023b). To deal with this, we created a variance-covariance matrix to add to
264 meta-analytic models by assuming sampling variances from the same studies have the
265 correlation $r = 0.5$, as suggested by Noble *et al.* (2017). For meta-analytic models, we calculated
266 the multilevel-model version of heterogeneity (I^2), which quantifies variance not due to
267 sampling error, for each random effect and the total heterogeneity following Nakagawa and
268 Santos (2012). Based on these analyses, only species identity, record ID, and observation ID
269 were retained. For subsequent analyses (i.e., meta-regressions), we dropped the phylogenetic
270 effect of species and group ID as these accounted for <0.01% of the heterogeneity.

271 To explain the observed heterogeneity (I^2), we created a set of meta-regression models. The
272 moderators considered were: cue modality, trait type (behaviour, life history or physiology),
273 treatment duration (in days), sex of the focal individual (male, female, or both), type of
274 predator used (i.e., whether the predator targets adults, eggs/nestlings or both), predator guild,
275 study design (within-subject versus among-subject), season (breeding versus non-breeding),
276 setting (field, lab or semi-natural), and control type (blank, disturbance control, or non-predator
277 control).

278 To address our main question, we first tested for the effect of cue modality. We did this in
279 multiple steps. We first constructed a model including all six treatment levels for which we had
280 estimates: acoustic (A), visual (V), olfactory (O), acoustic + visual (AV), olfactory + visual (OV),
281 and acoustic + visual + olfactory (AVO). However, because there were few estimates for
282 treatments involving olfactory cues either on their own or in combination with other cue types
283 (see Results), we also constructed models that were restricted to estimates from studies based
284 on A, V and AV treatment levels. For this dataset, we considered both homoscedastic and
285 heteroscedastic models because visualizations using orchard plots revealed a clear difference in
286 variability among different treatment levels (Nakagawa *et al.* 2015; Nakagawa *et al.* 2023a).
287 As a secondary analysis, we considered all the other moderators above, and where appropriate,
288 we considered both homoscedastic and heteroscedastic models (see Supporting Information
289 SI4; <https://itchyshin.github.io/multimodality/>). For all models, we assessed the importance of
290 moderators by calculating marginal R^2 (*sensu* Nakagawa & Schielzeth 2013). We visualized
291 meta-analytic results as well other relevant results mainly using the R packages *ggplot2*
292 (Wickham 2016), *orchaRd* (Nakagawa *et al.* 2021; Nakagawa *et al.* 2023a), *ggalluvial* (Brunson &

293 Reac 2023), and ggtree (Yu *et al.* 2017). Data and reproducible analyses are provided in
294 Supplementary Information SI4 (<https://itchyshin.github.io/multimodality/>).

295

296 **(4) Publication bias**

297 We evaluated evidence for publication bias by assessing funnel plot asymmetry and tested the
298 significance of the asymmetry using a multilevel version of Egger's regression (Nakagawa *et al.*
299 2022). We included the square root of the effective sample size (effective N) as a fixed effect in
300 Egger's regression and also included the following random effects based on the variables that
301 contributed most to heterogeneity in the null model described above: species ID, study ID, and
302 observation ID. We assessed the presence of a time lag effect by regressing standardized effect
303 sizes (Hedge's g) against publication year (Jennions & Møller 2002; Yang *et al.* 2023), also
304 known as a decline effect (Koricheva & Kulinskaya 2019), with the same random effects as
305 Egger's regression model (species ID, study ID, and observation ID). Furthermore, we conducted
306 a leave-one-study-test to see whether a particular study had a major impact on the overall
307 effect (see Supplementary Information SI4; <https://itchyshin.github.io/multimodality/>)

308

309 **Results**

310 Our extraction criteria yielded 645 estimates from 116 studies representing 87 species (Figure
311 3A), and 29 countries/regions (Figure 3B). Estimates were not evenly distributed amongst the
312 types of unimodal cues or their multimodal combinations (Figure 4). Most estimates were for
313 experimental manipulations using acoustic cues ($k = 302$), followed by visual cues ($k = 190$),
314 then combined acoustic and visual cues ($k = 108$). A smaller number of estimates were obtained

315 from experimental manipulations of olfactory cues alone ($k = 18$), or olfactory cues in
316 combination with visual cues ($k = 15$) or both visual and acoustic cues ($k = 7$). Within the three
317 treatment levels for which we had a large number of estimated effect sizes (A, V, and AV),
318 estimates were relatively balanced across all putative moderators (see Supporting Information
319 SI4; <https://itchyshin.github.io/multimodality/>) such that observed treatment effects were
320 unlikely to be due to confounding effects of these moderators.

321 ***(1) Responses to different cues of predation risk: how is information integrated?***

322 Overall, there was strong support that birds responded in the predicted direction (see Figure 4)
323 to manipulations of perceived predation risk (standardised mean difference, SMD or $g = 0.418$,
324 95% confidence interval, CI = [0.288, 0.548]). Total heterogeneity was high ($I^2_{[total]} = 92.82$),
325 phylogeny ($I^2_{[phylogeny]} < 0.01$) species ($I^2_{[species]} = 1.22$) and subject ID ($I^2_{[group]} = 0.00$) accounted
326 for very little variation. Substantial heterogeneity was observed across studies ($I^2_{[across-study]} =$
327 15.58), with most heterogeneity remaining unexplained ($I^2_{[residuals]} = 75.54$).

328 As per our *a priori* assumptions about the level of certainty each cue modality would convey
329 about current predation risk, we first assessed whether different cue modalities elicited
330 different magnitudes of response. Contra to our predictions, there was no support that the
331 mean magnitude of response differed as a function of the modality of cue(s) presented (Figure
332 4). No pairwise contrasts between treatment categories (types of uni-modal cues or contrast
333 between unimodal and multimodal cues) were significantly different from one another (all $p \geq$
334 0.30, see Supporting Information SI4; <https://itchyshin.github.io/multimodality/> for exact p-

335 values for each pairwise contrast. SI4 also includes multi-moderator analyses and sensitivity
336 analyses).

337 Given the lack of estimates in response to olfactory cues either alone ($k = 18$) or in combination
338 with visual ($k = 15$) and in combination with both visual and acoustic ($k = 7$) cues, we restricted
339 subsequent analyses to estimates derived from the three most common treatment types: A, V
340 and AV. The exclusion of treatments, including olfactory cues (alone or in combination) due to
341 low sample size did not alter the interpretations related to the three most commonly used
342 treatments (A, V and AV). Analyses restricted to the three most common treatment levels
343 reveal that while the mean response to each of these three treatments did not differ, there was
344 strong support for heterogeneous variances (LRT: 18.86, $p < 0.0001$). Specifically, among-study
345 variance in response to acoustic cues alone ($\sigma^2_{[\text{residuals}]} = 0.75$) and visual cues ($\sigma^2_{[\text{residuals}]} = 0.86$)
346 were comparable in magnitude. However, when acoustic and visual cues were provided
347 together, among-study variance in responses was less than half in magnitude ($\sigma^2_{[\text{within-study}]} =$
348 0.35) (Figure 4).

349 ***(2) Exploring the effects of moderators on the responses to manipulations of perceived***
350 ***predation risk.***

351 As a secondary analysis, we explored the effects of several potential moderators on the
352 response to experimental manipulations of perceived predation risk. We found that response
353 to manipulations of perceived predation risk varied as a function of the type of response
354 measured. Specifically, behavioural responses were significantly stronger than physiological
355 responses (estimated difference: $\beta = 0.458$, 95% CI = [0.193, 0.723]), with life-history responses

356 being intermediate in magnitude and not significantly different from either behavioural
357 (estimated difference: $\beta = 0.178$, 95% CI = [-0.062, 0.418]) or physiological responses (estimated
358 difference: $\beta = 0.280$, 95% CI = [-0.025, 0.586]) (Figure 5A). Responses also varied as a function
359 of treatment duration, with longer treatments eliciting significantly smaller responses ($\beta = -$
360 0.046 , 95% CI = [-0.076, -0.015], $R^2_{\text{[marginal]}} = 3.43$) (Figure 5B). However, response type and
361 treatment duration were confounded, making it difficult to disentangle their effects from one
362 another (Figure 5B).

363 We also evaluated support for several additional putative moderators. There was no support
364 that additions to the visual treatment (e.g., movement of model predator), setting (lab, field, or
365 semi-natural), season (breeding or non-breeding), study design (within-subject versus among-
366 subject), response period (during or after treatment), control type (blank, control for
367 disturbance, non-predator control), sex of focal individuals (male, female or both), age (adults
368 or nestlings), or predator type (predator to adults, predator to nestlings, or both) on the
369 magnitude of response to manipulations of perceived predation risk (see Supporting
370 Information SI4; <https://itchyshin.github.io/multimodality/>).

371

372 **(3) Publication bias**

373 Visual assessment of funnel plots did not provide evidence for publication bias (Figure 6A).
374 Results of the Egger regression were consistent with this. The slope of the regression was not
375 significantly different from zero ($\beta = -0.03$, 95% CI = [-0.08, 0.03], $R^2_{\text{[marginal]}} = 0.30\%$) (Figure 6B).
376 We also found no evidence of a time lag effect (Year: $\beta = -0.01$, 95% CI = [-0.03, 0.01], $R^2_{\text{[marginal]}}$

377 = 0.59% (Figure 6C; for more relevant results, see Supplementary Information SI4;
378 <https://itchyshin.github.io/multimodality/>).

379

380 **Discussion**

381 We used meta-analyses to quantify the effect of experimental manipulations of perceived
382 predation risk in birds on behavioural, physiological and life-history traits, and explored the
383 effects of several putative moderators for the relationship. We found strong overall support
384 that birds respond in the predicted direction to manipulated predation risk. However, contrary
385 to our predictions (Figure 1), we found no evidence that the modality of information about
386 predation risk (acoustic, visual, or olfactory) influenced the mean magnitude of response, nor
387 did combining cues alter the mean magnitude of response (Figure 4). Interestingly, we found
388 strong support that providing multi-modal cues of predation risk reduced among-study variance
389 in response to manipulations. We discuss the implications of these findings for our
390 understanding of how multimodal cues affect uncertainty and shape animal decision-making in
391 a wide range of contexts.

392 ***Responses to unimodal cues***

393 We assumed that different types of manipulations of perceived predation risk would convey
394 different degrees of certainty about the current level of risk. Specifically, we assumed that
395 visual cues, such as predator mounts, would provide the highest certainty about the current
396 presence of a predator. In contrast, olfactory cues would provide the lowest level of certainty
397 as these cues can persist in even after the predator has left the area. Acoustic cues, such as

398 mobbing calls by conspecifics, were expected to provide an intermediate level of information.
399 On the one hand, they provide social information about current predation risk, but they can be
400 unreliable as they can be given as false alarms (Munn 1986; Møller 1988), or may reduce
401 perceived risk as they indicate that the threat is already being attended to (Arteaga-Torres *et al.*
402 2020).

403 Accordingly, we predicted that the response to visual cues of predation would be greater than
404 the response to olfactory cues, with acoustic cues producing intermediate-level responses.

405 Although the response to olfactory cues tended to be lower compared with either visual or
406 acoustic cues, the 95% CI around the estimated effects overlapped broadly, indicating a lack of
407 support for a difference in response level. The estimated response to acoustic versus visual
408 cues was quantitatively very similar, indicating strong support for no difference. Therefore,
409 contrary to our expectation, risk assessment based on either acoustic or visual cues alone was
410 similar. We suggest this similarity may be because the acoustic cues used were typically
411 mobbing and/or alarm calls of groups of conspecifics. Although single individuals may produce
412 false alarms, the risk of a group of conspecifics producing false alarms may be lower. A
413 consensus among group members about current risk (expressed by group mobbing calls) may
414 provide relatively high certainty about current risk such that the response to this social
415 information is, on average, similar to direct, personal information (Rieucau & Giraldeau 2011).

416 ***Integration of multimodal cues***

417 We were also interested in understanding how access to multimodal cues would shape
418 responses to manipulations of perceived predation risk. There needed to be more studies that

419 used olfactory cues in combination with other cues (olfactory + visual: K = 3 studies, olfactory +
420 acoustic + visual: K = 4 studies) to allow meaningful analyses of these multimodal cue
421 combinations. However, when comparing responses to either acoustic or visual cues alone
422 versus acoustic and visual cues combined, there was no support for an effect on the mean
423 magnitude of response. This finding is consistent with the notion that the two cues provide
424 redundant information (Figure 1), which could be expected given that each cue in isolation
425 elicited quantitatively similar responses (Figure 4). However, our analyses also show that
426 among-study variance in response to multimodal cues was significantly lower compared with
427 responses to unimodal cues (Figure 4).

428 This result may be explained by maximum-likelihood estimation (MLE) integration (see Box 1
429 for description). Under MLE integration, the probability densities of predation risk associated
430 with cues presented in isolation yield combined estimates that integrate information about the
431 mean and variance estimations derived from either cue alone (Ernst & Banks 2002). Under MLE
432 integration, estimates with less variance are given higher weight, so that if the two estimates
433 have different means from their probability distribution, the mean derived through the
434 integration of both estimates will be closer to the mean from the higher certainty cue (Figure
435 7A). Importantly, the variance of the combined estimate is always reduced relative to either of
436 the independent estimates from which it is derived. Thus, even if acoustic and visual cues of
437 predation risk have equal means and variances in the probability distributions for estimated
438 predation risk, multimodal cues that combine information from visual and acoustic cues will still
439 have lower variance than either unimodal cue alone (Figure 7B). However, cue integration
440 occurs at the level of individuals. Thus, under MLE integration, we would expect a reduction in

441 among-individual variance when combining cues with equal probability distributions (Ernst &
442 Banks 2002). Assuming different study populations had access to the same cues with the same
443 probability distributions, we would not predict MLE integration of multimodal cues to lead to a
444 reduction in among-study variance (Box 1, Figure 7).

445 However, we argue that the assumption that the probability distributions of cues used across
446 studies are identical is unrealistic for several reasons. First, even within cue types, studies vary
447 in numerous features that are likely to affect risk assessment. For example, we found that
448 response magnitude was affected by treatment duration, with longer exposure to cues
449 resulting in smaller responses (Figure 5B). Furthermore, numerous studies have shown that the
450 same species of predator can elicit different responses depending on postural cues about
451 current threat level and/or the distance at which the predator is first detected (e.g., Robinson
452 1980; Helfman 1989; Helfman & Winkelman 1997; Edelaar & Wright 2006; Stankowich & Coss
453 2007; Mathot *et al.* 2009). Such variation also exists among studies and may be expected to
454 contribute to among-study variance in response. For field studies, particularities of the study
455 site, including habitat features that affect the ability of birds to detect or evade predators, year-
456 specific environmental conditions that affect the risk of energy shortfall, or among-study
457 differences in population size that influence dilution of predation risk, among others, are all
458 likely to have biologically important impacts on perception of predation risk (Lima & Dill 1990;
459 Caro 2005). Thus, we can expect large among-study variance in risk assessment even when the
460 same cue modality is used (Figure 8A & 8B). Indeed, our analyses support this interpretation
461 because study ID accounted for substantial heterogeneity among estimates. Under MLE
462 integration, high among-study variance in the perceived risk associated with a given cue type

463 would result in similar mean responses to unimodal versus multimodal cues but lower among-
464 study variance under MLE integration (Figure 7C).

465 ***Moderators of the effects of perceived predation risk in birds***

466 We also explored the effects of several putative moderators on the magnitude of response to
467 manipulations of perceived predation risk. Surprisingly, several moderators previously
468 described as important were not found to affect the magnitude of response in the present
469 meta-analysis (Supporting Information S14; <https://itchyshin.github.io/multimodality/>).
470 Specifically, we found no evidence that adding movement to the visual manipulations of
471 predation risk, such as side-to-side head movement or gliding movement by the model
472 predator, consistently affected the mean response significantly. Similarly, whether the control
473 treatment was a blank control, a control for the disturbance associated with the predator
474 treatment, or an equivalent stimulus from a non-predator species did not systematically affect
475 mean response levels. Both of these findings are at odds with results from earlier empirical
476 studies showing the birds can exhibit graded responses to stimuli representing differing levels
477 of risk and/or disturbance (Mathot *et al.* 2009; Kyle & Freeberg 2016; Kyle 2020). We suggest
478 that the lack of effects reported here again can be attributed to high among-study variance
479 such that uncontrolled among-study variance had a larger impact on response to manipulations
480 of perceived predation risk than specific features of the experimental treatment (e.g., predator
481 posture or type of control), reducing our power to detect these effects.

482 In fact, only two of the explored moderators had detectable effects on mean response to
483 manipulations of perceived predation risk: duration of treatment and response type. Longer

484 treatment durations were associated with significantly smaller effect sizes (Figure 5B). This
485 result is consistent with the notion that animals may habituate to cues that are presented
486 repeatedly for extended periods of time (e.g., Raderschall *et al.* 2011), or that lower allocation
487 to predator avoidance is adaptive when high-risk situations are frequent and/or lengthy (Lima
488 & Bednekoff 1999). However, another possibility is that researchers design their studies based
489 on expected responses, such that traits that are expected to exhibit small and/or slow
490 responses to manipulations of risk are typically studied using experiments with longer
491 treatment durations. Indeed, we found that treatment duration was the longest for studies
492 investigating life history responses to perceived predation risk, followed by studies of
493 physiological responses, with studies of behavioural responses tending to have the shortest
494 duration (Figure 5B). While our analyses did detect an effect of response type on response
495 magnitude, with behavioural traits exhibiting the largest effect sizes (Figure 5A), because
496 response type was confounded with treatment duration, we cannot conclusively tease apart
497 their effects from one another.

498 ***Limitations and future directions***

499 Our meta-analysis revealed significant heterogeneity in responses to manipulations of
500 perceived predation risk, with most heterogeneity existing at the level of the observation (i.e.,
501 single estimates), followed by study ID. This indicates that responses are context-specific and
502 that among-study variance in ecological context and particularities of how treatments were
503 carried out have important consequences for how birds respond to experimental manipulations
504 of predation risk. Importantly, there were several limitations to the available data. First, the
505 lack of studies that included olfactory cues, either alone or in combination with other cues,

506 meant we could not evaluate whether integration of information of olfactory cues differed
507 from other cue modalities. This is important as previous authors have suggested that olfactory
508 cues may be less informative than acoustic or visual cues (Kats & Dill 1998), however, more
509 studies are needed to test whether birds exhibit systematically lower responses to olfactory
510 cues. Additionally, we did not detect a phylogenetic effect of species on responses to perceived
511 predation risk. However, Passeriformes in particular, were over-represented within the studies
512 included in the meta-analysis (Figure 3A), which may have limited our power to detect
513 phylogenetic effects.

514 Further, while our meta-analysis did synthesize studies from 29 countries from five continents,
515 the representation was heavily skewed towards North America and Europe (Figure 3B). Given
516 that our analysis indicates an important effect of study ID, which we presume is due to study-
517 specific context (e.g., baseline predation risk, flock size, food availability, ambient conditions,
518 etc.), a more balanced global representation of studies would help ascertain the generality of
519 our results. Finally, at least two potential moderators of the effect of manipulations of
520 perceived predation risk on birds were confounded in our available our dataset; treatment
521 duration and response type. More studies employing relatively short-term manipulations of
522 perceived predation risk to investigate physiological and life-history responses are needed to
523 better understand the causal effect that each of these moderators (treatment duration and
524 response type) exert independently.

525 We found no evidence that the type of unimodal cue affected mean response, nor did
526 multimodal cues differ in mean response compared to unimodal cues (Figure 4). However,
527 there was strong support that among-study heterogeneity was lower for responses to

528 multimodal cues compared to unimodal cues. This finding is consistent with maximum
529 likelihood estimation (MLE) integration. Importantly, the MLE integration hypothesis applies
530 across multiple levels of biological organization, including cue integration at the level of
531 individuals, populations, and studies. A logical next step to formally test this hypothesis would
532 involve manipulating unimodal and multimodal cues in different contexts (e.g., predation risk,
533 mate choice, etc.) and across different scales (within-individuals, among-individuals within the
534 same population, and across studies) to test 1) whether multimodal cues lead to lower variance
535 in responses across each of these scales as predicted by MLE integration and 2) the generality
536 of MLE for information integration problems.

537 ***Conclusions***

538 Our meta-analysis shows that providing two complementary cues about predation risk does not
539 alter mean responses but leads to lower among-study variance in response. Our finding
540 provides a powerful demonstration that explicit consideration of variance can yield important
541 biological insights (Cleasby & Nakagawa 2011; Westneat *et al.* 2015). Based on these meta-
542 analytic insights, we outline a framework for cue integration that incorporates effects of cue
543 integration on both means and variances in response: maximum likelihood estimation (MLE)
544 integration. Although the MLE framework has been shown to apply to the integration of visual
545 and haptic cues in humans (Ernst & Banks 2002), to date, studies of cue integration in non-
546 human animal systems have not explicitly considered the impact of cue integration on variance
547 in responses. Given that MLE integration can apply at different scales, from individuals to
548 populations, it may be relevant to understanding information integration in animal decision
549 making in a wide range of contexts.

550

551 **Data accessibility**

552 All data and scripts required to replicate the analyses are available at the GitHub repository
553 (<https://github.com/itchyshin/multimodality>) and will be archived in Zenodo upon final
554 acceptance.

555

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561

562 **References**

563 **References with asterisks were used to calculate effect-sizes in the meta-analysis.**

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1155 **Figure Legends:**

1156 **Figure 1:** Illustration of three types of multimodal cue integration. We assume that the
1157 unimodal cues differ in information quality (i.e., certainty), such that stimulus II has higher
1158 certainty and elicits a stronger response on its own compared to stimulus I. Panel A illustrates
1159 signal redundancy (or equivalence), whereby the multimodal stimulus does not increase
1160 certainty relative to the higher certainty stimulus (II) on its own. Panel B illustrates
1161 enhancement, where the multimodal stimulus increases certainty relative to either stimulus on
1162 their own, thereby eliciting a stronger response. Panel C illustrates antagonism, whereby the
1163 multimodal cue results in a lower estimation of risk than the more certain unimodal cue on its
1164 own. Note, that any reduction in the response to the multimodal cue relative to the more
1165 certain stimulus (II) would be considered antagonism even if it is higher than the response to
1166 the lower certainty cue (I).

1167 **Figure 2:** PRISMA flow chart showing the number of articles discovered and/or retained at each
1168 phase of the systematic review. All studies included in the meta-analysis are indicated with
1169 asterisks in the References section, and the list of all studies that were rejected after reading
1170 the full text can be found in Table S3 including the reason for the rejection.

1171 **Figure 3:** Illustration of phylogenetic and geographic breadth of estimates included in meta-
1172 analysis. Panel A) shows the phylogenetic relationships used in the meta-regression, grouped by
1173 order, and the associated mean effect size for response to manipulations of perceived
1174 predation risk for k estimates from K studies. Panel B) shows the geographic distribution of
1175 estimates, where the colour of the country on a gradient from yellow to red represents the

1176 total number of estimates (k). Grey is used for countries from which no estimates were
1177 obtained. Silhouettes representing different bird orders were obtained from PhyloPic.org
1178 ([https://www.phylopic.org/permalinks/4d2aebec1e2f2da818396c344eb377c61d6ce0d70ddb15](https://www.phylopic.org/permalinks/4d2aebec1e2f2da818396c344eb377c61d6ce0d70ddb15d09d7671defdf00ed2)
1179 [d09d7671defdf00ed2](https://www.phylopic.org/permalinks/4d2aebec1e2f2da818396c344eb377c61d6ce0d70ddb15d09d7671defdf00ed2)).

1180 **Figure 4:** Orchard plot of meta-analytic mean effect sizes, standardised mean difference (SMD
1181 or Hedge's g) for each of six treatment levels for experimental manipulations of perceived
1182 predation risk: A = acoustic, AV = acoustic + visual, AVO = acoustic + visual + olfactory, O =
1183 olfactory, OV = olfactory + visual, and V = visual. The circle denotes the meta-analytic means,
1184 and the black rectangle represent the 95% confidence intervals, and the whiskers denote the
1185 prediction intervals. Total number of estimates (k) is given on to the right of each plot with the
1186 number of studies contributing estimates in parentheses. Panel A) shows results from meta-
1187 analysis including all treatment levels. Panels B) and C) illustrate results from analyses restricted
1188 to the three most common cue types (A, V, and AV). Panel B) shows estimated effects from
1189 homoscedastic model, and panel C) shows estimated effects from heteroscedastic model.

1190 **Figure 5:** Illustration of the effect of significant moderators of the effect of manipulations of
1191 perceived predation risk in birds. Magnitude of response varies as a function of (A) response
1192 type (behaviour, life history, or physiology), and (B) declines with increasing treatment
1193 duration. However, different treatment durations tend to be associated with different response
1194 types as shown in panel (B), making it difficult to tease apart their effects. In panel A, the circle
1195 denotes the meta-analytic means, and the black rectangle represent the 95% confidence
1196 intervals, and whiskers denote the prediction intervals. In panel B, the regression is plotted with
1197 95% confidence intervals (inner dotted line) and 95% prediction intervals (outer dotted line).

1198 Total number of estimates (k) is given on to the right of each plot, with the number of studies
1199 contributing estimates in parentheses.

1200 **Figure 6:** Assessing publication bias. (A) Funnel plot. (B) Egger regression to assess funnel
1201 asymmetry. 95% confidence intervals are depicted by the two outer dotted lines. (C) Regression
1202 to test time lag effect of published effect sizes, with 95% confidence intervals depicted by the
1203 two inner dotted lines and 95% prediction intervals depicted by the two outer dotted lines
1204 (these are non-linear as the predictions are derived from multi-moderator models).

1205 **Figure 7:** Illustration of multimodal cue integration under two scenarios. A) Acoustic cues
1206 provide a lower mean estimate of risk and higher uncertainty/variance (blue dotted line)
1207 compared with visual cues (red dashed line). The estimated risk that integrates both these
1208 sources of information using maximum likelihood estimation (MLE) integration will have lower
1209 variance than either alone, and the mean will be closer to the mean of the higher certainty
1210 unimodal cue (solid black line). B) Acoustic (blue dotted line) and visual (red dashed line)
1211 provide similar means and variances in estimated risk. Under multimodal cue integration using
1212 MLE integration (solid black line), mean estimated risk remains unchanged, but has lower
1213 variance relative to both unimodal cues.

1214 **Figure 8:** Illustration of how maximum likelihood estimation integration (MLE) could result in
1215 lower among-study variance in response to manipulations of perceived predation risk when
1216 two redundant cues are integrated relative to the among-study variance when either cue type
1217 is presented alone. Each panel illustrates five hypothetical populations (shown in five distinct
1218 colours). If there is across study heterogeneity in the probability function associated with study-

1219 specific unimodal cues as shown in panels A (Acoustic) and B (Visual), then even if the mean
1220 and among-study variance in response to each of the two unimodal cues are identical,
1221 maximum likelihood integration will result in lower among-study variance, as shown in panel C.
1222



Figure 1

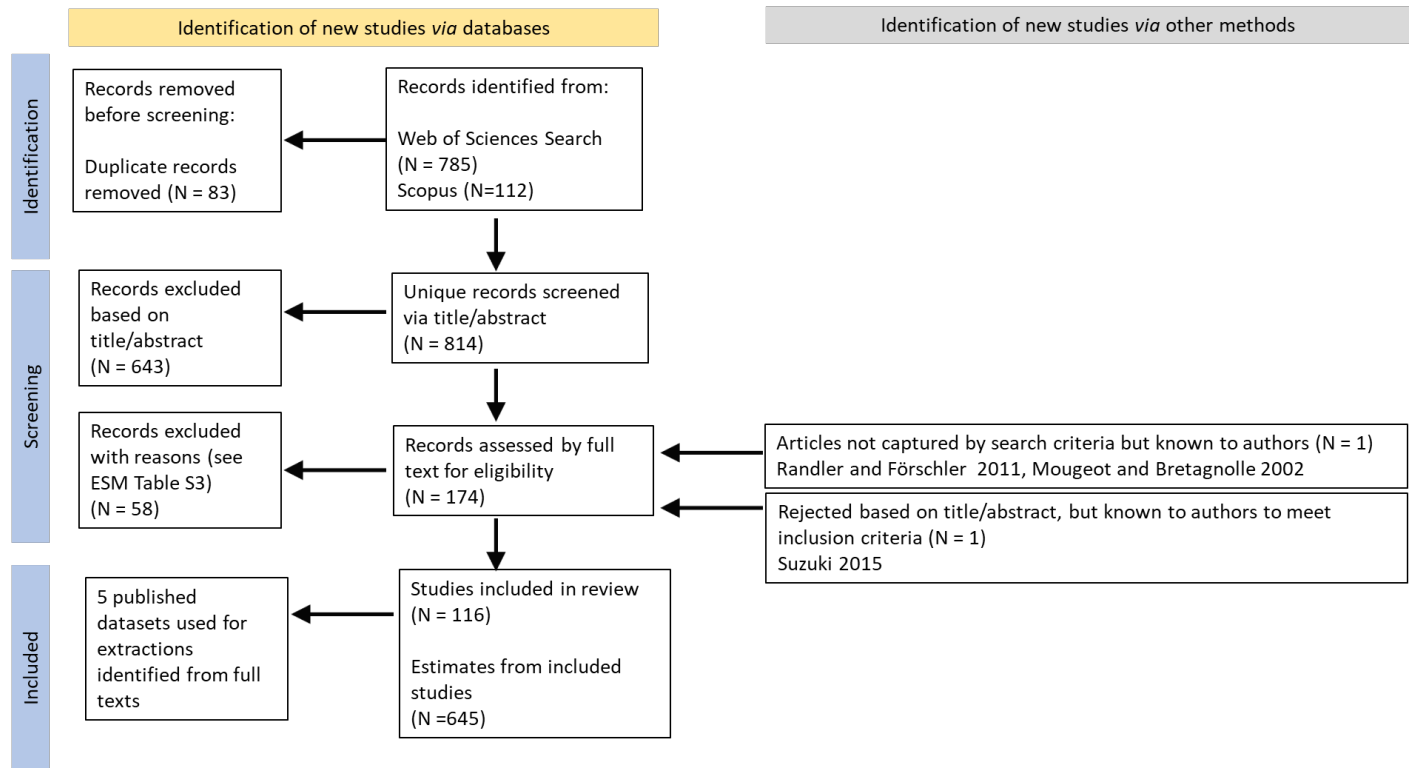


Figure 2

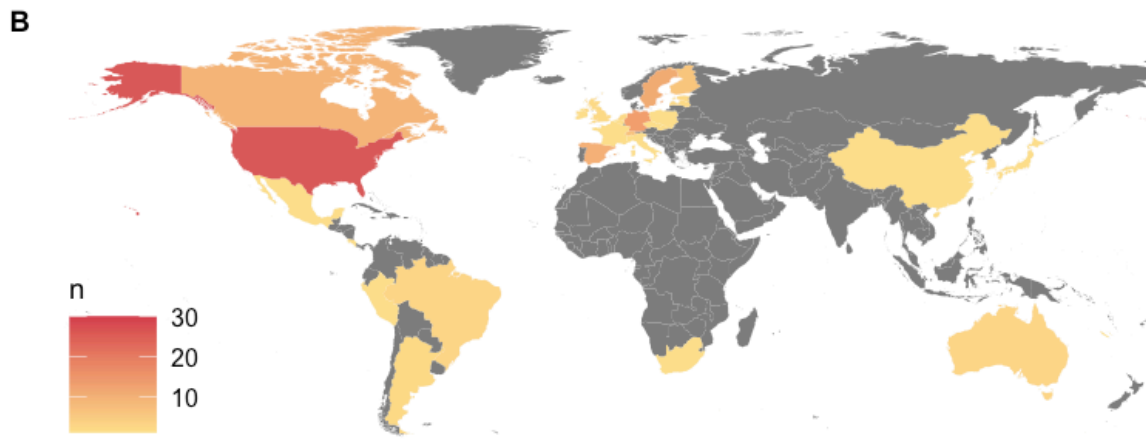
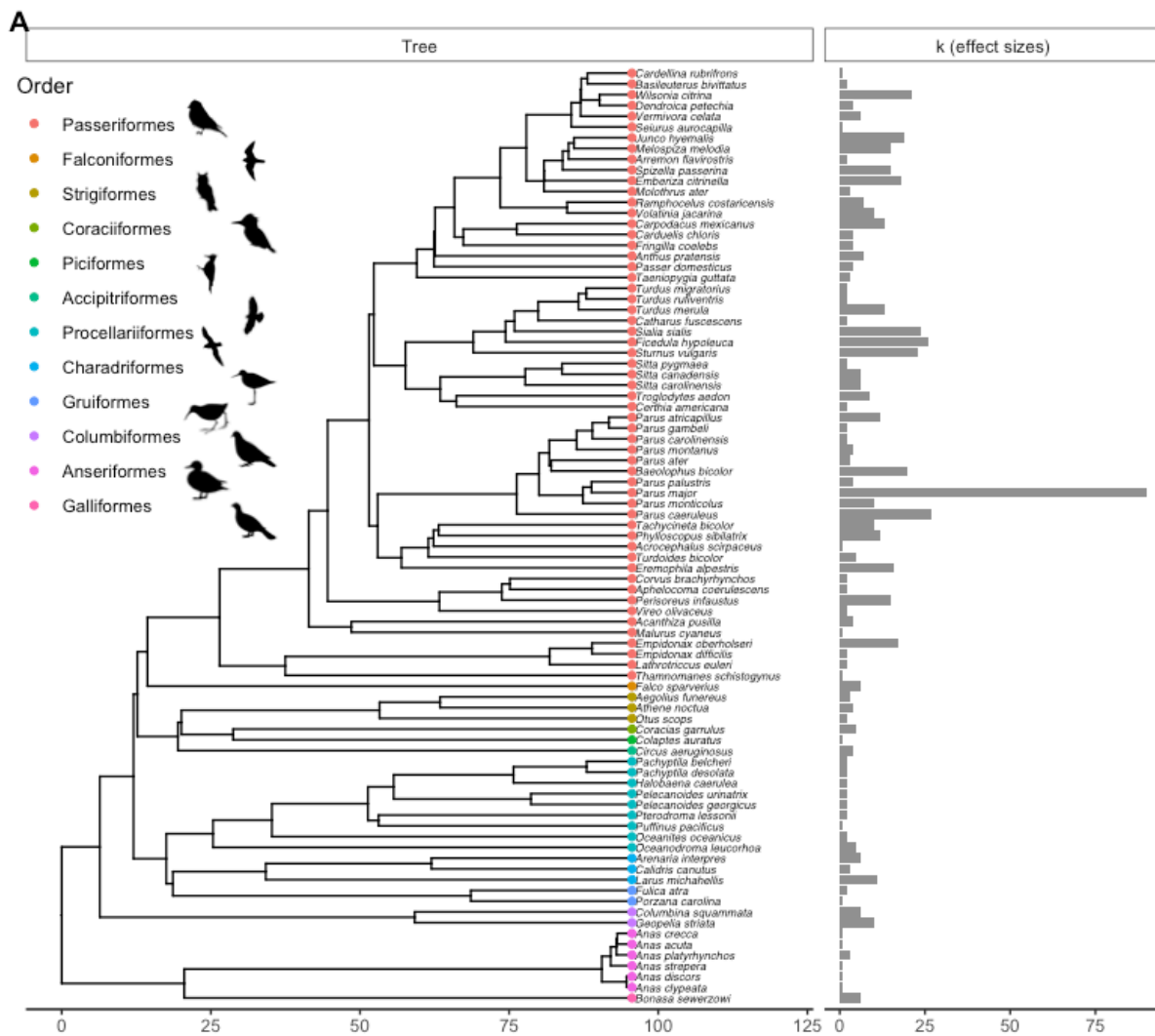


Figure 3

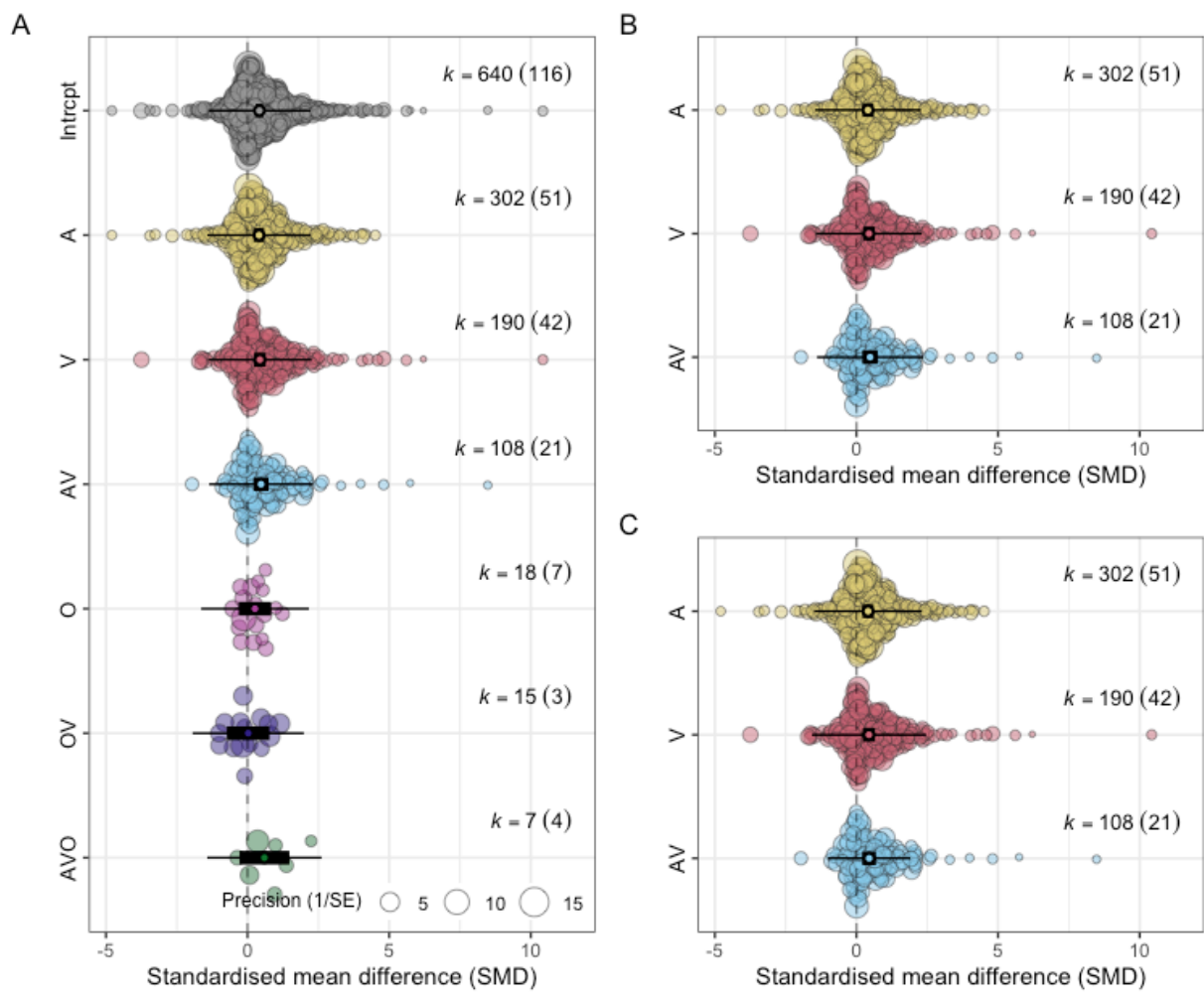


Figure 4

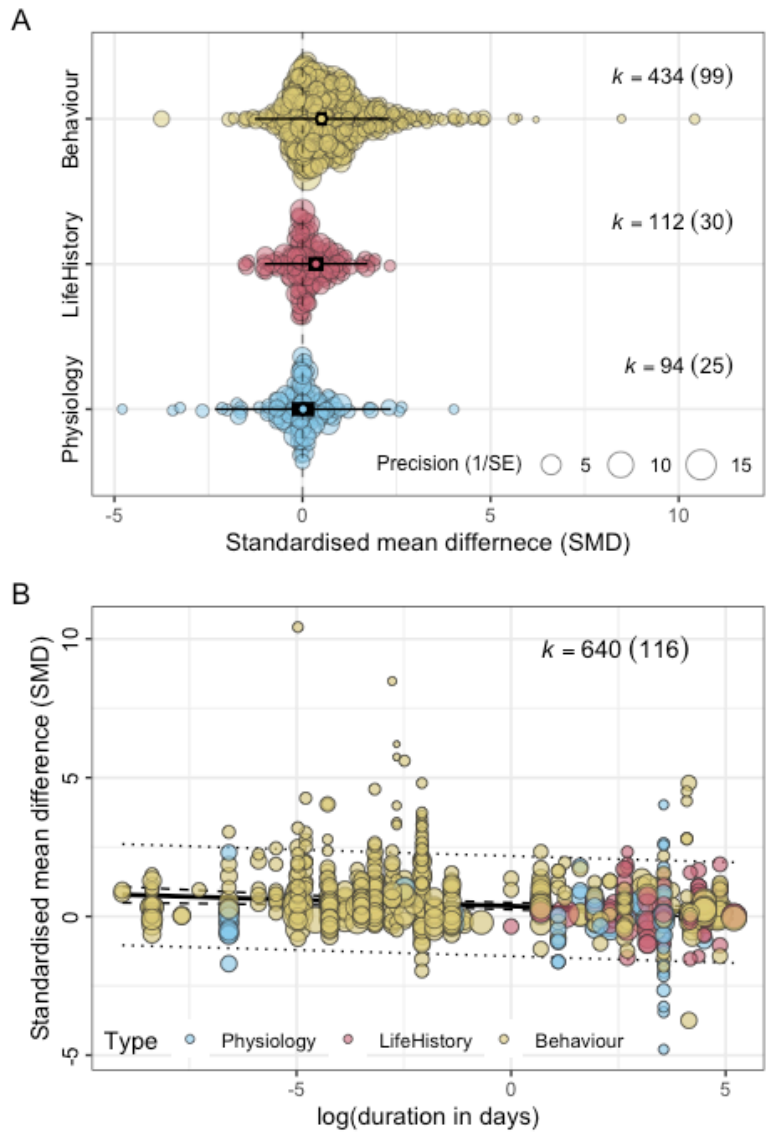


Figure 5

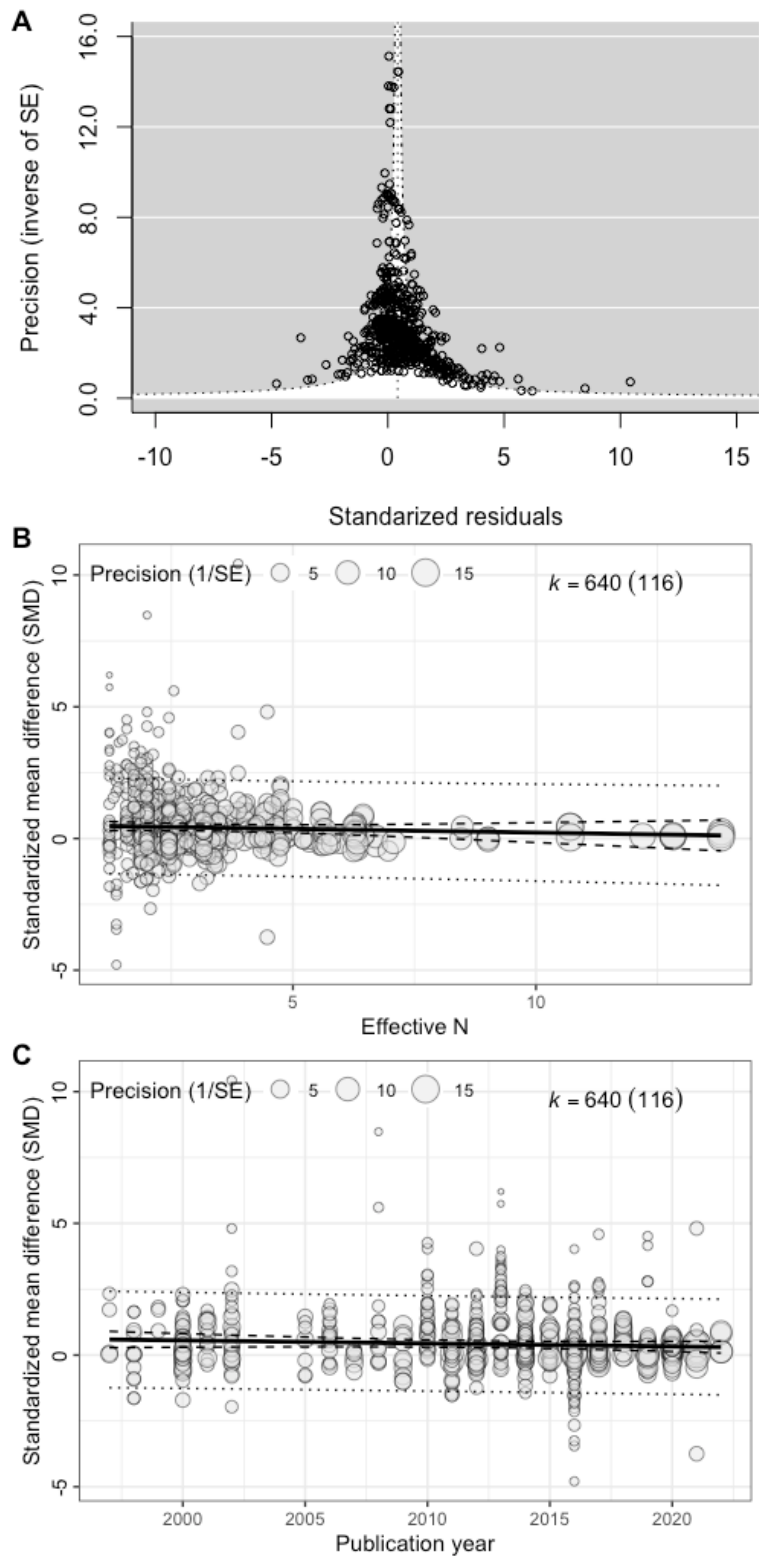


Figure 6.

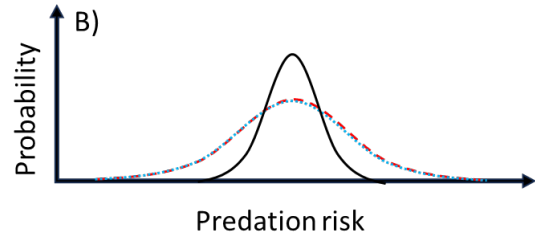
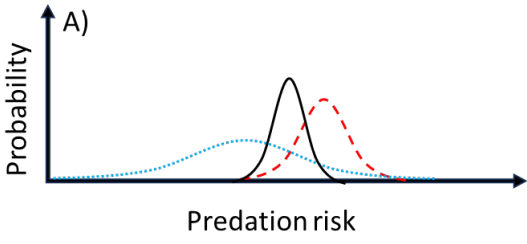


Figure 7

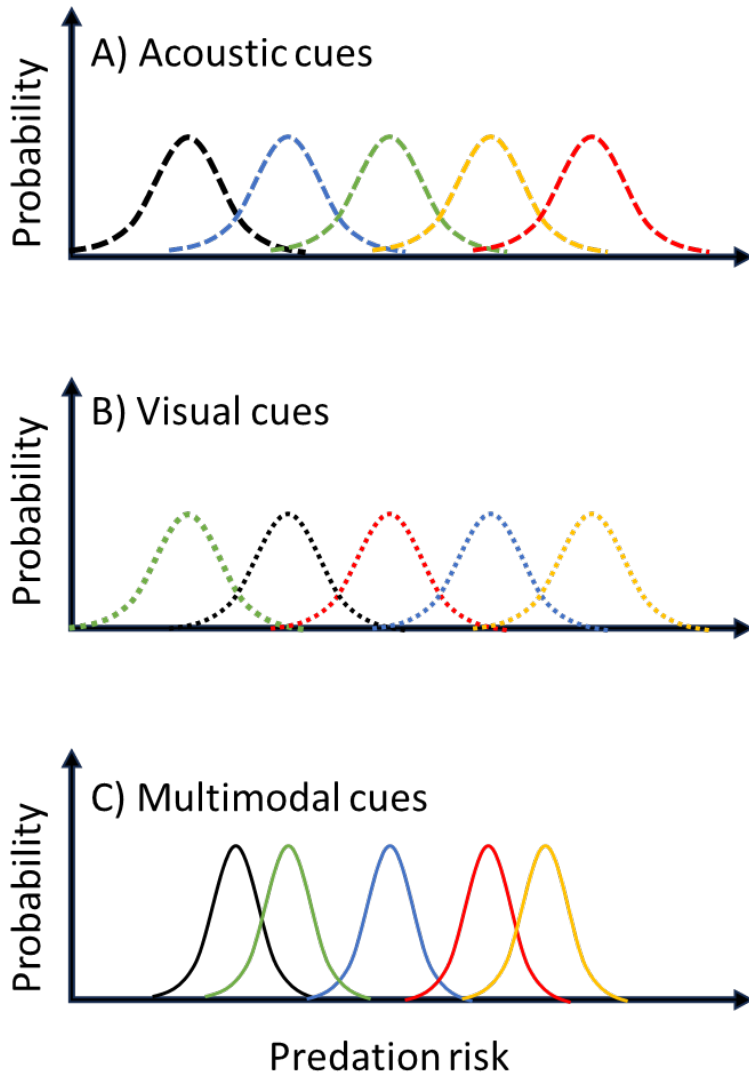


Figure 8

Box 1: What is maximum likelihood estimation?

Maximum likelihood estimation (MLE) is a statistical method for estimating the parameters of a probability distribution given some observed data (e.g., observing a particular cue). MLE determines the parameters for which the observed data have the highest probability, or likelihood. MLE integration refers to a process by which independent probability distributions are integrated to produce a probability distribution that combines the information from independent estimates (van Dam *et al.* 2014). Specifically, if each of independent probability distributions is Gaussian, the combined estimate mean will correspond to the weighted average of the independent estimate means, with the weights being inversely proportional to the amount of uncertainty, or variance, associated with each independent estimate (Eq. 1). Furthermore, the variance of the combined estimate is always reduced relative to either of the independent estimates from which it is derived (Eq. 2). Thus, under MLE integration, responses to multimodal cues are always expected to have lower variance than responses to any unimodal cue presented alone.

$$\mu_{AV} = \left(\frac{\frac{1}{\sigma_A^2}}{\left(\frac{1}{\sigma_A^2} + \frac{1}{\sigma_V^2} \right)} \right) \mu_A + \left(\frac{\frac{1}{\sigma_V^2}}{\left(\frac{1}{\sigma_A^2} + \frac{1}{\sigma_V^2} \right)} \right) \mu_V \quad \text{Eq. 1}$$

$$\sigma_{AV}^2 = \frac{\sigma_A^2 \sigma_V^2}{\sigma_A^2 + \sigma_V^2} \quad \text{Eq. 2}$$

Table S1. PRISMA Eco-Evo reporting checklist based on O'Dea *et al.* (2021).

Checklist item	Sub-item number	Sub-item	Reported by authors?	Notes
Title and abstract	1.1	Identify the review as a systematic review, meta-analysis, or both	Yes	
	1.2	Summarise the aims and scope of the review	Yes	
	1.3	Describe the data set	Yes	
	1.4	State the results of the primary outcome	Yes	
	1.5	State conclusions	Yes	
	1.6	State limitations	Yes	
Aims and questions	2.1	Provide a rationale for the review	Yes	
	2.2	Reference any previous reviews or meta-analyses on the topic	Yes	
	2.3	State the aims and scope of the review (including its generality)	Yes	
	2.4	State the primary questions the review addresses (e.g. which moderators were tested)	Yes	
	2.5	Describe whether effect sizes were derived from experimental and/or observational comparisons	Yes	Details provided in the methods section
Review registration	3.1	Register review aims, hypotheses (if applicable), and methods in a time-stamped and publicly accessible archive and provide a link to the registration in the methods section of the manuscript. Ideally registration occurs before the search, but it can be done at any stage before data analysis.	No	
	3.2	Describe deviations from the registered aims and methods	No	
	3.3	Justify deviations from the registered aims and methods	No	
Eligibility criteria	4.1	Report the specific criteria used for including or excluding studies when screening titles and/or abstracts, and full texts, according to the aims of the systematic review (e.g. study design, taxa, data availability)	Yes	
	4.2	Justify criteria, if necessary (i.e. not obvious from aims and scope)	Yes	

Finding studies	5.1	Define the type of search (e.g. comprehensive search, representative sample)	Yes	
	5.2	State what sources of information were sought (e.g. published and unpublished studies, personal communications)	Yes	
	5.3	Include, for each database searched, the exact search strings used, with keyword combinations and Boolean operators	Yes	
	5.4	Provide enough information to repeat the equivalent search (if possible), including the timespan covered (start and end dates)	Yes	
Study selection	6.1	Describe how studies were selected for inclusion at each stage of the screening process (e.g. use of decision trees, screening software)	Yes	
	6.2	Report the number of people involved and how they contributed (e.g. independent parallel screening)	Yes	
Data collection process	7.1	Describe where in the reports data were collected from (e.g. text or figures)	Yes	
	7.2	Describe how data were collected (e.g. software used to digitize figures, external data sources)	Yes	
	7.3	Describe moderator variables that were constructed from collected data (e.g. number of generations calculated from years and average generation time)	Yes	Treatment duration calculated in days. Where duration < 1 day, proportion of day calculated assuming 12hr daylength
	7.4	Report how missing or ambiguous information was dealt with during data collection (e.g. authors of original studies were contacted for missing descriptive statistics, and/or effect sizes were calculated from test statistics)	Yes	
	7.5	Report who collected data	Yes	
	7.6	State the number of extractions that were checked for accuracy by co-authors	Yes	
Data items	8.1	Describe the key data sought from each study	Yes	
	8.2	Describe items that do not appear in the main results, or which could not be extracted due to insufficient information	Yes	

	8.3	Describe main assumptions or simplifications that were made (e.g. categorising both ‘length’ and ‘mass’ as ‘morphology’)	Yes	
	8.4	Describe the type of replication unit (e.g. individuals, broods, study sites)	Yes	
Assessment of individual study quality	9.1	Describe whether the quality of studies included in the systematic review or meta-analysis was assessed (e.g. blinded data collection, reporting quality, experimental vs. observational)	No	All studies included were experimental
	9.2	Describe how information about study quality was incorporated into analyses (e.g. meta-regression and/or sensitivity analysis)	No	Information on quality was not incorporated into analyses
Effect size measures	10.1	Describe effect size(s) used	Yes	
	10.2	Provide a reference to the equation of each calculated effect size (e.g. standardised mean difference, log response ratio) and (if applicable) its sampling variance	Yes	
	10.3	If no reference exists, derive the equations for each effect size and state the assumed sampling distribution(s)	NA	A reference for the effect size and its sampling variance was available, so no derivation was required
Missing data	11.1	Describe any steps taken to deal with missing data during analysis (e.g. imputation, complete case, subset analysis)	NA	There were no missing data
	11.2	Justify the decisions made to deal with missing data	NA	There were no missing data
Meta-analytic model description	12.1	Describe the models used for synthesis of effect sizes	Yes	
	12.2	The most common approach in ecology & evolution will be a random-effects model, often with a hierarchical/multilevel structure. If other types of models are chosen (e.g. common/fixed effects model, unweighted model), provide justification for this choice	Yes	
Software	13.1	Describe the statistical platform used for inference (e.g. R)	Yes	
	13.2	Describe the packages used to run models	Yes	
	13.3	Describe the functions used to run models	Yes	
	13.4	Describe any arguments that differed from the default settings	Yes	

	13.5	Describe the version numbers of all software used	Yes
Non-independence	14.1	Describe the types of non-independence encountered (e.g. phylogenetic, spatial, multiple measurements over time)	Yes
	14.2	Describe how non-independence has been handled	Yes
	14.3	Justify decisions made	Yes
Meta-regression and model selection	15.1	Provide a rationale for the inclusion of moderators (covariates) that were evaluated in meta-regression models	Yes
	15.2	Justify the number of parameters estimated in models, in relation to the number of effect sizes and studies (e.g. interaction terms were not included due to insufficient sample sizes)	Yes
	15.3	Describe any process of model selection	Yes
Publication bias and sensitivity analyses	16.1	Describe assessments of the risk of bias due to missing results (e.g. publication, time-lag, and taxonomic biases)	Yes
	16.2	Describe any steps taken to investigate the effects of such biases (if present)	Yes
	16.3	Describe any other analyses of robustness of the results, e.g. due to effect size choice, weighting or analytical model assumptions, inclusion or exclusion of subsets of the data, or the inclusion of alternative moderator variables in meta-regressions	Yes
Clarification of <i>post hoc</i> analyses	17.1	When hypotheses were formulated after data analysis, this should be acknowledged.	Yes
Metadata, data, and code	18.1	Share metadata (i.e. data descriptions)	Yes
	18.2	Share data required to reproduce the results presented in the manuscript	Yes
	18.3	Share additional data, including information that was not presented in the manuscript (e.g. raw data used to calculate effect sizes, descriptions of where data were located in papers)	Yes
	18.4	Share analysis scripts (or, if a software package with graphical user interface (GUI) was used, then describe full model specification and fully specify choices)	Yes
Results of study selection process	19.1	Report the number of studies screened	Yes
	19.2	Report the number of studies excluded at each stage of screening	Yes
	19.3	Report brief reasons for exclusion from the full-text stage	Yes

	19.4	Present a Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA)-like flowchart (www.prisma-statement.org).	Yes	
Sample sizes and study characteristics	20.1	Report the number of studies and effect sizes for data included in meta-analyses	Yes	
	20.2	Report the number of studies and effect sizes for subsets of data included in meta-regressions	Yes	
	20.3	Provide a summary of key characteristics for reported outcomes (either in text or figures; e.g. one quarter of effect sizes reported for vertebrates and the rest invertebrates)	Yes	
	20.4	Provide a summary of limitations of included moderators (e.g. collinearity and overlap between moderators)	Yes	
	20.5	Provide a summary of characteristics related to individual study quality (risk of bias)	NA	The quality of studies included in the meta-analysis was not assessed
Meta-analysis	21.1	Provide a quantitative synthesis of results across studies, including estimates for the mean effect size, with confidence/credible intervals	Yes	
Heterogeneity	22.1	Report indicators of heterogeneity in the estimated effect (e.g. I^2 , τ^2 and other variance components)	Yes	
Meta-regression	23.1	Provide estimates of meta-regression slopes (i.e. regression coefficients) and confidence/credible intervals	Yes	
	23.2	Include estimates and confidence/credible intervals for all moderator variables that were assessed (i.e. complete reporting)	Yes	
	23.3	Report interactions, if they were included	NA	No interactions were included
	23.4	Describe outcomes from model selection, if done (e.g. R^2 and AIC)	Yes	
Outcomes of publication bias & sensitivity analyses	24.1	Provide results for the assessments of the risks of bias (e.g. Egger's regression, funnel plots)	Yes	
	24.2	Provide results for the robustness of the review's results (e.g. subgroup analyses, meta-regression of study quality, results from alternative methods of analysis, and temporal trends)	Yes	
Discussion	25.1	Summarise the main findings in terms of the magnitude of effect	Yes	

	25.2	Summarise the main findings in terms of the precision of effects (e.g. size of confidence intervals, statistical significance)	Yes	
	25.3	Summarise the main findings in terms of their heterogeneity	Yes	
	25.4	Summarise the main findings in terms of their biological/practical relevance	Yes	
	25.5	Compare results with previous reviews on the topic, if available	Yes	
	25.6	Consider limitations and their influence on the generality of conclusions, such as gaps in the available evidence (e.g. taxonomic and geographical research biases)	Yes	
Contributions and funding	26.1	Provide names, affiliations, and funding sources of all co-authors	Yes	
	26.2	List the contributions of each co-author	Yes	
	26.3	Provide contact details for the corresponding author	Yes	
	26.4	Disclose any conflicts of interest	NA	There were no conflicts of interest
References	27.1	Provide a reference list of all studies included in the systematic review or meta-analysis	Yes	
	27.2	List included studies as referenced sources (e.g. rather than listing them in a table or supplement)	Yes	

Reference

1.

O'Dea, R.E., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W.A., Parker, T.H. *et al.* (2021). Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biol. Rev. Camb. Philos. Soc.*, 96, 1695-1722.

Table S2. Descriptions of trait categories used for coding response variables. When the variable was scored in a way that was inverse to the investment in the trait it measured, the direction of the estimate was corrected by multiplying by -1 (indicated in parentheses following the example description as applicable). For example, inter-scan-interval is inversely related to investment in vigilance, and was therefore multiplied by -1. The predicted effect of an increased perceived predation risk on a category of response variable is indicated in the column “Predicted effect”. In order to allow to estimate global effects in our meta-analyses, all variables were coded so that effects in the predicted direction were positive. This means that estimates for categories where the predicted effect was “Decrease” were all multiplied by -1 prior to analysis.

Type	Category (<i>definition</i>)	Subcategories	Predicted Effect	Examples
Behaviour	Antipredator (<i>Behaviours that mitigate predation risk by increasing likelihood of detecting predator, increasing likelihood of avoiding predator, or decreasing likelihood that predator can mount a successful attack</i>)	Vigilance Avoidance Mobbing/ alarming	Increase	Scanning rate Inter-scan interval (-1) Mean scan bout duration Inspection behaviour Choice of non-predator location Choice of predator location (-1) Use of cover Avoidance of cover (-1) Dispersal Escape flight behaviour Settlement (density of breeding pairs) (-1) Settlement timing Probability of building a nest (-1) Nest abandonment Time out of refuge (-1) Freezing behaviour Probability of approaching to speaker/mount Call rate Wing flicking Recruitment of conspecifics
	Costly Behaviours (<i>Behaviours that expend net energy but that are not involved in mitigating predation risk</i>)	Courtship Activity	Decrease	Number of songs Songs per bird Count of mate attraction calls Duration of courtship display Singing rate Exploration Number of movements Latency to begin activity (-1) Proportion of time active
	Intake	Foraging Begging	Decrease	Foraging rates Latency to resume feeding (-1)

	<i>(Behaviours that bring in net energy but that are not involved in mitigating predation risk)</i>			Giving up density (-1) Probability of returning to feeder (-1) Begging per hour Begging rate Gapes per sec
	Parental Care <i>(Care provided to eggs or offspring)</i>	Incubation/ brooding Provisioning	Decrease	Number of incubation bouts Mean incubation bout duration Proportion of time incubating Probability of abandoning nest (-1) Number of brooding bouts Total time brooding Number/rate of incubation feeds Provisioning rate Provisioning biomass delivery Provisioning load size Latency to resume provisioning (-1)
Life History	Reproduction <i>(Measures of reproductive success)</i>	ClutchSize EggSize Nestlings	Decrease	Clutch size Mean clutch size Clutch size change across years Egg mass Egg volume Brood size Number of nestlings Number of fledglings Hatching Success Prop chicks dead (-1) Prop eggs not hatched (-1) Clutch mass Fledging success Brood mass Hatching success
	Phenology <i>(Measures of timing of key life history events)</i>	LayDate Developmental timing	Increase	Lay date Clutch initiation date Nest initiation date Duration of incubation Duration of nestling Age at fledging Rate of ageing (telomere length) Time to hatching
Physiology	Condition <i>(Measure of body condition of individuals)</i>	Mass Growth	Decrease	Morning mass Average mass Evening mass Rate of mass gain (adults) Lean mass Fat mass Body mass Residual fat

				Asymptotic body mass (nestlings) Mass gain (nestlings) Sing growth rate Tarsus growth rate Structural body size
	Hormones <i>(Measure of hormone levels in vivo)</i>	Corticosterone	Increase	Corticosterone Basal corticosterone Stress corticosterone Maximum corticosterone level

Table S3: List of studies that were excluded from the meta-analysis based on reading of full text, and their reasons for exclusion.

Reference	Reason for Exclusion
Amo <i>et al.</i> (2011a)	Predator treatment is novel to focal species
Amo <i>et al.</i> (2011b)	Predator treatment is novel to focal species
Andreasson <i>et al.</i> (2019)	Response variable (Tb) not replicated in other studies
Antze and Koper (2018)	Mobbing calls used were generic response to humans
Atkins <i>et al.</i> (2017)	Doesn't meet minimum sample size requirements. Level of analysis is "site", with N = 1 treatment and N = 2 control.
Aviles <i>et al.</i> (2019)	Mixed species level data
Berziņš <i>et al.</i> (2010)	No control treatment
Blackwell <i>et al.</i> (2018)	Results do not allow for extraction of effects for each level of treatment separately
Breviglieri and Romero (2016)	Mixed species level data.
Cimprich <i>et al.</i> (2005)	Season (migration) had insufficient independent studies for inclusion (K = 2)
Coslovsky and Richner (2011)	Not eligible – study of transgenerational effect of predator treatments. Traits investigated in nestlings that were not exposed to cues of predation directly.
da Cunha <i>et al.</i> (2017)	Mixed species level data
Davies and Welbergen (2008)	Mixed species level data
Dutour <i>et al.</i> (2016)	Mixed species level data
Fardell <i>et al.</i> (2021)	Mixed species level data
Forsman and Monkkonen (2001)	Mixed species level data
Forsman <i>et al.</i> (1998)	Mixed species level data
Fransson and Weber (1997)	Season (migration) had insufficient independent studies for inclusion (K = 2)
Ghalambor and Martin (2001)	Mixed species level data
Gomez-Serrano (2021)	Experimental portion of study used humans as "predator" treatment
Griesser (2008)	for experiments 1: treatment and control observations cannot be compared (different observation durations), for experiment 2: testing information content of calls
Griesser (2013)	No control
Groenewoud <i>et al.</i> (2019)	No predator treatment
Holthuijzen (2018)	No relevant treatment, assessing if birds recognize heterospecific alarm calls
Hua <i>et al.</i> (2013)	Mixed species level data
Huang <i>et al.</i> (2012)	Test of heterospecific information use
Hunts <i>et al.</i> (2019)	Mixed species level data

Ibanez-Alamo <i>et al.</i> (2013)	Response type (fecal sac removals) not replicated in any other study. Also, no clear predicted direction of effect based on theory.
Iglesias <i>et al.</i> (2014)	No control
Jones and Sieving (2019)	Species level data cannot be extracted for control/treatment contrasts
Journey <i>et al.</i> (2013)	No s.e. (standard error) provided for species level data
Keen <i>et al.</i> (2020)	Social learning of novel cue
Kerman <i>et al.</i> (2018)	No control
Leavesley and Magrath (2005)	No treatment: study tests whether trills convey predator information
Macleod <i>et al.</i> (2005)	Response variable is cumulative mass gain expressed as percentage (i.e., control and treatment scaled to same range from 0 to 100)
Madden <i>et al.</i> (2005)	mobbing calls used for treatment were generated in response to humans
Martinez <i>et al.</i> (2017)	Could not extract species level data- figure resolution too low to extract overlapping data points
McIntyre <i>et al.</i> (2014)	Effect direction not extractable
Morosinotto <i>et al.</i> (2016)	response variable = testosterone excluded because no clear predicted effect (authors themselves stated no single prediction)
Nilsson and Nord (2017)	Not relevant - no predator treatment
Nocera and Ratcliffe (2010)	Mixed species level data
Pascual and Senar (2013)	Manipulation is distance to cover
Poysa <i>et al.</i> (2001)	Not relevant - no predator treatment
Rajala <i>et al.</i> (2003)	No control
Rands and Cuthill (2001)	manipulation is human threat
Roncalli <i>et al.</i> (2019)	Response variables not relevant (egg touches, egg rejection)
Schneider and Griesser (2014)	Cannot extract behavioural response to treatments in isolation
Serra and Fernandez (2011)	manipulation is human threat
Sieving <i>et al.</i> (2010)	Response variables is structure of acoustic response -species specific, not generalizable
Thompson <i>et al.</i> (2013)	Not relevant - no predator treatment
Tilgar and Moks (2015)	Mixed species level data
Tilgar <i>et al.</i> (2010)	manipulation is human threat
Tolvanen <i>et al.</i> (2018)	Not relevant - no predator treatment
Turney and Godin (2014)	Mixed species level data
Tvardikova and Fuchs (2011)	Mixed species level data
Williams and Lindell (2018)	Not relevant - no predator treatment
Williamson and Fagan (2017)	Mixed species level data
Zanette <i>et al.</i> (2019)	Response subcategory (cFOS levels) not used in any other study, also, no clear directional prediction

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