



## Predator cue studies reveal strong trait-mediated effects in communities despite variation in experimental designs<sup>☆</sup>



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Nonconsumptive or trait-mediated effects of predators on their prey often outweigh density-mediated interactions where predators consume prey. For instance, predator presence can alter prey behaviour, physiology, morphology and/or development. Despite a burgeoning literature, our ability to identify general patterns in prey behavioural responses may be influenced by the inconsistent methodologies of predator cue experiments used to assess trait-mediated effects. We therefore conducted a meta-analysis to highlight variables (e.g. water type, predator husbandry, exposure time) that may influence invertebrate prey's behavioural responses to fish predator cues. This revealed that changes in prey activity and refuge use were remarkably consistent overall, despite wide differences in experimental methodologies. Our meta-analysis shows that invertebrates altered their behaviour to predator cues of both fish that were fed the focal invertebrate and those that were fed other prey types, which suggests that invertebrates were not responding to specific diet information in the fish cues. Invertebrates also altered their behaviour regardless of predator cue addition regimes and fish satiation levels. Cue intensity and exposure time did not have significant effects on invertebrate behaviour. We also highlight that potentially confounding factors, such as parasitism, were rarely recorded in sufficient detail to assess the magnitude of their effects. By examining the likelihood of detecting trait-mediated effects under large variations in experimental design, our study demonstrates that trait-mediated effects are likely to have pervasive and powerful influences in nature.

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The impact of nonconsumptive or trait-mediated effects of predators on their prey can be strong, often outweighing the effect of density-mediated interactions where predators directly consume prey (Preisser et al. 2005). Trait-mediated effects have an impact on prey populations because predators influence prey behaviour, development, morphology and/or physiology (Peacor & Werner 2001; Werner & Peacor 2003; Frommen et al. 2011). Additionally, trait-mediated indirect effects may radiate throughout the community as predators affect competitors of the prey and resources (Schmitz et al. 2004; Mowles et al. 2011; Gosnell & Gaines 2012). For

example, increased refuge use by small-mouthed salamanders, *Ambystoma barbouri*, in response to predation risk was shown to have positive effects on their isopod prey (Huang & Sih 1991). There is much current interest in the role such trait-mediated indirect effects play in community ecology; they may be important drivers of population dynamics (Alexander et al. 2013) and community structure (Ohgushi et al. 2012), influential components of host–parasite interactions (Hatcher & Dunn 2011) and drivers of biological invasions (White et al. 2006; Dunn et al. 2012).

A standard method for quantifying trait-mediated effects is measuring behavioural responses to predator cues (e.g. Richmond & Lasenby 2006; Dalesman et al. 2007; Dunn et al. 2008). Despite a burgeoning literature in this research field (>180 predator cue studies in aquatic environments, ISI Web of Science), considerable variation in prey responses to predator cues exists. For instance, some studies report increased prey activity in response to predator cues (e.g. Scrimgeour & Culp 1994; Miyasaka & Nakano 2001),

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whereas others report decreased prey activity (e.g. Åbjörnsson et al. 2000; Dezfuli et al. 2003). Although these differences may be partially explained by predator-specific responses of prey (e.g. refuge use by aquatic snails increases in response to a pelagic fish predator, but decreases to avoid a benthic crayfish predator, Turner et al. 1999), variation in experimental design may further confound the outcome of predator cue studies. These confounding factors include cue intensity, degradation rate, addition regime and presence of predator diet cues or alarm substances from consumed conspecifics or heterospecifics released during predation events, the water type, prey functional feeding group and familiarity with the predator and satiation level of the predator, among others.

Predator cue intensity varies widely among studies, and therefore may affect the ability of prey to detect predators and estimate their relative proximity (Dickey & McCarthy 2007; Ferrari et al. 2007). Similarly, cue degradation time frames are likely to be influenced by differences in sunlight and microbial activity affecting cue breakdown rates (Ferrari et al. 2007), coupled with varying cue exposure times (e.g. 4 weeks, Åbjörnsson et al. 2000; 5 min, Dunn et al. 2008). Despite this, few studies assess predator cue efficacy (e.g. Hazlett 1999; Ferrari et al. 2007; Wisenden et al. 2009), with most studies relying instead on the prompt use of a cue after its production. Although long-term studies may avoid cue degradation effects by housing predators with focal prey, additional problems of habituation to predator cues may confound results (e.g. *Gammarus pulex* amphipods no longer reduced leaf consumption following 4 weeks of continuous exposure to sculpin, *Cottus gobius*, Åbjörnsson et al. 2000). Furthermore, some water types (e.g. indoor experiments using dechlorinated tap water) may alter natural degradation processes to extend cue efficacies beyond their natural 'shelf lives' (Ferrari et al. 2007), offering an explanation as to why prey exposed to old/frozen cues display antipredator responses (e.g. Wudkevich et al. 1997; Pettersson et al. 2000).

Predator cue studies rarely consider how prey functional feeding group (e.g. carnivore, omnivore, filter-feeder; MacNeil et al. 1997) may influence whether prey respond to cues as a predation threat or a potential food resource. Additionally, the information that the cue conveys about the predator, and thus the potential risk of predation to the prey, varies with predator satiation level (e.g. Åbjörnsson et al. 1997), as well as the presence/absence of diet or alarm cues from consumed conspecifics or heterospecifics (e.g. Huryn & Chivers 1999). Indeed, studies may provide predators with either the focal invertebrates (e.g. Åbjörnsson et al. 2000; Bernot & Turner 2001) or heterospecific invertebrates as a food source (e.g. Gyssels & Stoks 2005; Wohlfahrt et al. 2006), or hold predators without food entirely (e.g. Mathis & Hoback 1997; Miyasaka & Nakano 2001). Furthermore, predator identity may be important for prey to mount appropriate behavioural responses to known predators (Henry et al. 2010), whereas prey may be unable to recognize predation risks posed by novel predators (Cox & Lima 2006). However, prey exposed to unfamiliar predators may benefit from diet information provided in the cue to convey predation risk or, alternatively, display fixed antipredator responses that can be activated with novel predators (Sih et al. 2010).

To determine whether the experimental design of predator cue studies influences whether trait-mediated effects will be detected, we undertook a quantitative literature review using a 'flexible' (sensu Nakagawa et al. 2007) meta-analytical approach. Specifically, we examined the influence of 10 experimental design factors, including water type, fish satiation, cue intensity and exposure time, on invertebrate prey activity and refuge use observed in fish predator cue experiments. We also assessed publication bias, which is a common source of criticism in meta-analyses since studies with significant results are more likely to be published (the 'file drawer' problem, Rosenthal 1979).

## METHODS

### Data Collection

Studies investigating the behavioural responses of aquatic invertebrates to predator cues were obtained from literature databases and internet searches (pre June 2012), and were primarily selected according to the following criteria: (1) published in English; (2) predator cues derived from fish; (3) macroinvertebrate prey; (4) experimental study of a freshwater system rather than field-based observations (meta-analysis search terms: (fish\*) AND (aquatic OR freshwater) AND (cue OR kairomones OR odour) AND (invertebrate\* OR macroinvertebrate\* OR insect\*)). We focused on chemical odour cues since turbidity and/or a prey's visual ability in aquatic environments often impairs visual recognition of predators (Chivers & Smith 1998; Wisenden 2000). We included only those studies that measured the effect of predator cue on invertebrate activity or refuge use, because we did not consider other behavioural measures, such as latency of pairing, to be immediate responses to predation threats. Furthermore, our final data set includes only those studies that reported the control and treatment sample sizes, and the effect size, or another measure from which the effect size could be calculated (e.g. test statistic, mean and standard deviation or error). We also contacted corresponding authors of publications where data required to calculate effect sizes could not be extracted from published text or figures.

### Calculation of Effect Sizes

We calculated the effect size Cohen's *d* (also known as Hedge's *g*, maximum likelihood estimator) for each measure of activity or refuge use (e.g. change in drift rate or position on substrate), then converted each effect size into the standardized mean difference effect size *g*. As effect sizes (the standardized mean difference between control and treatment group) were seldom reported in published papers, we calculated the effect size for each study by (1) transforming the reported statistic (e.g. *t*, *F*), or (2) the reported mean and SE or SD of the control and treatment groups using methods outlined by Rosenthal (1994). As *F* statistics were often reported from more than one treatment (e.g. control versus cue from multiple predator types;  $df > 1$ ), effect sizes were also calculated from control and treatment means extracted from figures using DataThief (Tummers 2006).

### Moderator Variables

We selected 10 moderator variables (fixed effects) from the original studies that potentially influence aquatic invertebrate responses to fish cue (see Appendix Table A1). Another unaccounted variable, parasite infection status, may be relevant but was seldom reported unless the influence of parasitism was the focus of the investigation, with such studies removed from further analysis.

### Statistical Procedures

All statistical analyses were computed in R (version 2.13.1, R Development Core Team 2011). Linear mixed-effect models were used to conduct mixed-effects meta-analyses (Pinheiro et al. 2013). Outliers were removed (by visual inspection of funnel plots) before we fitted models for *g* using the restricted maximum likelihood estimation. Our preliminary analysis demonstrated that effects of fish cue were unlikely to be revealed from the pooled invertebrate data set because pooling effect sizes from invertebrates that respond differently to the threat of predation would generate 95% confidence intervals that bounded zero (see Appendix Tables A2,

A3). Therefore, we used absolute effect sizes to examine the effect of experimental design, as the magnitude of the change in behaviour rather than the direction of change (i.e. increasing or decreasing activity or refuge use appropriate to the invertebrate) was of interest.

To estimate between-study variability, we used Study ID as a random factor in our analysis. Although prey species and predator species might be considered random factors (see Nakagawa et al. 2007; Nakagawa & Hauber 2011), there were insufficient observations to fit these predictors without overparameterizing the model. The  $I^2$  statistic (Higgins et al. 2001; Nakagawa & Santos 2012) was used to calculate the heterogeneity (degree of consistency among studies). Delta Akaike information criterion ( $\Delta$ AIC; mixed model–random only model) fitted with maximum likelihood estimation was used to examine whether any of the a priori fixed effects improved model fits (see Appendix Table A1). Each fixed effect was included in a separate meta-analytical model, because few studies provided information on all predictor variables, with a minimum of eight studies for each predictor considered necessary for analysis (Nakagawa et al. 2007). Continuous variables (cue intensity, exposure time) were centred on the mean and scaled by two times the standard deviation (Gelman 2008). We report the effect size estimates for each model representing intercepts for categorical factors, and slopes for continuous variables. To determine whether estimates were different from zero (i.e. no effect) we used 95% confidence intervals and tested statistical significance using  $P$  values from  $z$  approximations of  $t$  values because degrees of freedom are difficult to specify from mixed-effect models. Contrast analyses were constructed for each model to assess whether the factors in each predictor variable differed, with significant contrasts indicated in the results only (see Appendix Tables A4, A5).

Publication bias was assessed by constructing funnel plots to examine graphically the relationship between effect size (original  $g$ ) and sample size for activity and refuge use, with absence of publication bias indicated by decreasing effect sizes with increasing sample size (Sterne et al. 2005). We also calculated the Spearman rank correlation to examine statistically the relationship between effect size and sample size. If a significant relationship was detected, we then used the Rosenberg (2005) fail-safe number calculator (metafor package, Viechtbauer 2010) to estimate the number of additional studies averaging null results that would be required to reduce the significance level of the average effect size to the commonly accepted level of statistical significance of  $\alpha = 0.05$ . We assumed that, if the fail-safe number was larger than  $5n + 10$  where  $n$  is the number of studies, the results were robust regardless of publication bias.

## RESULTS

### Meta-analysis

Twenty-eight original studies met the criteria for inclusion in the meta-analysis. These involved a total of 28 invertebrate and 29 fish species, from which 66 effect size estimates of activity and 39 refuge use responses were obtained (see Appendix Tables A2, A3). The majority of studies involved Ephemeroptera ( $N = 7$ ), Gastropoda ( $N = 7$ ), Amphipoda ( $N = 5$ ) and Odonata ( $N = 5$ ).

### Activity

Overall, we found that fish cues altered invertebrate prey activity ( $t$  test:  $z = 6.05$ ,  $P < 0.0001$ ), with the  $I^2$  statistic indicating that Study ID accounts for most of the heterogeneity in the data (Table 1, Fig. 1a). Of the three invertebrate types for which there were sufficient studies, Amphipoda and Ephemeroptera altered

activity in the presence of a cue ( $t$  test:  $z = 4.11$ ,  $P < 0.0001$ ;  $z = 4.53$ ,  $P < 0.0001$ ), while Odonata did not ( $z = 0.93$ ,  $P = 0.352$ ). All invertebrate functional feeding groups altered activity in the presence of a cue (Table 1, Fig. 1a).

Invertebrates altered their activity in response to cues from familiar fish species (Table 1; insufficient data to test for a response to novel fish), regardless of whether the fish were fed conspecific invertebrates or other food sources, whether or not the fish was starved, or whether the fish cue was added once or continuously, with no difference in the magnitude of the effects within each predictor. Invertebrates were more likely to alter their activity when the fish cue was provided from a fish not physically present in the experimental tank (contrast [effect size<sub>Fish in tank Yes</sub> – effect size<sub>Fish in tank No</sub>]:  $t$  test:  $z = 2.12$ ,  $P = 0.034$ ). Fish cues provided in tap water resulted in highly variable, nonsignificant effect sizes, whereas invertebrates exposed to a fish cue in dechlorinated, ground or stream water showed altered activity. Neither cue intensity nor exposure time showed a relationship with activity effect sizes.

### Refuge Use

Fish cues altered invertebrate refuge use overall, with the  $I^2$  statistic also indicating that the random factor Study ID accounts for much of the heterogeneity between studies (Table 2, Fig. 1b). Gastropoda and Ephemeroptera (insufficient data for Amphipoda) both altered refuge use in the presence of a cue; however, the cue had a greater influence on Gastropoda (contrast [effect size<sub>Ephemeroptera</sub> – effect size<sub>Gastropoda</sub>]:  $t$  test:  $z = 2.02$ ,  $P = 0.004$ ). Invertebrates in the functional feeding group ‘grazer’ also altered their refuge use in the presence of a fish cue ( $t$  test:  $z = 5.02$ ,  $P < 0.0001$ ; insufficient studies for other groups).

Invertebrates altered their refuge use regardless of familiarity to the fish species, whether or not the fish was in the experimental tank, fish satiation levels or cue addition regime, with no difference in the magnitude of the effects within each predictor. Cues from fish that were fed invertebrate conspecifics and cues provided in stream water significantly altered refuge use effect sizes (insufficient data for fish that were fed other invertebrates and other water types). Cue intensity and exposure time did not have a significant effect on invertebrate refuge use.

### Publication Bias

The Spearman rank correlation coefficient for activity suggested a relationship between effect size and sample size across studies ( $r_s = 0.349$ ,  $N = 66$ ,  $P = 0.004$ ). However, visual inspection of the funnel plot (Fig. 2a) showed that this publication bias was not severe. This conclusion was also supported by the Rosenberg fail-safe number, which indicated an additional 1214 studies averaging null results would be required to reduce the significance of the average effect size below  $\alpha = 0.05$ . For refuge use, the funnel plot (Fig. 2b) and Spearman rank correlation coefficient ( $r_s = -0.250$ ,  $N = 39$ ,  $P = 0.124$ ) indicated the absence of publication bias.

## DISCUSSION

Predator cue studies are a frequently utilized approach when assessing the potential trait-mediated effects of predators on prey (e.g. Trussel et al. 2003; Dalesman et al. 2007; Griffen et al. 2012). Our meta-analyses indicate that, despite the very considerable differences in methodologies employed in predator cue experiments, effect sizes were remarkably consistent (with the exception of tap water), indicating that predator cue experiments are relatively robust to differences in experimental design. Variation in tap

**Table 1**  
Results of mixed-effect meta-analyses (LMMs with REML) of invertebrate activity response to fish predator cue

Variable	Variable level	<i>k</i>	<i>m</i>	<i>n</i>	Effect size <i>g</i> ( <i>d</i> )	<i>z</i> ( <i>p</i> )	95% CI for <i>g</i> ( <i>d</i> )	ΔAIC <i>g</i>	<i>I</i> <sup>2</sup> <i>g</i>
<b>Overall</b>		66	18	3094	<b>0.72 (0.75)</b>	6.05 (<0.0001)	<b>0.49 to 0.96</b> (0.50 to 0.99)	—	5.33
<b>Invert. type</b>	<b>Amphipoda</b>	17	5	500	<b>0.80 (0.82)</b>	4.11 (<0.0001)	<b>0.42 to 1.18</b> (0.41 to 1.23)	−1.81	1.95
	Dytiscidae	2		34					
	<b>Ephemeroptera</b>	24	8	782	<b>0.63 (0.65)</b>	4.53 (<0.0001)	<b>0.35 to 0.90</b> (0.36 to 0.93)		
	Gastropoda	3		336					
	Isopoda	5		60					
	Odonata	15	1	1382	0.23 (0.26)	0.93 (0.352)	−0.28 to 0.79 (−0.32 to 0.84)		
<b>Invert. FFG.</b>	<b>Grazer</b>	21	9	878	<b>0.72 (0.75)</b>	4.28 (<0.0001)	<b>0.39 to 1.05</b> (0.40 to 1.10)	2.92	5.21
	<b>Omnivore</b>	25	7	680	<b>0.79 (0.81)</b>	4.27 (<0.0001)	<b>0.43 to 1.16</b> (0.42 to 1.20)		
	<b>Carnivore</b>	20	3	1536	<b>0.59 (0.62)</b>	2.63 (0.008)	<b>0.15 to 1.03</b> (0.16 to 1.08)		
<b>Familiar fish</b>	<b>Yes</b>	41	15	1350	<b>0.78 (0.81)</b>	5.17 (<0.0001)	<b>0.49 to 1.08</b> (0.50 to 1.12)	—	6.94
	No	5		294					
<b>Fish in tank</b>	Yes	28	5	1628	0.32 (0.30)	1.72 (0.085)	−0.04 to 0.68 (−0.08 to 0.69)	−2.01	1.97
	No	38	14	1466	<b>0.77 (0.80)</b>	7.10 (<0.001)	<b>0.56 to 0.99</b> (0.58 to 1.03)		
<b>Fish fed invert.</b>	<b>Yes</b>	17	9	894	<b>0.75 (0.77)</b>	4.99 (<0.001)	<b>0.46 to 1.04</b> (0.47 to 1.08)	0.57	3.33
	No	33	8	2042	<b>0.51 (0.52)</b>	3.27 (0.001)	<b>0.21 to 0.82</b> (0.20 to 0.84)		
<b>Fish starved</b>	<b>Yes</b>	12	5	280	<b>0.56 (0.56)</b>	2.33 (0.020)	<b>0.09 to 1.02</b> (0.07 to 1.04)	1.80	2.23
	No	38	11	2656	<b>0.63 (0.65)</b>	5.04 (<0.0001)	<b>0.39 to 0.88</b> (0.40 to 0.91)		
<b>Water type</b>	Artificial	3	2	336				5.10	8.86
	<b>Dechlorinated</b>	34	7	1930	<b>0.74 (0.79)</b>	3.40 (0.001)	<b>0.31 to 1.17</b> (0.33 to 1.25)		
	<b>Ground</b>	10	2	288	<b>1.12 (1.18)</b>	2.60 (0.009)	<b>0.27 to 1.96</b> (0.28 to 2.08)		
	<b>Stream</b>	11	5	470	<b>0.59 (0.61)</b>	2.41 (0.016)	<b>0.11 to 1.08</b> (0.10 to 1.12)		
	Tap	8	2	70	1.00 (0.98)	1.92 (0.055)	−0.02 to 2.02 (−0.16 to 2.11)		
<b>Cue addition</b>	<b>Single</b>	26	8	1092	<b>0.80 (0.84)</b>	4.53 (<0.0001)	<b>0.46 to 1.15</b> (0.47 to 1.20)	1.50	5.45
	<b>Constant</b>	40	10	2002	<b>0.66 (0.67)</b>	3.95 (<0.0001)	<b>0.33 to 0.98</b> (0.32 to 1.01)		
Cue intensity		61	17	3034	0.02 (0.02)	0.14 (0.890)	−0.28 to 0.3 (−0.29 to 0.34)	−12.15	3.42
Exposure time		66	18	3094	0.21 (0.19)	0.99 (0.324)	−0.21 to 0.63 (−0.25 to 0.64)	0.91	5.82

The table shows the number of effect sizes (*k*), studies (*m*) and individuals or observations (*n*) used in the meta-analyses. Cue intensity and exposure time were scaled (continuous variables). Statistically significant effect sizes ( $\alpha = 0.05$ ) are in bold.

water quality offers an explanation of the inconsistency of tap water effect sizes, since tap water may be chlorinated in some locations, whereas it may be sourced directly from ground water elsewhere. The consistent signal of predator cue effects on prey behaviour, despite variations in experimental design, lends further weight to current proposals that trait-mediated indirect effects are pervasive and powerful influences in nature (Dunn et al. 2012; Ohgushi et al. 2012).

When the original effect sizes of invertebrates in predator cue studies are examined, it may appear that few invertebrate taxa or functional feeding groups show consistent behavioural responses to predator cues (see Appendix Tables A2, A3). However, these differences are likely to reflect both the prey- and/or predator-specific responses (e.g. fast-moving prey increase activity to escape predators; prey increase refuge use to avoid pelagic predators). Prey exhibiting inappropriate or unnecessary predator avoidance behaviour may face penalties in terms of reduced foraging and reproductive outputs (Dunn et al. 2008), in addition to increased predation risk from other predators (Chivers & Smith 1995; Åbjörnsson et al. 2004). Therefore, prey benefit from the ability to detect and respond appropriately to cues that indicate potential predation risk (e.g. Wisenden et al. 1997; Mirza & Chivers 2003; Richmond & Lasenby 2006).

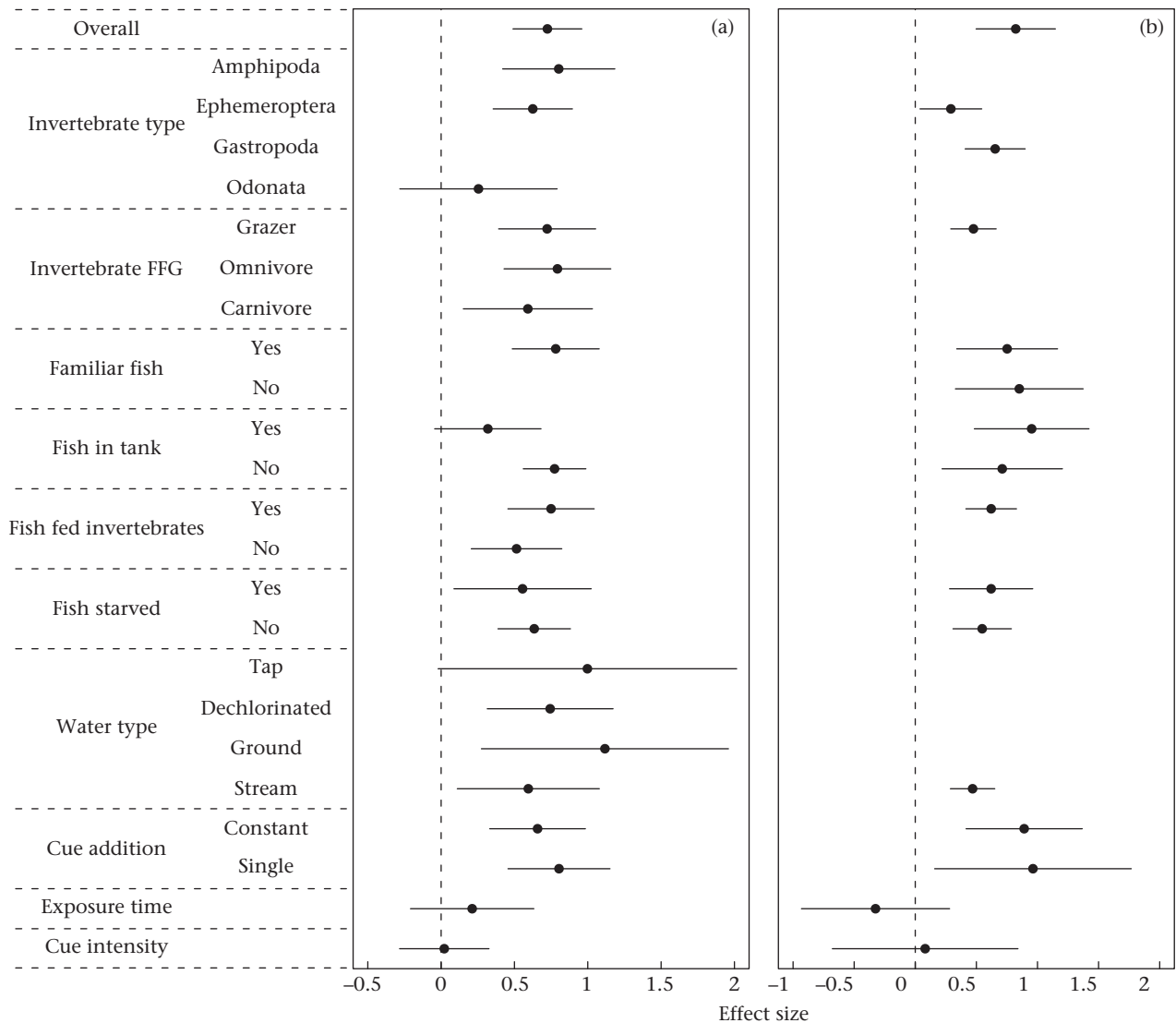
However, the appropriateness of a particular behavioural response of an invertebrate to a 'predator' cue may not be fully evaluated since few studies consider the functional feeding group of the invertebrate species itself. This is of particular importance in studies that focus on the behaviour of invertebrates known to consume tissues of live and/or dead fish (e.g. *Gammarus* amphipods, reviewed in MacNeil et al. 1997; notonectid waterbugs, Papáček 2001; odonates, Mobley et al. 2013). With such omnivorous 'prey' species, conclusions must be cautiously drawn from cue studies, since observed behaviour may not be strictly that of an invertebrate prey avoiding a fish predator, and may in fact be a feeding response.

Invertebrates showed behavioural responses to the cues of both familiar and unfamiliar fish species, indicating a general ability to perceive and respond to the potential risk of predation posed by novel predators, which may become increasingly important as freshwater communities face mounting pressure from the introduction of exotic species (Strayer 2010). Previous studies have suggested that invertebrates may display innate (general) predator responses to novel predation threats, or use diet cues to learn and respond rapidly to novel predator cues (Wisenden & Millard 2001; Sih et al. 2010). Our meta-analysis shows that invertebrates altered their behaviour to predator cues of both fish that were fed the focal invertebrate and those that were fed other prey types, which suggests that invertebrates were not responding to specific diet information in the fish cues. Additionally, satiation levels of the fish did not have a strong influence on whether invertebrates altered their behaviour.

Both the presence and absence of the predatory fish in the experimental tank resulted in invertebrates altering their refuge use, whereas invertebrates altered their activity only when fish were not in the tank. This suggests that invertebrates may adjust their predator avoidance strategies based on additional information obtained from their physical environment. If the exact location of the fish is unknown (i.e. is outside the experimental tank or behind an opaque barrier), and only a chemical cue of its presence is available, then the best strategy for an invertebrate to avoid predation may be to alter its behaviour.

Previous studies have suggested that changes in cue intensity provide prey with a method of assessing predation risk based on the density of the predators, as well as their temporal and spatial proximity (Ferrari et al. 2006). In contrast, our results suggest that invertebrates respond in a similar fashion regardless of the intensity of the cue. This behavioural trait is likely to be advantageous in avoiding being consumed since the appropriate behavioural response required to avoid a single predator is likely to be relevant if there are multiple predators (of the same species) present. If prey





**Figure 1.** Visual presentation of the relationship between absolute effect size ( $g$ ) and (a) invertebrate activity and (b) refuge use in response to fish cue. Error bars are 95% confidence intervals. FFG: functional food group.

respond differently to predator number or proximity, then our results suggest that cue intensity alone may not be sufficient for prey to distinguish between these threats. Indeed, prey may respond to predation threats by utilizing multiple cues in an additive manner as proposed in the 'sensory complement' hypothesis (Lima & Steury 2005). However, we cannot discount the possibility that the intensity of cues used in these studies was sufficiently high to mask otherwise subtle effects of predator number or proximity (i.e. studies should use more realistic (low) concentrations of predator cue).

In this study, our ability to evaluate fully the influence of a number of experimental design factors was limited owing to a lack of studies, which in some cases was further confounded by available studies failing to report effect sizes or statistics and/or figures from which effect sizes could be estimated. For example, fewer than eight refuge use studies used water types other than 'stream' and thus the influence of other water types could not be evaluated. In contrast, sufficient invertebrate activity studies were available for four different water types, which indicated that experiments should avoid tap water since highly variable effect sizes were likely

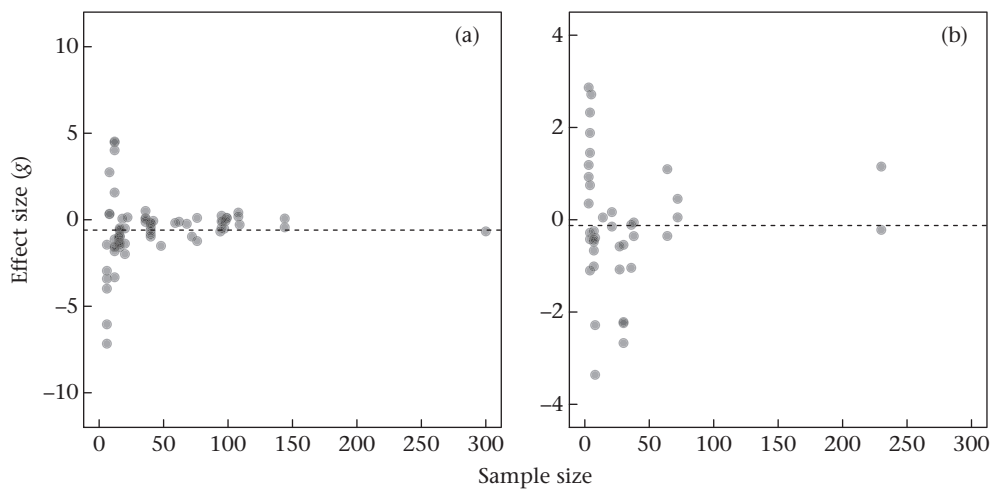
to be generated. The ability for meta-analyses to assess the overall effect of predator cues on prey behaviour relies directly on the access to effect size statistics, and thus their inclusion should be encouraged in future studies. In other instances, factors such as cue degradation are not routinely assessed when designing predator cue studies, and thus little inference could be made on their effect.

Likewise, we found parasite infection status was rarely reported, despite trophically transmitted parasites frequently altering the behaviour of their intermediate hosts to enhance their transmission to the predatory definitive host (e.g. Thomas et al. 2005). For example, *G. pulex* amphipods infected with the fish acanthocephalan *Pomphorhynchus laevis* prefer water containing the odour of perch, *Perca fluviatilis* (a known definitive host, Baldauf et al. 2007); while Medoc & Beisel (2008) demonstrated increased escape performance of *Polymorphus minutus* infected with *Gammarus roeseli* amphipods in response to a nonhost predator. Indeed, there is growing evidence that many parasites, including many that are not trophically transmitted, influence host behaviour and thereby induce trait-mediated indirect effects on species with which the host interacts (reviewed in Hatcher & Dunn 2011). This is

**Table 2**  
Results of mixed-effect meta-analyses (LMMs with REML) of invertebrate refuge use response to fish predator cue

Variable	Variable level	<i>k</i>	<i>m</i>	<i>n</i>	Effect size <i>g</i> ( <i>d</i> )	<i>z</i> ( <i>p</i> )	95% CI for <i>g</i> ( <i>d</i> )	ΔAIC <i>g</i>	<i>I</i> <sup>2</sup> <i>g</i>
<b>Overall</b>		39	15	2352	<b>0.82 (0.88)</b>	4.97 (<0.0001)	<b>0.50 to 1.15</b> (0.53 to 1.24)		14.97
<b>Invert. type</b>	Amphipoda	6		196				−2.07	0
	Diptera	6		132					
	<b>Ephemeroptera</b>	14	5	430	<b>0.29 (0.29)</b>	2.26 (0.024)	<b>0.04 to 0.54</b> (0.03 to 0.55)		
	<b>Gastropoda</b>	12	6	1522	<b>0.65 (0.64)</b>	5.22 (<0.0001)	<b>0.41 to 0.90</b> (0.39 to 0.90)		
	Plecoptera	1		72					
<b>Invert. FFG</b>	Detritivore	6		132				—	0
	<b>Grazer</b>	26	11	1952	<b>0.48 (0.48)</b>	5.02 (<0.0001)	<b>0.29 to 0.66</b> (0.28 to 0.67)		
	Omnivore	6		196					
	Carnivore	1		72					
<b>Familiar fish</b>	<b>Yes</b>	19	11	1656	<b>0.75 (0.83)</b>	3.57 (0.0003)	<b>0.34 to 1.16</b> (0.36 to 1.28)	−4.60	21.46
	<b>No</b>	18	5	614	<b>0.85 (0.90)</b>	3.19 (0.001)	<b>0.33 to 1.37</b> (0.32 to 1.47)		
<b>Fish in tank</b>	<b>Yes</b>	19	8	1570	<b>0.95 (1.01)</b>	3.98 (0.0001)	<b>0.48 to 1.42</b> (0.50 to 1.53)	1.38	18.20
	<b>No</b>	20	7	782	<b>0.71 (0.78)</b>	2.83 (0.005)	<b>0.22 to 1.20</b> (0.23 to 1.33)		
<b>Fish fed invert.</b>	<b>Yes</b>	30	12	1876	<b>0.62 (0.63)</b>	5.88 (<0.0001)	<b>0.41 to 0.83</b> (0.41 to 0.84)	—	0
	<b>No</b>	2		288					
<b>Fish starved</b>	<b>Yes</b>	16	5	346	<b>0.62 (0.64)</b>	3.57 (0.0004)	<b>0.28 to 0.96</b> (0.28 to 0.99)	−24.54	0
	<b>No</b>	17	8	1826	<b>0.55 (0.55)</b>	4.49 (<0.0001)	<b>0.31 to 0.79</b> (0.30 to 0.79)		
<b>Water type</b>	Artificial	2	1	288				—	0
	Dechlorinated	5		56					
	Ground	4		32					
	<b>Stream</b>	17	7	1670	<b>0.47 (0.48)</b>	5.06 (<0.0001)	<b>0.29 to 0.65</b> (0.30 to 0.67)		
	50% tap, 50% river	1		10					
	Tap	6		132					
<b>Cue addition</b>	<b>Single</b>	27	10	1742	<b>0.96 (1.10)</b>	2.35 (0.019)	<b>0.16 to 1.77</b> (0.21 to 2.00)	1.99	32.46
	<b>Constant</b>	11	4	362	<b>0.89 (0.95)</b>	3.68 (0.0002)	<b>0.42 to 1.37</b> (0.43 to 1.48)		
	Daily	2		256					
Cue intensity		39	14	2352	0.08 (0.13)	0.21 (0.835)	−0.68 to 0.84 (−0.71 to 0.96)	1.93	17.63
Exposure time		39	14	2352	−0.33 (−0.35)	1.05 (0.293)	−0.93 to 0.28 (−1.01 to 0.31)	1.21	30.75

The table shows the number of effect sizes (*k*), studies (*m*) and individuals or observations (*n*) used in the meta-analyses. Cue intensity and exposure time were scaled (continuous variables). Statistically significant effect sizes ( $\alpha = 0.05$ ) are in bold.



**Figure 2.** Funnel plots of original effect size (*g*) versus sample size for (a) activity and (b) refuge use of aquatic invertebrates.

particularly relevant for predator–prey studies because parasites can alter both host vulnerability to predation and, for predatory host species, their predation rate. Thus, future predator cue studies would benefit from ensuring prey are not parasitized when the influence of parasitism is not of interest.

In conclusion, our study highlights that when variations resulting from choice of cue and response variables, and adaptive underpinning of response in relation to prey functional or taxonomic group, are properly accounted for, fish predator–invertebrate prey studies are remarkably robust to differences in experimental design. Thus, the standardization of predator cue experimental designs may not be required in order to assess the

strong influences of predator cue on prey behaviour. Furthermore, this study provides evidence to suggest that trait-mediated effects are powerful drivers of ecological and evolutionary processes that define prey populations, and the resources with which they interact.

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## APPENDIX

Table A1

Predictor variables used to investigate the influence of fish cue on invertebrate behaviour

	Variable level	Original study feature
<b>Categorical variables</b>		
Invertebrate type	Amphipoda	
	Diptera	
	Dytiscidae	
	Ephemeroptera	
	Odonata	
	Plecoptera	
Invertebrate functional feeding group	Gastropoda	
	Detritivore	Consumes fine particulate organic matter
Familiar fish	Shredder/grazer	Consumes coarse particulate organic matter or epilithon
	Omnivore	Consumes animal and plant material
Fish fed invertebrate	Carnivore	Consumes other invertebrates
	Yes	Fish species known to prey (i.e. present at invertebrate collection site)
Fish starved	No	Fish species novel to prey (i.e. absent at invertebrate collection site)
	Yes	Fish fed study invertebrate species
Fish in tank	No	Fish fed nonstudy invertebrate species or other food
	Yes	Fish held without food before experiment
Water type	No	Fish were fed before experiment
	Yes	Fish present in experimental arena
	No	Fish absent from experimental arena (e.g. in separate holding tank)
Cue addition	Artificial	Tap water with artificial additives to mimic 'stream' water (see below)
	Tap	Tap water
	Dechlorinated	Tap water with chlorine removed (e.g. spring or well)
Exposure time	Ground	Water from subterranean source (e.g. stream, lake)
	Stream	Water from surface water body (e.g. stream, lake)
Cue intensity	Single	Single cue addition to experimental arena
	Constant	Constant cue addition to experimental arena
Exposure time	Daily	Cue added daily
	NA	Mean fish weight (g) per litre of water in experimental arena
Exposure time	NA	Experimental duration (min)



**Table A2**

Studies used in the meta-analyses of the influence of predator cue experimental design on invertebrate activity

Study ID	Invert. species	Invert. type	Invert. FFG	Fish species	Familiar fish	Fish in tank	Fish fed invert.	Fish starved	Water type	Cue addition	Cue intensity	Exposure time	Original statistic	Control; Treatment	$N_c; N_t$	$g$	Source
1	<i>G. pulex</i>	A	O	<i>S. trutta</i>	Yes	No	Yes	No	D	S	0.024	10	X±SE	-1.34±4.19; -24.77±5.60	8; 8	-1.583	Ábjörnsson et al. 2000
1	<i>G. pulex</i>	A	O	<i>S. trutta</i>	Yes	No	No	Yes	D	S	0.024	10	X±SE	-1.34±4.19; -36.12±17.34	8; 7	-1.012	Ábjörnsson et al. 2000
1	<i>G. pulex</i>	A	O	<i>S. trutta</i>	Yes	No	No	No	D	S	0.024	10	X±SE	-1.34±4.19; -31.15±9.11	8; 8	-1.406	Ábjörnsson et al. 2000
1	<i>G. pulex</i>	A	O	<i>C. gobio</i>	Yes	No	No	Yes	D	S	0.006	10	X±SE	-1.34±4.19; -33.47±11.76	8; 7	-1.323	Ábjörnsson et al. 2000
1	<i>G. pulex</i>	A	O	<i>C. gobio</i>	Yes	No	Yes	No	D	S	0.006	10	X±SE	-1.34±4.19; -21.07±8.93	8; 8	-0.945	Ábjörnsson et al. 2000
1	<i>G. pulex</i>	A	O	<i>C. gobio</i>	Yes	No	No	No	D	S	0.006	10	X±SE	-1.34±4.19; -10.63±6.66	8; 8	-0.559	Ábjörnsson et al. 2000
2	<i>A. sulcatus</i>	Dy	C	<i>P. fluviatilis</i>	Yes	No	No	Yes	T	C	0.135	10	X±SE	119.38±22.75; 66.97±11.14	8; 8	-0.978	Ábjörnsson et al. 1997
2	<i>A. sulcatus</i>	Dy	C	<i>P. fluviatilis</i>	Yes	No	No	No	T	C	0.135	10	X±SE	73.06±20.14; 76.81±18.01	9; 9	0.062	Ábjörnsson et al. 1997
3	<i>L. stagnalis</i>	G	G	<i>T. tinca</i>	No	No	No	No	A	S	0.870	120	X±SE	1.00±0.00; 0.55±0.09	24; 24	-1.510	Dalesman et al. 2006
4	<i>L. stagnalis</i>	G	G	<i>T. tinca</i>	No	No	No	No	A	S	0.870	120	X±SE	0.98±0.01; 0.76±0.08	72; 72	-0.440	Dalesman et al. 2007
4	<i>L. stagnalis</i>	G	G	<i>T. tinca</i>	Yes	No	No	No	A	S	0.870	120	X±SE	0.94±0.03; 0.96±0.03	72; 72	0.071	Dalesman et al. 2007
5	<i>E. stammeri</i>	A	O	<i>L. cephalus</i>	NA	No	Yes	No	D	C	2.588	4320	X±SE	0.05±0.05; 0.00±0.00	8; 8	-0.492	Dezfuli et al. 2003
5	<i>E. stammeri</i>	A	O	<i>L. cephalus</i>	NA	No	Yes	No	D	C	2.588	4320	X±SE	0.67±0.29; 0.27±0.09	8; 8	-0.633	Dezfuli et al. 2003
6	<i>G. duebeni</i>	A	O	<i>G. aculeatus</i>	Yes	No	Yes	No	D	S	0.043	5	X±SE	8.77±0.64; 4.24±0.44	150; 150	-0.672	Dunn et al. 2008
7	<i>G. minus</i>	A	O	<i>L. cyanellus</i>	Yes	No	NA	NA	D	S	1.293	15	F	7.87	8; 8	-1.311	Holomuzki & Hoyle 1990
7	<i>G. minus</i>	A	O	<i>L. cyanellus</i>	Yes	No	NA	NA	D	S	1.293	15	F	142.16	11; 11	0.140	Holomuzki & Hoyle 1990
8	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	Yes	Yes	Yes	Yes	S	C	0.249	720	X±SE	1.24±0.82; 0.83±0.70	18; 18	-0.125	Huhta et al. 1999
8	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	Yes	Yes	Yes	Yes	S	C	0.249	720	X±SE	3.08±1.49; 3.38±1.47	18; 18	0.047	Huhta et al. 1999
8	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	Yes	Yes	Yes	Yes	S	C	0.249	720	X±SE	0.29±0.11; 0.36±0.22	18; 18	0.093	Huhta et al. 1999
8	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	Yes	Yes	Yes	Yes	S	C	0.249	720	X±SE	0.34±0.22; 2.42±1.32	18; 18	0.508	Huhta et al. 1999
9	<i>Siphonurus</i> spp.	E	O	<i>S. fontinalis</i>	Yes	No	Yes	No	G	S	0.021	5	<i>t</i>	-3.12	20; 20	-0.975	Huryñ & Chivers 1999
9	<i>Siphonurus</i> spp.	E	O	<i>S. fontinalis</i>	Yes	No	No	No	G	S	0.021	5	<i>t</i>	-0.72	20; 20	-0.422	Huryñ & Chivers 1999
9	<i>Siphonurus</i> spp.	E	O	<i>S. fontinalis</i>	Yes	No	No	No	G	S	0.021	5	<i>t</i>	-1.40	20; 20	-0.196	Huryñ & Chivers 1999
9	<i>Siphonisca</i> spp.	E	C	<i>S. fontinalis</i>	Yes	No	Yes	No	G	S	0.021	5	<i>t</i>	-2.52	20; 20	-0.827	Huryñ & Chivers 1999
9	<i>Siphonisca</i> spp.	E	C	<i>S. fontinalis</i>	Yes	No	No	No	G	S	0.021	5	<i>t</i>	-0.67	20; 20	-0.624	Huryñ & Chivers 1999
9	<i>Siphonisca</i> spp.	E	C	<i>S. fontinalis</i>	Yes	No	No	No	G	S	0.021	5	<i>t</i>	-1.95	20; 20	-0.206	Huryñ & Chivers 1999
10	<i>B. bicaudatus</i>	E	G	<i>O. clarkii pleuriticus</i>	Yes	No	Yes	No	S	C	3.908	1080	X±SE	14.98±1.64; 5.54±1.21	10; 10	-1.983	McIntosh & Peckarsky 2004

(continued on next page)

Table A2 (continued)

Study ID	Invert. species	Invert. type	Invert. FFG	Fish species	Familiar fish	Fish in tank	Fish fed invert.	Fish starved	Water type	Cue addition	Cue intensity	Exposure time	Original statistic	Control; Treatment	$N_c; N_t$	$g$	Source
10	<i>B. bicaudatus</i>	E	G	<i>S. fontinalis</i>	Yes	No	Yes	No	S	C	4.094	1080	X±SE	14.98±1.64; 8.69±1.05	10; 10	-1.381	McIntosh & Peckarsky 2004
10	<i>B. bicaudatus</i>	E	G	<i>C. auratus</i>	No	No	No	No	S	C	4.466	1080	X±SE	14.98±1.64; 12.26±1.64	10; 10	-0.501	McIntosh & Peckarsky 2004
11	<i>B. bicaudatus</i>	E	G	<i>S. fontinalis</i>	Yes	No	Yes	No	S	C	0.008	2880	X±SE	23.26±1.53; 11.56±1.52	38; 38	-1.232	McIntosh & Peckarsky 1996
11	<i>B. bicaudatus</i>	E	G	<i>S. fontinalis</i>	No	No	Yes	No	S	C	0.008	2880	X±SE	5.23±0.86; 5.99±1.41	38; 38	0.105	McIntosh & Peckarsky 1996
12	<i>B. thermicus</i>	E	G	<i>O. masou</i>	Yes	No	No	Yes	G	C	0.032	1440	X±SE	20.79±1.83; 35.76±4.73	6; 6	1.573	Miyasaka & Nakano 2001
12	<i>B. thermicus</i>	E	G	<i>C. nozawae</i>	Yes	No	No	Yes	G	C	0.031	1440	X±SE	20.04±3.51; 76.15±6.57	6; 6	4.016	Miyasaka & Nakano 2001
12	<i>B. thermicus</i>	E	G	<i>C. nozawae</i>	Yes	Yes	No	Yes	G	C	0.031	1440	X±SE	20.04±3.51; 77.02±5.80	6; 6	4.477	Miyasaka & Nakano 2001
12	<i>B. thermicus</i>	E	G	<i>O. masou</i>	Yes	Yes	No	Yes	G	C	0.032	1440	X±SE	20.79±1.83; 59.06±4.12	6; 6	4.521	Miyasaka & Nakano 2001
13	<i>B. bicaudatus</i>	E	G	<i>S. fontinalis</i>	Yes	No	Yes	No	S	C	0.019	8640	X±SE	6.00±0.84; 2.22±0.34	36; 36	-0.973	Peckarsky & McIntosh 1998
14	<i>B. tricaudatus</i>	E	G	<i>R. cataractae</i>	Yes	No	NA	NA	D	S	3.888	1	X±SE	3.00±1.30; 3.80±0.80	4; 4	0.322	Scrimgeour & Culp 1994
14	<i>P. heteronea</i>	E	G	<i>R. cataractae</i>	Yes	No	NA	NA	D	S	3.888	1	X±SE	0.20±0.20; 0.50±0.50	4; 4	0.343	Scrimgeour & Culp 1994
14	<i>E. aurivillii</i>	E	G	<i>R. cataractae</i>	Yes	No	NA	NA	D	S	3.888	1	X±SE	0.60±0.40; 4.20±0.70	4; 4	2.746	Scrimgeour & Culp 1994
15	<i>L. fontinalis</i>	I	O	<i>L. megalotis</i>	NA	No	NA	NA	D	S	NA	3	X±SE	111.00±3.60; 57.40±7.80	6; 6	-3.325	Short & Holomuzki 1992
15	<i>L. fontinalis</i>	I	O	<i>S. atromaculatus</i>	Yes	No	NA	NA	D	S	NA	3	X±SE	89.10±9.00; 57.40±2.30	6; 6	-1.819	Short & Holomuzki 1992
15	<i>L. fontinalis</i>	I	O	<i>C. anomalum</i>	NA	No	NA	NA	D	S	NA	3	X±SE	110.70±3.90; 88.00±6.80	6; 6	-1.543	Short & Holomuzki 1992
15	<i>L. fontinalis</i>	I	O	<i>C. carolinae</i>	NA	No	NA	NA	D	S	NA	3	X±SE	118.10±11.20; 83.60±11.80	6; 6	-1.130	Short & Holomuzki 1992
15	<i>L. fontinalis</i>	I	O	<i>L. cyanellus</i>	Yes	No	NA	NA	D	S	NA	3	X±SE	107.40±7.40; 70.00±10.10	6; 6	-1.592	Short & Holomuzki 1992
16	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	Yes	Yes	Yes	Yes	S	C	0.252	30	X±SE	2.22±0.52; 2.06±0.55	21; 21	-0.066	Tikkanen et al. 1994
17	<i>G. pseudolimnaeus</i>	A	O	<i>S. namaycush/fontinalis</i>	Yes	Yes	NA	NA	T	C	2.326	5760	X±SE	146.60±8.00; 27.10±7.40	3; 3	-7.163	Williams & Moore 1985
17	<i>G. pseudolimnaeus</i>	A	O	<i>Notropis</i> spp.	Yes	Yes	NA	NA	T	C	2.326	5760	X±SE	217.80±13.60; 53.60±11.40	3; 3	-6.044	Williams & Moore 1985
17	<i>G. pseudolimnaeus</i>	A	O	<i>O. mykiss</i>	Yes	Yes	NA	NA	T	C	2.326	5760	X±SE	119.10±16.40; 10.90±6.80	3; 3	-3.981	Williams & Moore 1985
17	<i>G. pseudolimnaeus</i>	A	O	<i>P. taeniatus</i>	No	Yes	NA	NA	T	C	2.326	5760	X±SE	160.90±17.20; 48.40±13.00	3; 3	-3.408	Williams & Moore 1985
17	<i>G. pseudolimnaeus</i>	A	O	<i>Rhinichthys</i> spp.	Yes	Yes	NA	NA	T	C	2.326	5760	X±SE	115.00±12.20; 50.00±7.60	3; 3	-2.954	Williams & Moore 1985
17	<i>G. pseudolimnaeus</i>	A	O	<i>Etheostoma</i> spp.	Yes	Yes	NA	NA	T	C	2.326	5760	X±SE	198.90±25.80; 119.30±25.20	3; 3	-1.442	Williams & Moore 1985
18	<i>C. puella</i>	O	C	<i>S. erythrophthalmus</i>	NA	Yes	No	No	D	C	2.942	150	X±SE	4.66±0.43; 2.80±0.36	46; 48	-0.680	Wohlfahrt et al. 2006
18	<i>C. puella</i>	O	C	<i>P. fluviatilis</i>	NA	Yes	No	No	D	C	2.086	150	X±SE	4.66±0.43; 3.09±0.43	46; 51	-0.517	Wohlfahrt et al. 2006
18	<i>C. puella</i>	O	C	<i>G. gobio</i>	NA	Yes	No	No	D	C	0.810	150	X±SE	4.66±0.43; 3.23±0.43	46; 49	-0.478	Wohlfahrt et al. 2006

18	<i>L. depressa</i>	O	C	<i>S. erythrophthalmus</i>	NA	Yes	No	No	D	C	2.942	150	X±SE	3.46±0.50; 2.50±0.40	54; 55	−0.286	Wohlfahrt et al. 2006
18	<i>S. striolatum</i>	O	C	<i>P. fluviatilis</i>	NA	Yes	No	No	D	C	2.086	150	X±SE	3.96±0.61; 3.11±0.61	32; 36	−0.235	Wohlfahrt et al. 2006
18	<i>S. striolatum</i>	O	C	<i>G. gobio</i>	NA	Yes	No	No	D	C	0.810	150	X±SE	3.96±0.61; 3.28±0.74	32; 27	−0.185	Wohlfahrt et al. 2006
18	<i>S. striolatum</i>	O	C	<i>S. erythrophthalmus</i>	NA	Yes	No	No	D	C	2.942	150	X±SE	3.96±0.61; 3.56±0.63	32; 30	−0.115	Wohlfahrt et al. 2006
18	<i>P. pennipes</i>	O	C	<i>S. erythrophthalmus</i>	NA	Yes	No	No	D	C	2.942	150	X±SE	0.83±0.20; 0.71±0.16	48; 47	−0.092	Wohlfahrt et al. 2006
18	<i>P. pennipes</i>	O	C	<i>G. gobio</i>	NA	Yes	No	No	D	C	0.810	150	X±SE	0.83±0.20; 0.72±0.13	48; 48	−0.090	Wohlfahrt et al. 2006
18	<i>L. sponza</i>	O	C	<i>S. erythrophthalmus</i>	NA	Yes	No	No	D	C	2.942	150	X±SE	3.24±0.52; 2.98±0.40	49; 49	−0.079	Wohlfahrt et al. 2006
18	<i>L. sponza</i>	O	C	<i>G. gobio</i>	NA	Yes	No	No	D	C	0.810	150	X±SE	3.24±0.52; 3.55±0.40	49; 50	0.095	Wohlfahrt et al. 2006
18	<i>L. sponza</i>	O	C	<i>P. fluviatilis</i>	NA	Yes	No	No	D	C	2.086	150	X±SE	3.24±0.52; 3.62±0.43	49; 50	0.111	Wohlfahrt et al. 2006
18	<i>L. depressa</i>	O	C	<i>P. fluviatilis</i>	NA	Yes	No	No	D	C	2.086	150	X±SE	3.46±0.50; 4.19±0.59	54; 54	0.181	Wohlfahrt et al. 2006
18	<i>P. pennipes</i>	O	C	<i>P. fluviatilis</i>	NA	Yes	No	No	D	C	2.086	150	X±SE	0.83±0.20; 1.22±0.29	48; 47	0.230	Wohlfahrt et al. 2006
18	<i>L. depressa</i>	O	C	<i>G. gobio</i>	NA	Yes	No	No	D	C	0.810	150	X±SE	3.46±0.50; 5.26±0.67	54; 54	0.413	Wohlfahrt et al. 2006

Invertebrate (invert.) type: Amphipoda (A), Dytiscidae (Dy), Ephemeroptera (E), Gastropoda (G); invertebrate functional feeding group (FFG): carnivore (C), grazer (G), omnivore (O); water type: artificial (A), dechlorinated (D), ground (G), stream (S), tap (T); cue addition: constant (C), single (S).

**Table A3**

Studies used in the meta-analyses of the influence of predator cue experimental design on invertebrate refuge use

Study ID	Invert. Species	Invert. type	Invert. FFG	Fish species	Familiar fish	Fish in tank	Fish fed invert	Fish starved	Water type	Cue addition	Cue intensity	Exposure time	Original statistic	Control; Treatment	$N_c; N_t$	$g$	Source
1	<i>G. pulex</i>	A	O	<i>C. gobio</i>	No	Yes	NA	NA	NA	C	0.781	10	X±SE	63.00±11.40; 15.20±1.90	11; 30	−2.217	Andersson et al. 1986
1	<i>G. pulex</i>	A	O	<i>C. gobio</i>	No	Yes	NA	NA	NA	C	0.782	10	X±SE	69.10±10.60; 16.90±1.50	11; 30	−2.672	Andersson et al. 1986
1	<i>G. pulex</i>	A	O	<i>C. gobio</i>	No	Yes	NA	NA	NA	C	0.782	10	X±SE	62.40±7.70; 20.90±2.70	11; 30	−2.241	Andersson et al. 1986
1	<i>G. pulex</i>	A	O	<i>C. gobio</i>	No	Yes	NA	NA	NA	C	0.782	10	X±SE	41.00±5.60; 30.90±3.30	11; 30	−0.544	Andersson et al. 1986
2	<i>P. integra</i>	G	G	<i>L. gibbosus</i>	Yes	Yes	Yes	No	S	C	0.033	11 520	X±SE	0.59±0.04; 0.48±0.02	230; 230	−0.220	Bernot & Turner 2001
2	<i>P. integra</i>	G	G	<i>L. gibbosus</i>	Yes	Yes	Yes	No	S	C	0.033	11 520	X±SE	0.24±0.02; 0.65±0.03	230; 230	1.152	Bernot & Turner 2001
3	<i>P. canaliculata</i>	G	G	<i>A. testudineus</i>	NA	No	Yes	No	50% T, 50% S	S	0.004	30	X±SE	1.43±2.22; 56.12±11.29	5; 5	2.716	Carlsson et al. 2004
4	<i>L. stagnalis</i>	G	G	<i>T. tinca</i>	Yes	No	No	No	A	S	0.870	120	X±SE	0.01±0.004; 0.01±0.01	72; 72	0.052	Dalesman et al. 2007
4	<i>L. stagnalis</i>	G	G	<i>T. tinca</i>	No	No	No	No	A	S	0.870	120	X±SE	0.003±0.01; 0.11±0.04	72; 72	0.453	Dalesman et al. 2007
5	<i>C. riparius</i>	Di	D	<i>R. rutilus</i>	No	No	Yes	Yes	T	C	0.0001	120	X±SE	17.38±1.28; 13.32±1.38	27; 27	−0.579	Hölker & Stief 2005
5	<i>C. riparius</i>	Di	D	<i>R. rutilus</i>	No	No	Yes	Yes	T	C	0.0001	4320	X±SD	6.05±0.57; 7.19±1.27	3; 3	0.928	Hölker & Stief 2005

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Table A3 (continued)

Study ID	Invert. Species	Invert. type	Invert. FFG	Fish species	Familiar fish	Fish in tank	Fish fed invert	Fish starved	Water type	Cue addition	Cue intensity	Exposure time	Original statistic	Control; Treatment	$N_c$ ; $N_t$	$g$	Source
5	<i>C. riparius</i>	Di	D	<i>R. rutilus</i>	No	No	Yes	Yes	T	C	0.0001	7200	$X \pm SD$	10.27±1.68; 10.81±0.47	3; 3	0.352	Hölker & Stief 2005
5	<i>C. riparius</i>	Di	D	<i>R. rutilus</i>	No	No	Yes	Yes	T	C	0.0004	120	$X \pm SE$	17.38±1.28; 9.36±1.54	27; 27	-1.077	Hölker & Stief 2005
5	<i>C. riparius</i>	Di	D	<i>R. rutilus</i>	No	No	Yes	Yes	T	C	0.0004	4320	$X \pm SD$	6.05±0.57; 8.97±1.01	3; 3	2.867	Hölker & Stief 2005
5	<i>C. riparius</i>	Di	D	<i>R. rutilus</i>	No	No	Yes	Yes	T	C	0.0004	7200	$X \pm SD$	10.27±1.68; 12.19±0.74	3; 3	1.187	Hölker & Stief 2005
6	<i>G. pulex</i>	A	O	<i>C. gobio</i>	Yes	Yes	Yes	Yes	D	C	0.909	90	$X \pm SE$	4.63±0.46; 0.63±0.32	8; 8	-3.361	Kaldonski et al. 2007
7	<i>B. bicaudatus</i>	E	G	<i>S. fontinalis</i>	Yes	No	Yes	No	S	C	0.008	2880	$X \pm SE$	28.42±2.27; 22.84±2.76	38; 38	-0.355	McIntosh & Peckarsky 1996
7	<i>B. bicaudatus</i>	E	G	<i>S. fontinalis</i>	No	No	Yes	No	S	C	0.008	2880	$X \pm SE$	16.80±1.93; 15.90±2.90	38; 38	-0.059	McIntosh & Peckarsky 1996
8	<i>B. bicaudatus</i>	E	G	<i>S. fontinalis</i>	Yes	No	Yes	No	S	C	0.019	8640	$X \pm SE$	19.21±1.77; 17.87±2.19	36; 36	-0.111	Peckarsky & McIntosh 1998
8	<i>M. signata</i>	P	C	<i>S. fontinalis</i>	NA	No	Yes	No	S	C	0.019	8640	$X \pm SE$	0.95±0.05; 0.62±0.05	36; 36	-1.042	Peckarsky & McIntosh 1998
9	<i>G. pulex</i>	A	O	<i>C. gobio</i>	Yes	Yes	Yes	Yes	D	C	0.909	95	$X \pm SD$	39.61±9.06; 18.09±8.76	8; 8	-2.284	Perrot-Minnot et al. 2007
10	<i>P. heteronea</i>	E	G	<i>R. cataractae</i>	Yes	No	NA	NA	D	S	3.888	1	$X \pm SE$	5.40±0.40; 3.80±0.80	4; 4	-1.100	Scrimgeour & Culp 1994
10	<i>B. tricaudatus</i>	E	G	<i>R. cataractae</i>	Yes	No	NA	NA	D	S	3.888	1	$X \pm SE$	9.60±1.00; 8.80±0.60	4; 4	-0.422	Scrimgeour & Culp 1994
10	<i>E. aurivillii</i>	E	G	<i>R. cataractae</i>	Yes	No	NA	NA	D	S	3.888	1	$X \pm SE$	6.80±0.70; 6.00±1.60	4; 4	-0.282	Scrimgeour & Culp 1994
11	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	Yes	Yes	Yes	Yes	S	C	0.252	30	$X \pm SE$	2.00±0.49; 1.69±0.41	21; 21	-0.148	Tikkanen et al. 1994
11	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	Yes	Yes	Yes	Yes	S	C	0.252	30	$X \pm SE$	2.23±0.47; 2.68±0.66	21; 21	0.166	Tikkanen et al. 1994
12	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	No	Yes	Yes	Yes	S	C	0.252	0	$X \pm SE$	72.12±6.62; 65.15±4.61	7; 7	-0.432	Tikkanen et al. 1994
12	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	No	Yes	Yes	Yes	S	C	0.252	20	$X \pm SE$	3.90±3.23; 4.42±2.10	14; 14	0.049	Tikkanen et al. 1994
12	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	No	Yes	Yes	Yes	S	C	0.252	120	$X \pm SE$	73.05±5.97; 59.93±2.54	7; 7	-1.012	Tikkanen et al. 1994
12	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	No	Yes	Yes	Yes	S	C	0.252	240	$X \pm SE$	76.87±5.73; 67.30±4.32	7; 7	-0.668	Tikkanen et al. 1994
12	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	No	Yes	Yes	Yes	S	C	0.252	360	$X \pm SE$	72.83±5.62; 66.69±3.19	7; 7	-0.476	Tikkanen et al. 1994
12	<i>B. rhodani</i>	E	G	<i>P. phoxinus</i>	No	Yes	Yes	Yes	S	C	0.252	1020	$X \pm SE$	52.66±8.57; 47.75±5.14	7; 7	-0.245	Tikkanen et al. 1994
13	<i>P. acuta</i>	G	G	<i>L. gibbosus</i>	Yes	No	Yes	No	G	S	0.005	720	$X \pm SE$	0.35±0.03; 0.59±0.05	4; 4	2.324	Turner & Montgomery 2003
13	<i>P. acuta</i>	G	G	<i>L. gibbosus</i>	Yes	No	Yes	No	G	S	0.005	1440	$X \pm SE$	0.35±0.03; 0.53±0.05	4; 4	1.882	Turner & Montgomery 2003
13	<i>P. acuta</i>	G	G	<i>L. gibbosus</i>	Yes	No	Yes	No	G	S	0.005	2880	$X \pm SE$	0.35±0.03; 0.48±0.04	4; 4	1.450	Turner & Montgomery 2003
13	<i>P. acuta</i>	G	G	<i>L. gibbosus</i>	Yes	No	Yes	No	G	S	0.005	5760	$X \pm SE$	0.35±0.03; 0.42±0.04	4; 4	0.749	Turner & Montgomery 2003
14	<i>P. gyrina</i>	G	G	<i>L. gibbosus</i>	Yes	Yes	Yes	No	S	D	0.033	12960	$X \pm SE$	7.65±1.56; 3.86±1.07	64; 64	-0.352	Turner et al. 1999



14 *P. gyryina* G G *L. gibbosus* Yes Yes Yes No S 0.033 12.960 X±SE 22.20±4.21; 70.22±6.44 64; 64 1.096 Turner et al. 1999  
 15 *P. gyryina* G G *L. gibbosus* Yes Yes Yes No S 0.033 10.080 X±SE 15.52±1.52; 13.62±1.73 8; 8 -0.391 Turner et al. 2000

Invertebrate (invert.) type: Amphipoda (A), Diptera (Di), Ephemeroptera (E), Gastropoda (G), Plecoptera (P); invertebrate functional feeding group (FFG): carnivore (C), detritivore (D), grazer (G), omnivore (O); water type: artificial (A), dechlorinated (D), ground (G), stream (S), tap (T); cue addition: constant (C), daily (D), single (S).

**Table A4**  
Invertebrate activity effect size contrast analysis results

Variable	Variable level	Contrast	SE	t	P(z)
Invertebrate type	<b>Model 1</b>				
	Amphipoda (intercept)	0.80	0.19	4.11	<0.0001
	Ephemeroptera	-0.18	0.24	0.74	0.458
	Odonata	-0.55	0.34	1.63	0.103
Prey FFG	<b>Model 2</b>				
	Ephemeroptera (intercept)	0.63	0.14	4.53	<0.0001
	Odonata	-0.37	0.31	1.21	0.227
	<b>Model 1</b>				
Fish in tank	Grazer (intercept)	0.72	0.17	4.28	<0.0001
	Omnivore	0.07	0.25	0.28	0.780
	Carnivore	-0.13	0.28	0.47	0.640
	<b>Model 2</b>				
Fish fed invertebrates	Omnivore (intercept)	0.79	0.18	4.27	<0.0001
	Carnivore	-0.20	0.23	0.89	0.373
	Yes (intercept)	0.32	0.18	1.72	0.085
	<b>No</b>	<b>0.45</b>	0.21	<b>2.12</b>	<b>0.034</b>
Fish starved	Yes (intercept)	0.75	0.15	4.99	<0.0001
	No	-0.24	0.19	-1.27	0.205
Water type	Yes (intercept)	0.56	0.24	2.33	0.020
	No	0.08	0.26	0.30	0.763
	<b>Model 1</b>				
	Dechlorinated (intercept)	0.74	0.22	3.40	<0.0001
	Ground	0.37	0.48	0.77	0.439
	Stream	-0.15	0.33	-0.45	0.652
	Tap	0.25	0.56	0.45	0.652
	<b>Model 2</b>				
	Ground (intercept)	1.12	0.43	2.60	0.009
	Stream	-0.52	0.50	-1.05	0.292
	Tap	-0.12	0.67	-0.18	0.859
	<b>Model 3</b>				
Stream (intercept)	0.59	0.25	2.41	0.016	
Tap	0.40	0.58	0.70	0.484	
Cue addition	Single (intercept)	0.804	0.18	4.53	<0.0001
	Constant	-0.14	0.24	-0.60	0.548

Statistically significant effect sizes ( $\alpha = 0.05$ ) are in bold.

**Table A5**  
Invertebrate refuge use effect size contrast analysis results

Variable	Variable level	Contrast	SE	t	P(z)
<b>Invertebrate type</b>	Ephemeroptera (intercept)	0.29	0.13	2.26	0.024
	<b>Gastropoda</b>	0.36	0.18	2.02	<b>0.004</b>
Familiar fish	Yes (intercept)	0.75	0.21	3.57	0.0004
	No	0.10	0.31	0.32	0.747
Fish in tank	Yes (intercept)	0.95	0.24	3.98	<0.0001
	No	-0.24	0.35	-0.69	0.488
Fish starved	Yes (intercept)	0.62	0.17	3.57	0.0004
	No	-0.07	0.21	-0.35	0.730
Cue addition	Constant (intercept)	0.96	0.41	2.35	0.019
	Single	-0.70	0.48	-0.15	0.880

Statistically significant effect sizes ( $\alpha = 0.05$ ) are in bold.