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RESEARCH ARTICLE

Prey responses to direct and indirect predation risk cues reveal the importance of multiple information sources

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Abstract

1. Prey can use several information sources (cues) to assess predation risk and avoid predation with a variety of behavioural responses (e.g., changes in activity, foraging, vigilance, social behaviour, space use, and reproductive behaviour). Direct cues produced by predators and indirect cues from environmental features or conspecific and heterospecific prey generally provide different types of information about predation risk. Despite widespread interest in understanding behavioural antipredator responses to direct and indirect cues, a clear general pattern of relative response strength across taxa and environments has yet to emerge.
2. We conducted a meta-analysis of studies (*N* = 113 articles and 999 effect sizes taken from a search of over 7500 articles) testing behavioural responses to direct and indirect cues of predation risk, and their combination, across terrestrial and aquatic ecosystems. We further contrasted if effects were moderated by ecosystem type (terrestrial, marine, or freshwater), cue source (predator, conspecific, heterospecific, or environmental feature), or sensory modality (visual, auditory, or chemosensory).
3. Overall, there were strong effects of risk cues on prey behaviour. We found that prey responded more strongly when both types of cues were presented together compared with either cue in isolation, which was driven by changes in prey activity levels but not other behaviours. There was no general pattern in response strength to direct compared with indirect cues. Responses to these cues were moderated by interactions between environment, cue source, and cue sensory modality (e.g., visual cues elicited stronger responses than other modalities, and responses to conspecific chemosensory cues were stronger than those to predator chemosensory cues in aquatic systems).
4. These results suggest that rather than a broad framework of direct and indirect cues, the specific context of the system should be considered in tests and predictions of how prey respond to risk to elucidate general patterns of antipredator responses.

KEYWORDS
antipredator behaviour, direct cue, indirect cue, information, predation risk, sensory

1 | INTRODUCTION

Accurate assessment and response to predation risk is a ubiquitous concern for animals (Lima, 1998; Lima & Dill, 1990; Peckarsky et al., 2008). Behavioural antipredator responses, such as avoidance, vigilance, and refuge use, can improve prey survival by reducing the probability of predation; however, antipredator responses also can carry significant fitness costs (e.g., reduced reproductive output and lower body condition) (Dill, 1987; Ives & Dobson, 1987; Lima & Dill, 1990; Persons et al., 2002; Sih, 1994). The intensity of these responses can determine the strength of non-consumptive effects of predation and their consequences for prey population dynamics, community structure, and ecosystem function (Preisser et al., 2005; Schmitz et al., 2004; Weissburg et al., 2014; Werner & Peacor, 2003).

Animals use many sources of information to assess predation risk and likely respond differently depending on the type of risk cue and the information that can be obtained from it (Lima & Dill, 1990; Sih et al., 2010; Verdolin, 2006). Direct cues are stimuli emitted by predators (e.g., predator urine and faeces, kairomones, vocalizations, and visual cues) and are frequently used by prey to assess potential threats (Kats & Dill, 1998). Prey also use indirect cues, which are stimuli produced by conspecific or heterospecific prey (e.g., alarm calls and damage release chemicals) or other aspects of the environment associated with a generally higher probability of predation (e.g., vegetation cover and illumination) (Barrera et al., 2011; Chivers & Smith, 1998; Schmidt et al., 2008; Thorson et al., 1998). Despite widespread interest in understanding antipredator responses to direct and indirect cues, a clear general pattern of relative response strength across taxa has yet to emerge (cf. Barrera et al., 2011; Chivers & Smith, 1998; Grostal & Dicke, 1999; Orrock et al., 2004; Wirsing et al., 2021). Identifying the generality of direct and indirect cue effects is important to not only further our understanding of the mechanisms underlying non-consumptive effects but also to inform conservation and management efforts (Gaynor et al., 2021; Miller & Schmitz, 2019; Sih et al., 2010). Prey responsiveness to direct versus indirect cues may determine their ability to cope with changing environments, and conservation and management efforts may therefore target different strategies. For example, a reliance on direct cues may make prey more vulnerable to novel or invasive predators than a reliance on indirect cues that are not specific to particular predators (Castorani & Hovel, 2016; Parsons & Blumstein, 2010; Sih et al., 2010).

One potential reason for the absence of general predictions for these response patterns may be that the relative threat level, reliability, generalizability, and precision of information transmitted by direct and indirect cues could vary substantially (Figure 1). Several hypotheses concerning information use by prey may provide insight into the expected strengths of responses to direct and indirect cues (Table 1). The threat sensitivity hypothesis posits that cues that indicate a higher threat level (i.e., the magnitude of influence on prey fitness) should elicit a stronger antipredator response (Table 1) (Helfman, 1989). Alternatively, the generalized risk assessment hypothesis emphasizes that antipredator responses should be stronger when cues are more generalizable (i.e., provide information about threats from multiple sources of risk rather than a single, specific predator), whilst the information precision hypothesis states that cues containing more precise and accurate information should elicit stronger responses (Table 1) (Grason, 2017; Rainey et al., 2004; Sih et al., 2010). Following the logic of these hypotheses, indirect cues can provide information about risk from multiple predators whereas direct cues are more specific, which may make indirect cues more reliable indicators of high risk (Arvigo et al., 2019; Blumstein et al., 2008; Grason, 2017; Orrock et al., 2004). On the other hand, some indirect cues may be unreliable and can elicit costly responses in non-threatening situations. In these situations, prey may respond more strongly to predator-specific direct cues (Barrera et al., 2011; Beauchamp & Ruxton, 2007; Sih et al., 2010; Wheeler, 2009). Certain direct cues can also contain precise information about immediate predator presence, location, and identity and may indicate higher risk levels than indirect cues (Barrera et al., 2011; Makin et al., 2019; Rainey et al., 2004). Whilst there has been some evidence for these hypotheses with regard to direct and indirect cues (Table 1), it remains unclear the extent to which these hypotheses explain antipredator behaviours.

Direct and indirect cues are often available to prey simultaneously, and combined cues are typically assumed to generate stronger responses because they are more reliable indicators of risk and contain more information about the nature of the threat than a single cue (Brodin et al., 2006; Chivers et al., 2002; Schoeppner & Relyea, 2005; Sih, 1986). Combined direct and indirect cues may elicit enhanced responses in an additive manner, particularly if each cue provides unique information about the threat (Farnworth et al., 2020; Grason, 2017; Smith & Belk, 2001). However, cue combination may also enhance antipredator responses non-additively depending on the cost of assessing multiple cues and the threat levels indicated by those cues (Arteaga-Torres et al., 2020; Arvigo et al., 2019; Dalesman et al., 2006; Dzierżyńska-Białończyk et al., 2019; Ślusarczyk, 1999). For example, the cost of assessing multiple cues may be great enough that prey rely on single cues and exhibit responses equivalent to situations in which only one cue is available (Munoz & Blumstein, 2012).

The difference between responses to direct and indirect cues may also be moderated by other factors, such as the specific cue source, sensory modality, and environmental context (Barrera et al., 2011; Munoz & Blumstein, 2012). Whilst direct cues are always produced by predators, indirect cues include stimuli from several sources that may vary in their reliability (Barrera et al., 2011; Schmidt et al., 2008; Thorson et al., 1998). For example, cues from heterospecifics may be less reliable than cues from conspecifics as they are more likely to be unfamiliar or even false alarms (Flower, 2011; Magrath et al., 2009; Magrath et al., 2015). Additionally, environmental cues may be more general indicators of risk from multiple predators but lack information about the immediate presence of a predator (Orrock et al., 2004; Thorson et al., 1998). Both direct and indirect cues are transmitted through multiple sensory modalities, including visual, auditory, and chemosensory cues, which can influence the

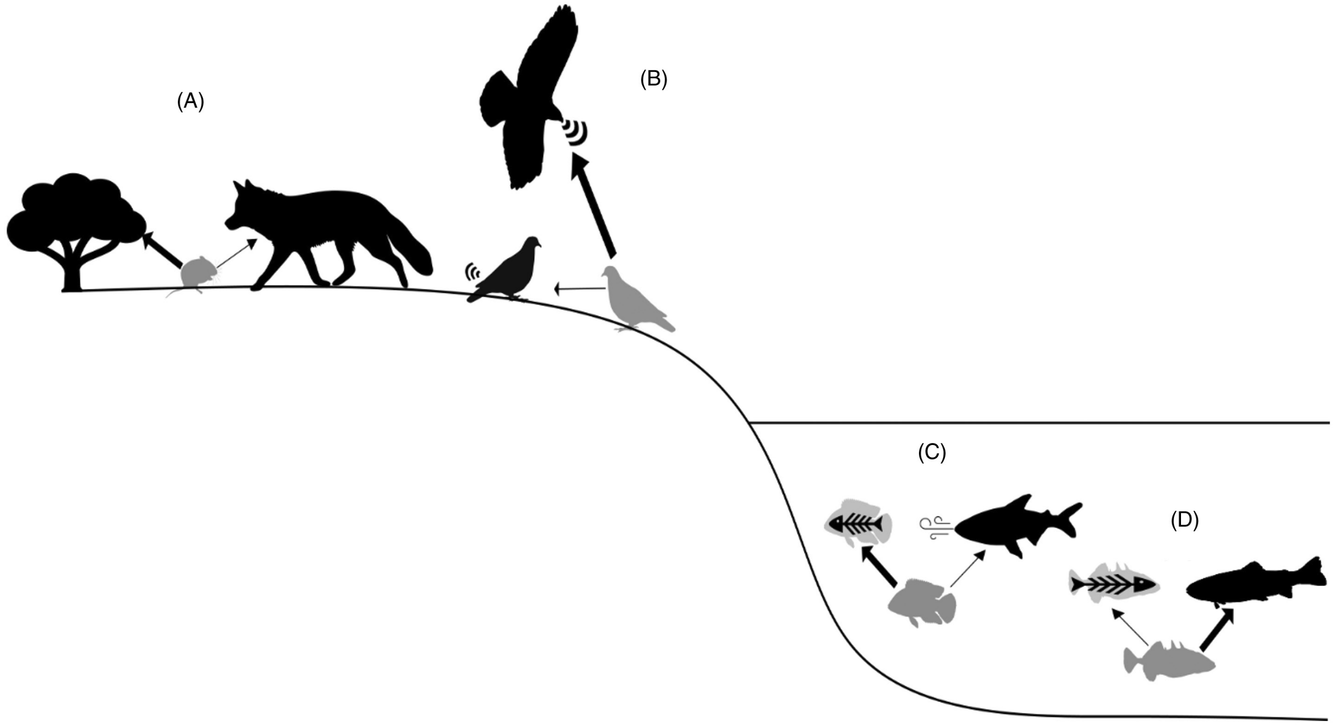


FIGURE 1 Examples of antipredator responses to direct and indirect risk cues that support the hypotheses presented in Table 1. Arrows represent responses of prey (light grey silhouettes) to cues of predation risk, with response strength indicated by the thickness of the arrow. (A) In line with the generalized risk assessment hypothesis, oldfield mice (*Peromyscus polionotus*) respond more strongly to the generalized, indirect cue of vegetation cover than the predator-specific direct cue of red fox (*Vulpes vulpes*) urine (Orrock et al., 2004). (B) In accordance with the information precision hypothesis, zenaida doves (*Zenaida aurita*) exhibited stronger vigilance responses to red-tailed hawk (*Buteo jamaicensis*) shrieks than conspecific wing whistles (Barrera et al., 2011). (C) In line with the threat sensitivity and generalized risk assessment hypotheses, pearl cichlids (*Geophagus brasiliensis*) exhibited a greater decrease in activity in response to a conspecific alarm substance, which is released after a skin injury and is indicative of an imminent threat from an actively foraging predator, than predator (*Hoplias malabaricus*) kairomones (Arvigo et al., 2019). (D) Three-spined sticklebacks (*Gasterosteus aculeatus*) responded more strongly (spine erection, predator inspection, and reduced foraging activity) to a visual predator cue (*Salmo trutta*) than a conspecific alarm substance, providing support for the information precision hypothesis (Landeira-Dabarca et al., 2019).

TABLE 1 Hypotheses concerning information use by prey and the expected relative strengths of behavioural antipredator responses to direct and indirect cues of predation risk.

Hypothesis	Predicted response strength	Reasoning	Examples
(A, C) *Generalized risk assessment*: Prey should respond more strongly to general cues that indicate risk from a variety of sources than specific cues that indicate risk from a particular predator (Sih et al., 2010)	Indirect > direct	Indirect cues provide more general information from a variety of risk sources	Ehlman et al. (2019), Grason (2017), Grason and Miner (2012), Orrock et al. (2004), Thorson et al. (1998)
(B, D) *Information precision*: Cues containing more precise, accurate information about a threat should elicit stronger responses (Rainey et al., 2004)	Direct > indirect	Direct cues contain precise information about immediate predator presence, location, and identity	Barrera et al. (2011), Makin et al. (2019), Rainey et al. (2004)
(C) *Threat sensitivity*: Prey should exhibit graded responses to predation risk cues according to the threat level indicated to balance the costs and benefits of antipredator responses (Helfman, 1989)	Indirect > direct	Indirect cues contain more reliable information about a predator's state and threat to prey and are more likely to be indicative of an actively foraging predator	Arvigo et al. (2019), Blumstein et al. (2008), Pereira et al. (2017), Schmidt et al. (2008)

Note: Letters A–D refer to the examples of antipredator responses illustrated in Figure 1.

information about a threat that prey obtain and the detection of this information (Kats & Dill, 1998; Munoz & Blumstein, 2012). Whilst direct visual and auditory cues may contain more precise information about a predator's current location, chemosensory cues persist longer in the environment and can contain more reliable information about the predator's foraging state (Munoz & Blumstein, 2012; Weissburg et al., 2014). Finally, the environment in which prey assess risk is likely to affect how direct and indirect cues persist in time and space (Preisser et al., 2005; Weissburg et al., 2014). For example, visual cues may be the most accurate and reliable sources of information in terrestrial environments, whereas chemosensory cues travel more easily through aquatic environments where visual cues may be more obscured (Munoz & Blumstein, 2020; Weissburg et al., 2014). Consideration of these factors and how they interact may help elucidate general patterns of antipredator responses to direct and indirect cues that may otherwise be obscured.

Here, we synthesize the general patterns of antipredator responses to direct and indirect predation risk cues using a meta-analysis. A previous meta-analysis by Verdolin (2006) found that prey foraging responses to indirect environmental cues of predation risk were stronger than direct cues from predators in terrestrial systems. We build on this and other work by expanding the range of behavioural responses considered, including foraging, activity, space use, vigilance, defensive behaviour, social behaviour, and reproductive behaviour, and looking across marine, freshwater, and terrestrial systems. We assessed the relative strength of behavioural antipredator responses to direct, indirect, and combined cues of risk. We hypothesized that direct and indirect cues contain unique information about threats, and thus combinations of these cues would elicit additive responses relative to either cue in isolation (Farnworth et al., 2020; Grason, 2017; Munoz & Blumstein, 2012). According to the threat sensitivity and generalized risk assessment hypotheses (Table 1), we hypothesized that responses would be stronger to indirect than direct cues because indirect cues typically indicate higher risk levels and provide information about a wider variety of threats (Blumstein et al., 2008; Grason, 2017; Helfman, 1989; Sih et al., 2010). We also predicted that combinations of direct and indirect cues would elicit stronger responses than either type of cue in isolation because each type of cue should contain some unique information about the threat and should be a more reliable source of information when available simultaneously (Brodin et al., 2006; Chivers et al., 2002; Schoeppner & Relyea, 2005; Sih, 1986). Alternatively, other aspects of risk cues, such as cue source and sensory modality, and the environment in which these cues are transmitted may moderate the relative responses to direct and indirect cues, as these factors are likely to influence the threat level, specificity, persistence, and familiarity of particular cues (Barrera et al., 2011; Munoz & Blumstein, 2012; Schoeppner & Relyea, 2005; Wirsing et al., 2021). Identifying broad patterns of information use can inform our understanding of non-consumptive effects and their consequences for prey population dynamics, community structure, and ecosystem function as well as the evolution of predator–prey interactions (Ehlman et al., 2019; Peacor et al., 2022; Preisser et al., 2005; Stankowich & Blumstein, 2005; Weissburg et al., 2014). Such patterns may also be helpful in applied contexts, such as the management of invasive species or the mitigation of human–wildlife conflict (Gaynor et al., 2021; Miller & Schmitz, 2019; Sih et al., 2010).

2 | MATERIALS AND METHODS

2.1 | Literature search and data collection

We followed reporting guidelines for meta-analyses in ecology and evolutionary biology and have included the PRISMA-EcoEvo checklist with details on our reporting in Table S1 (O'Dea et al., 2021). We searched Web of Science (April 29, 2024) using the search terms "predat* AND cue*" (Timespan: 1900-01-01–2024-04-29), which were chosen to encompass the broadest range of published articles focusing on the use of any type of external information (cues were not always referred to as direct or indirect in the articles themselves) in the context of predation risk. We selected relevant articles from the 7515 articles returned by this search using the following criteria. We selected articles that experimentally tested behavioural antipredator response(s) to at least one direct cue and at least one indirect cue that was assumed to be indicators of predation risk. For a full description of the number of papers excluded at each step in our search process, see the PRISMA diagram in Figure S1. Briefly, we first examined the titles and abstracts of all articles returned by our search terms and excluded those that did not meet the criteria noted above; when this was not clear from the title and abstract, we scanned the full text to assess whether or not certain criteria were met (typically whether an article included both a direct cue and an indirect cue of risk). We then examined the full texts of all remaining articles and excluded those that did not meet our search criteria. Of the articles that met these criteria, we were able to extract the appropriate data (from data reported in the article (text and/or figures), Supporting Information, raw data from repositories, or obtained through communication with authors) for 113 articles (see Supporting Information for a full list of references for the included articles). This study did not require ethical approval.

2.2 | Response and moderator variables

For each of these 113 articles, we extracted the mean and variance or relevant test statistic (e.g., *t*-statistic, Chi-squared statistic) for the behavioural responses to each cue (indirect, direct, combinations of direct and indirect cues, and control cues). When necessary, we extracted means and variances from figures using Plot Digitizer software (http://plotdigitizer.sourceforge.net/). The sample size for each treatment and control group was also recorded. When multiple cues of each type were reported, responses to all cues were recorded, and all behavioural responses measured within each article were recorded separately. Behavioural responses included changes in foraging behaviour, activity levels, space use, alert and/or defensive behaviours (e.g., vigilance, defensive posturing), social behaviours (e.g., aggregation), and reproductive behaviours (e.g., mate choice). We also extracted information that we predicted to explain variance in antipredator responses to direct and indirect predation risk cues. We recorded prey taxon, whether the experiment was conducted in terrestrial, marine, or freshwater environments, and the sensory modality (visual, auditory, chemosensory, multiple modalities, or other [tactile and hydrodynamic stimuli]) of each cue. We also recorded the specific source of the indirect cue (conspecifics, heterospecifics, or environmental factors) because this is a more heterogeneous group of cues than direct cues from predators, and prey responses may vary across these different types of indirect cues.

2.3 | Effect size calculation

We calculated effect sizes using Hedges' *d*, a measure of standardized difference in means that corrects for small sample sizes (Hedges & Olkin, 1985; Koricheva et al., 2013). Individual effect sizes were calculated as the difference between the mean response to the risk cue (direct, indirect, or combined) and the mean response of the control group. We also estimated the variance of each Hedges' *d* value as a measure of the effect's precision. Effect sizes and variances were calculated using the appropriate formula for Hedges' *d* depending on the type of reported response (mean and standard deviation, *t*-statistic, or Chi-squared statistic) (Koricheva et al., 2013; Wilson, 2020). A negative value of Hedges' *d* indicates a smaller value of the measured behavioural response in the treatment group compared with the control group, whereas a positive value indicates a greater value relative to the control. In some cases, antipredator responses were expected to result in a smaller value of the measured response relative to the control (e.g., time spent foraging or active), whilst in others a larger value indicated an antipredator response (e.g., vigilance behaviour, refuge use). To ensure correct interpretation of effect sizes, when a negative value of Hedges' *d* was expected to reflect a greater antipredator response, we reversed the sign of the effect size such that a positive Hedges' *d* value indicated an increase in antipredator behaviour relative to the control for all comparisons (Nunes et al., 2019).

2.4 | Phylogeny

To control for nonindependence related to shared evolutionary history amongst the 113 prey species considered, we incorporated phylogeny into our analysis (Koricheva et al., 2013). No single phylogenetic tree was available that included this wide range of species, so we created a supertree using data from the Open Tree of Life with the package rotl (Michonneau et al., 2016) in R version 3.5.1 (R Core Team, 2021). Since accurate branch lengths could not be obtained for this supertree, we first set all branch lengths to one, made the tree ultrametric, and estimated branch lengths with Grafen's method (Grafen, 1989) using the package Analyses of Phylogenetics and Evolution version 5.0 (Paradis & Schliep, 2019). The resulting phylogenetic relationships were incorporated in the meta-analysis of effect sizes as a variance–covariance matrix.

2.5 | Statistical analysis

To understand patterns in the strength of antipredator responses to different types of predation risk cues, we ran multilevel meta-analysis models using the *rma.mv* function in the metafor package with effect size (Hedges' *d*) as the response variable (Viechtbauer, 2010). We weighted effect sizes by their precision and included behavioural response, article, phylogeny, and observation ID as random effects. We included article identity as a random effect because many of the included articles measured multiple responses to risk cues, and we nested the identity of the behavioural response within the article because we recorded at least two effect sizes (for the indirect and direct cues) for every response measured in a given article. Species identity was included as a random effect to account for instances in which multiple articles used the same focal species. We also included an observation-level random effect to allow for the estimation of residual error. Initially, to assess whether there was a significant amount of variation in the effect sizes sampled that could be further investigated and potentially attributed to differences in risk cues (e.g., direct versus indirect cues), we used an intercept-only model to determine the overall effect size, assess the total variation in effect sizes, and examine the amount of variation explained by each random effect. We used the I^2 statistic from this model to assess the percentage of variation due to heterogeneity between effect sizes rather than sampling error and partitioned the variation amongst the four random effects, using the guideline of 25%, 50%, and 75% representing low, moderate, and high heterogeneity, respectively (Higgins et al., 2003; Nakagawa & Santos, 2012). We performed all analyses using the metafor package in R (Viechtbauer, 2010).

We then ran several meta-regression models to determine the influence of different factors related to the predation risk cues on effect size. All models included phylogeny, response type nested within the article, and observation ID as random effects. First, to assess whether responses to direct, indirect, and combined cues varied in strength, we included cue type as the only fixed effect. Next, to test whether other factors moderated variation in responses to direct and indirect cues, we excluded responses to combined cues, and we included the source of the cue (predator, conspecific, heterospecific, or environment), sensory modality (visual, auditory, chemosensory), and whether the study system was terrestrial, marine, or freshwater as fixed effects. We first tested for a three-way interaction between these factors, which was significant (Table 2). Then, to aid in the interpretation of how these factors influence antipredator responses, we analysed terrestrial, marine, and freshwater studies separately. In each model, we included an interaction between cue source and modality. We tested the significance of moderating factors using the Q_M statistic, which describes

TABLE 2 Summary of statistics for all meta-regression models that included the effect of moderator variables on effect sizes of antipredator responses.

Model	Moderator	Q_M	df	*p*	Pseudo-R^2
Direct, indirect, and combined cues					
Cue type	Cue type	25.74	2	<0.0001	0.00
Cue type × response	Cue type	26.23	2	<0.0001	0.00
	Response	18.97	5	0.0019	0.06
	Interaction	24.50	10	0.0064	0.07
Direct and indirect cues only					
Cue source × modality × environment	Cue source	11.16	3	0.0109	0.00
	Sensory modality	14.38	4	0.0062	0.01
	Environment	12.21	2	0.0022	0.00
	Interaction	9.46	1	0.0021	0.28
Cue source × modality					
Marine	Cue source	52.81	3	<0.0001	0.02
	Sensory modality	12.05	2	0.0024	0.00
	Interaction[a]	NA	NA	NA	NA
Freshwater	Cue source	9.52	2	0.0086	0.03
	Sensory modality	12.17	3	0.0068	0.00
	Interaction	7.60	1	0.0059	0.07
Terrestrial	Cue source	31.64	3	<0.0001	0.00
	Sensory modality	22.24	4	0.0002	0.06
	Interaction	29.64	6	<0.0001	0.12

[a] Because of a limited number of combinations of cue sources and sensory modalities in marine systems, we did not include an interaction between these factors for this subset of articles. NA reflects the lack of statistics for this untested interaction.

the amount of heterogeneity in effect sizes explained by the model (Koricheva et al., 2013). We then performed pairwise comparisons of effect sizes amongst factor levels with Wald Chi-squared tests using the *glht* function in the multcomp package (Hothorn et al., 2008). We also assessed whether antipredator responses to different cue types varied across the types of responses tested by including cue type and the type of behavioural response (foraging, activity, space use, alert/defensive behaviour, social behaviour, and reproductive behaviour) and their interaction as fixed effects (see Supporting Information). Finally, we tested for publication bias in our dataset by assessing whether effect sizes changed over time, if there was a bias against small effect sizes using tests of funnel plot asymmetry, and addressing a potential file drawer problem using Rosenthal's failsafe test (see Supporting Information for details).

3 | RESULTS

We collated 999 effect sizes, which included 398 responses to direct cues, 357 to indirect cues, and 244 to combinations of direct and indirect cues, from 113 articles. These effect sizes included 113 prey species, including 13 mammals, 7 birds, 18 amphibians, 22 fish, 13 insects, 2 arachnids, 24 molluscs, 9 crustaceans, and 5 echinoids. The overall mean effect size estimated from the random-effects-only model was 0.911 ± 0.332 ($x \pm$ SE), indicating that on average, the risk cues used in these articles had a large effect on prey behaviour (Cohen, 1988; Koricheva et al., 2013). The overall heterogeneity of effect sizes was high ($I^2 = 89.51\%$, Figure S2); this heterogeneity was attributable to observation-level differences (33.91%), phylogeny (22.40%), species (5.75%), article ID (18.40%), and response type (9.04%). Cue type (i.e., direct, indirect, or combined) explained a significant amount of heterogeneity in effect sizes (Table 2). Larger effect sizes were associated with combinations of direct and indirect cues compared with either direct (combined vs. direct cues: $z = 4.970$, $p < 0.0001$) or indirect (combined vs. indirect cues: $z = 4.207$, $p < 0.0001$) cues in isolation (Figure 2). When including both cue type and response type (foraging, activity, space use, alert/defensive behaviour, social behaviour, and reproductive behaviour) as fixed effects in a meta-regression, there was a significant interaction between cue type and the type of behavioural response ($Q_M = 24.504$, $p = 0.0064$). Larger effect sizes were associated with combinations of cues compared with either direct ($z = 4.491$, $p = 0.0011$) or indirect ($z = 4.758$, $p = 0.0003$) cues in isolation for responses related to activity levels but not other responses ($p > 0.1$) (Figure 3). There was no overall difference in the strength of responses to direct versus indirect cues ($z = 1.128$, $p = 0.778$, Figure 2). The strength of responses to direct versus indirect cues also did not vary depending on response type ($p > 0.3$, Figure 3).

When assessing the effects of cue attributes on responses to direct and indirect cues, we found a significant interaction between cue source (predator, conspecific, heterospecific, environment), sensory modality (visual, auditory, chemosensory), and environment

FIGURE 2 Predicted effect size (Hedges' *d*) (mean ± SE) for each type of predation risk cue: Direct, indirect, and combinations of direct and indirect cues. Numbers on the right side of the plot indicate the number of articles represented for each category.

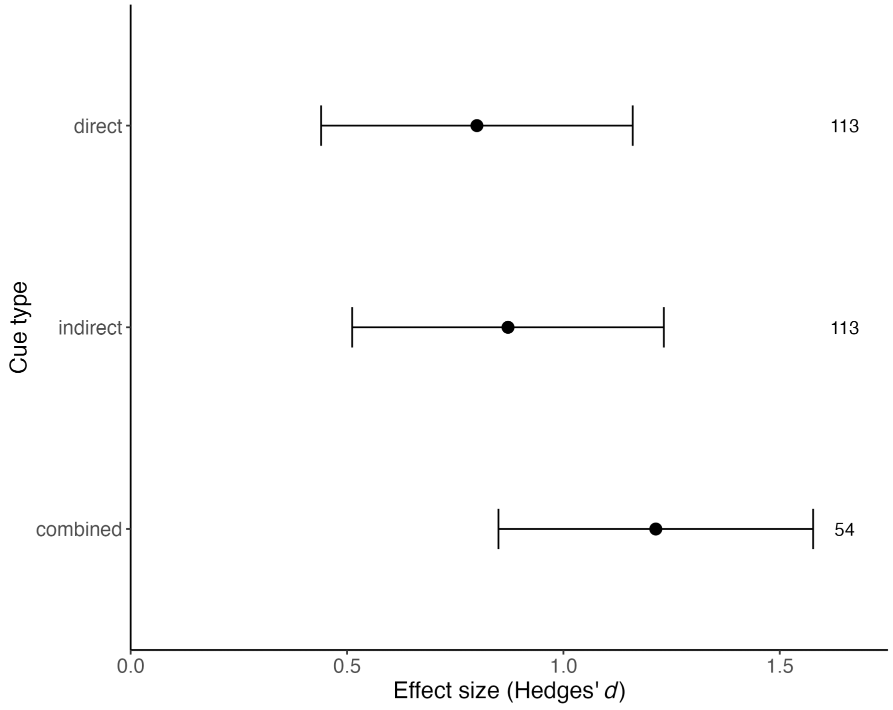
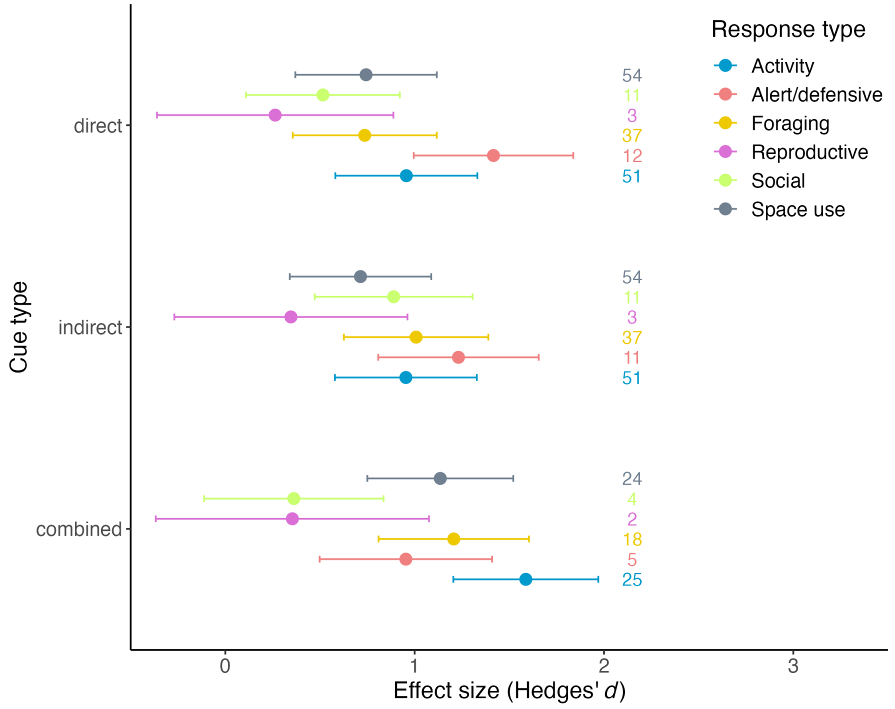


FIGURE 3 Predicted effect size (Hedges' *d*) (mean ± SE) for each type of predation risk cue (direct, indirect, and combinations of direct and indirect cues) and type of behavioural response measured. Numbers on the right side of the plot indicate the number of studies represented for each category.



(terrestrial, marine, freshwater) (Table 2). To better interpret the effects of these moderators, we then tested the effects of cue source and modality in marine, freshwater, and terrestrial studies separately. Considering only marine systems, there was a significant effect of cue source and sensory modality, and conspecific cues elicited stronger responses than predator or heterospecific cues (Table 2; Figure 4). For freshwater systems, there was an interaction between cue source and modality, such that responses were stronger to chemosensory cues from conspecifics than predators but not heterospecifics (Table 2; Figure 5). Additionally, in freshwater systems, responses to predator chemosensory cues were weaker than responses to visual cues of predators (Figure 5). There also was an interaction between cue source and modality for responses to cues in terrestrial systems (Table 2). In these cases, effect sizes for heterospecific cues were smaller than effect sizes for other indirect cues (conspecific and environmental cues) and predator cues (Figure 6). Furthermore, responses to chemosensory predator cues were weaker than responses to visual predator cues (Figure 6). We

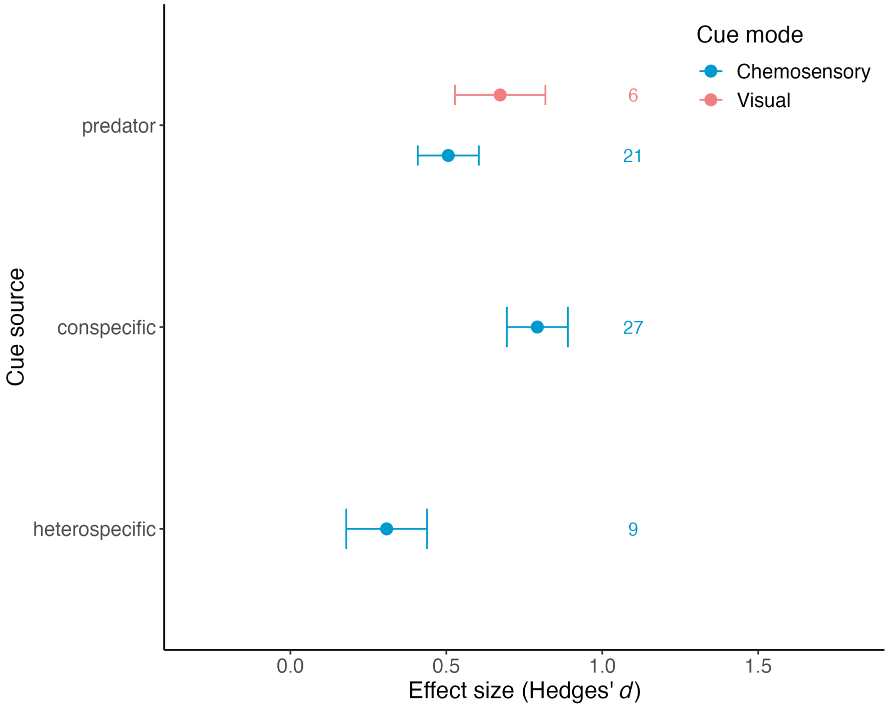


FIGURE 4 For marine systems, predicted effect size (Hedges' *d*) (mean ± SE) for specific sources of predation risk cue and cue sensory modalities. Numbers on the right side of the plot indicate the number of articles represented for each cue source and modality combination. Only combinations with data from three or more articles are shown here.

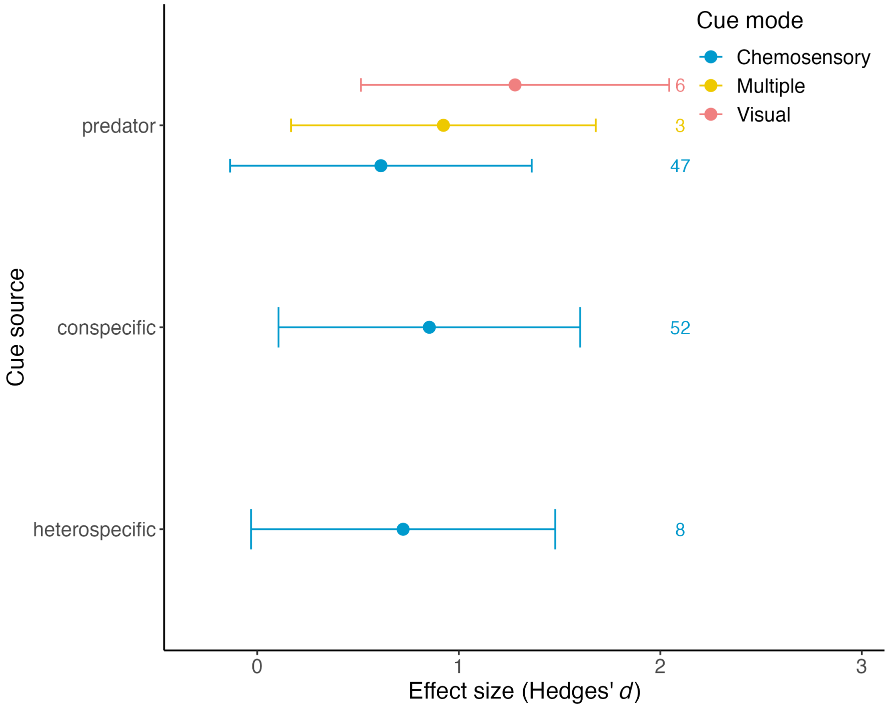


FIGURE 5 For freshwater systems, predicted effect size (Hedges' *d*) (mean ± SE) for specific sources of predation risk cue and cue sensory modalities. Numbers on the right side of the plot indicate the number of articles represented for each cue source and modality combination. Only combinations with data from three or more articles are shown here.

found mixed evidence for possible publication bias (see Supporting Information for details).

4 | DISCUSSION

This meta-analysis provides new insights into patterns of anti-predator behavioural responses to direct compared with indirect predation risk cues alone and in combination and emphasizes how the environment, cue source, and sensory modality may alter effects. We found that, as predicted, combinations of direct and indirect cues generally elicit responses that are ~1.5 times stronger than either type of cue in isolation, suggesting that each cue contains at least some unique information and uncertainty about a threat is reduced through assessment of multiple cues (Farnworth et al., 2020; Munoz & Blumstein, 2012). However, responses to these combined cues were weaker than the expectation for additive responses, which may indicate that there is some redundancy

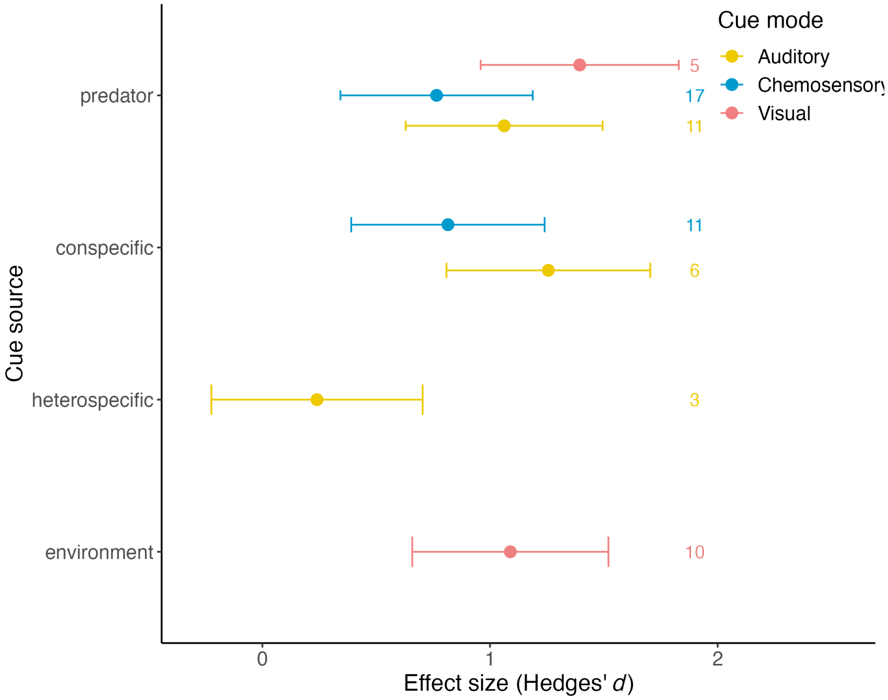


FIGURE 6 For terrestrial systems, predicted effect size (Hedges' *d*) (mean ± SE) for specific sources of predation risk cue and cue sensory modalities. Numbers on the right side of the plot indicate the number of articles represented for each cue source and modality combination. Only combinations with data from three or more articles are shown here.

or conflict between the information obtained from direct and indirect cues (Dalesman et al., 2006; Farnworth et al., 2020; Grason, 2017). For example, indirect cues from injured conspecific or heterospecific prey, which can indicate predator presence and foraging state, may overlap more with direct cues than environmental indirect cues (Farnworth et al., 2020). Alternatively, prey may rely primarily on only one cue to assess risk, particularly if the cost associated with assessing multiple cues is high (Munoz & Blumstein, 2012; Partan & Marler, 1999; Smith & Belk, 2001). In general, strengthened responses to combinations of direct and indirect cues suggest that prey rely on multiple sources of information to reduce uncertainty about predation risk, although the extent to which the information contained in these cues is unique or redundant and consistent versus conflicting is still unclear (Farnworth et al., 2020; Munoz & Blumstein, 2012).

When cues were presented in isolation, we found no consistent trend in the strength of behavioural antipredator responses to direct compared with indirect cues of predation risk. Although we expected indirect cues to elicit stronger responses than direct cues, the lack of a general trend in antipredator responses is not entirely surprising given the conflicting predictions and results from different study systems (Barrera et al., 2011; Grostal & Dicke, 1999; Orrock et al., 2004; Thorson et al., 1998). We expected antipredator responses to indirect cues to be stronger because they can alert prey to threats from multiple predators and often indicate higher threat levels compared with direct cues (Helfman, 1989; Schmidt et al., 2008; Sih et al., 2010; Thorson et al., 1998). Cues that are more generalizable and indicate greater threats should elicit stronger responses, according to the generalized risk assessment and threat sensitivity hypotheses, respectively (Helfman, 1989; Sih et al., 2010). However, direct cues often provide more precise information about predator identity and location and therefore may elicit stronger responses, supporting the information precision hypothesis (Barrera et al., 2011; Rainey et al., 2004). Rather than finding general support for any one of these hypotheses with respect to direct and indirect cues, our results suggest that the severity, generalizability, reliability, and precision of risk cues are more nuanced and context-dependent.

Nonetheless, we did find some support for these hypotheses when considering the ways in which responses to indirect and direct cues were moderated by other factors, including sensory modality and specific cue source, as well as environmental context (Wirsing et al., 2021). Our findings suggest that these factors explain additional variation in the strength of antipredator responses in ways that align with all three hypotheses: threat sensitivity, generalized risk assessment, and information precision (Figure 1). For example, antipredator responses to visual cues were generally stronger than any other sensory modality, which is in line with the information precision, threat sensitivity, and generalized risk assessment hypotheses. Visual predator cues may allow prey to obtain more precise information about predator presence, identity, and location, supporting the information precision hypothesis (Rainey et al., 2004); can provide information about the foraging state of a predator and thus the immediate threat level, supporting the threat sensitivity hypothesis (Etting & Isbell, 2014); and may be more general indicators of risk from multiple predators than auditory or chemosensory cues, supporting the generalized risk assessment hypothesis (Blumstein et al., 2000; Orrock et al., 2004; Thorson et al., 1998). In marine and freshwater studies, predator kairomones are the most commonly used direct cues, but these chemicals may not indicate the immediate presence or foraging state of predators, and a combination of these cues with prey-released chemicals (i.e., from injured or digested prey) is often required to induce an antipredator response (Brown et al., 1970; Crowl & Covich, 1990; Nielsen et al., 2015; Schoeppner & Relyea, 2009a, 2009b). Furthermore, in many cases, predator kairomones are not innately recognized but rather learned through experience and association with a threat (Chivers et al., 1996; Ferrari et al., 2009; Mathis & Smith, 1993).

In addition, direct chemosensory cues elicited weaker responses than chemosensory cues from conspecifics in marine and freshwater studies (Figures 4 and 5). Chemical alarm cues are released when animals are stressed, injured, or killed, and these cues can indicate higher threat levels (i.e., actively foraging predators) and are more general, familiar indicators of risk than direct cues, supporting the threat sensitivity and generalized risk assessment hypotheses, respectively (Arvigo et al., 2019; Grason, 2017; Wilson & Lefcort, 1993). Finally, across all studies, heterospecific cues tended to elicit the weakest responses, suggesting that overall, prey are least likely to rely on heterospecific cues when mounting antipredator responses. Interspecific eavesdropping on alarm cues has been observed across diverse taxa (Dalesman et al., 2007; Rainey et al., 2004; Schmidt et al., 2008). However, these cues are more likely to be unfamiliar or even false alarms, either because the threat is not relevant to the receiver or due to deception by the signaler, and thus may be less reliable than cues from conspecifics or predators (Flower, 2011; Magrath et al., 2009; Magrath et al., 2015; Schoeppner & Relyea, 2009a, 2009b). Consideration of this suite of factors may be important to understanding the relationship between risk cues and the threat level, generalizability, and precision of information prey can obtain from a given cue, which are all likely to determine if and how prey will respond (Table 1) (Helfman, 1989; Rainey et al., 2004; Sih et al., 2010).

We found some evidence of publication bias in this dataset, which could have influenced our findings and could indicate bias against either studies with small effects or sample sizes or missing studies with large effects and sample sizes. However, additional tests indicated no evidence of bias and that the data are robust against the file drawer problem. Given the limited evidence of publication bias and that our dataset only included articles that used both types of cues to allow for a direct comparison of direct and indirect cues, this bias likely did not have a strong influence on our test of differences between responses to direct and indirect cues. Although the moderators considered here (cue source, sensory modality, and environment) explained additional heterogeneity, most of the variation in effect sizes was still unexplained, suggesting that there are other factors that explain variation in antipredator responses to direct and indirect cues. For example, due to the limitations of our dataset and our focus on characteristics of the risk cues, we did not include information on prey or predator traits (e.g., body mass, prey age, predator hunting strategy), which are likely to influence how prey obtain and respond to information about predation risk (Brodin et al., 2006; Palmer & Packer, 2021; Preisser & Orrock, 2012). Matching predator and prey traits (e.g., ratio of predator to prey body size) would be a valuable additional avenue to explore when attempting to elucidate general patterns of antipredator responses but is beyond the scope of this study (Brousseau et al., 2018; Helfman, 1989; Persons & Rypstra, 2001). Furthermore, there was considerable variation in the sample sizes for different categories, limiting some conclusions we were able to make. For example, freshwater articles made up 47% of our sample, whereas only 27 marine and 28 terrestrial articles met all criteria for selection. Additionally, in marine and freshwater articles, most cues used were chemosensory (77% and 82%, respectively), whilst only 17% of cues in marine articles and 11% in freshwater articles were visual, limiting our understanding of the effects of sensory modality on response strength. Additional studies of underrepresented taxa, cue sources and modalities, and environments could provide a more complete understanding of prey responses to direct and indirect cues and how context modifies antipredator responses. For example, researchers should look outside of their own study systems for insights from other taxa to explore new avenues of sensory ecology across ecosystems (e.g., terrestrial ecologists further exploring associational learning that is emphasized in aquatic studies).

Despite long-standing interest in the use of direct and indirect cues of predation risk by prey, our findings suggest this distinction is not sufficient to describe patterns of antipredator responses across taxa and ecosystems (Barrera et al., 2011; Orrock et al., 2004; Thorson et al., 1998). However, combinations of these types of cues consistently elicit stronger responses than either cue in isolation, suggesting that these cues provide at least partially unique information about risk (Munoz & Blumstein, 2012). Given these findings, combinations of direct and indirect cues may be used by wildlife managers and conservationists to enhance the effectiveness of nonlethal management of invasive species or mitigation of human–wildlife conflict by producing stronger responses than single-risk cues (Farnworth et al., 2020; Lecker et al., 2015; Parsons & Blumstein, 2010). Additionally, there are consistent trends in antipredator responses to individual cues when accounting for cue source, sensory modality, and environment, which interact in complex ways to influence the strength of responses. Whilst indirect and direct cues did not neatly map onto the threat sensitivity, generalized risk assessment, and information precision hypotheses in ways supported by the data, predictions made by these hypotheses were supported when considering the exact source of the cue and its sensory modality, suggesting all three hypotheses provide a useful framework for understanding prey responses to risk. To better understand and predict antipredator responses and their consequences for ecological communities, predictions from these hypotheses should be made whilst considering the context of the targeted system, prey, and predator sensory abilities, and the availability and accessibility of information in the environment. Furthermore, the study of responses to combinations of direct and indirect cues from different sources, in single versus multiple modalities, and consideration of the order of cue presentation may help clarify nonlinear antipredator responses to cue combinations. Consideration of more nuances of particular predator–prey systems may allow meaningful patterns of prey information used to be elucidated and used in future research and management and conservation interventions.

AUTHOR CONTRIBUTIONS

Maggie M. Jones, Robert McCleery, Robert Fletcher, Jr., Alex Potash, and Muzi Sibiya conceived the ideas and designed the methodology; Maggie M. Jones, Alex Potash, and Muzi Sibiya collected the data; Maggie M. Jones analysed the data; Maggie M. Jones led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

We declare we have no competing interests.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.0000000c5 (Jones et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. PRISMA diagram for the literature search.

Figure S2. Funnel plot showing the relationship between effect size (Hedges' *d*) and study precision (inverse standard error), which increases with sample size.

Table S1. PRISMA-EcoEvo reporting checklist.

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