Predator cue studies reveal strong trait-mediated effects in communities despite variation in experimental designs

Paterson, R. A., Pritchard, D. W., Dick, J. T. A., Alexander, M., Hatcher, M. J., & Dunn, A. M. (2013). Predator cue studies reveal strong trait-mediated effects in communities despite variation in experimental designs. *Animal Behaviour, 86*(6), 1301-1313. https://doi.org/10.1016/j.anbehav.2013.09.036

Published in:
*Animal Behaviour*

Document Version:
Publisher's PDF, also known as Version of record

Queen's University Belfast - Research Portal:
Link to publication record in Queen's University Belfast Research Portal

Publisher rights
Copyright 2013 The Authors. Published on behalf of The Association for the Study of Animal Behaviour by Elsevier Ltd. Open access under CC BY license https://creativecommons.org/licenses/by/3.0/.

General rights
Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy
The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.
Predator cue studies reveal strong trait-mediated effects in communities despite variation in experimental designs

Rachel A. Paterson, Daniel W. Pritchard, Jaimie T. A. Dick, Mhairi E. Alexander, Melanie J. Hatcher, Alison M. Dunn

School of Biological Sciences, Queen’s University Belfast, U.K.
School of Planning, Architecture and Civil Engineering, Queen’s University Belfast, U.K.
Centre for Invasion Biology, Stellenbosch University, South Africa
School of Biological Sciences, University of Bristol, U.K.
School of Biology, University of Leeds, U.K.

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 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.

© 2013 The Authors. Published on behalf of The Association for the Study of Animal Behaviour by Elsevier Ltd. All rights reserved.

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),
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 reveal 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; Miyasaki & 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 (cne OR kairomones OR odour) AND (invertebrate* OR macroinvertebrate* OR insect*)). We focused on chemical cue odours 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,
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 variability 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 $t$ 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 predator. 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 $z_{\text{fish in tank}}$ − effect $z_{\text{fish in tank No}}$]: $t$ 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 $z_{\text{Ephemeroptera}}$ − effect $z_{\text{Gastropoda}}$]: $t$ 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
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 invertebrate activity suggests that 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.

### Table 1

| Variable | Variable level | k | m | n | Effect size g (d) | z (p) | 95% CI for g (d) | ΔAICc | I² g |
|----------|----------------|---|---|---|------------------|------|-----------------|-------|------|
| Overall  |                | 66| 18| 3094| 0.72 (0.75)      | 6.05 (<0.0001) | 0.49 to 0.96 (0.50 to 0.99) | –   | 5.33 |
| Invert. type | Amphipoda | 17 | 5 | 500 | 0.80 (0.82)      | 4.11 (<0.0001) | 0.42 to 1.18 (0.41 to 1.23) | –1.81 | 1.95 |
|           | Dytiidae       | 2 | 34 |    |                  |      |                  |       |      |
|           | Ephemeroptera  | 24 | 8 | 782 | 0.63 (0.65)      | 4.53 (<0.0001) | 0.35 to 0.90 (0.36 to 0.93) |       |      |
|           | Gastropoda     | 3 | 336|    |                  |      |                  |       |      |
|           | Isopoda        | 5 | 60 |    |                  |      |                  |       |      |
| Invert. FFG. | Grazer    | 21 | 9 | 878 | 0.72 (0.75)      | 4.28 (<0.0001) | 0.39 to 1.05 (0.40 to 1.10) | 2.92  | 5.21 |
|           | Omnivore       | 25 | 7 | 680 | 0.79 (0.81)      | 4.27 (<0.0001) | 0.43 to 1.16 (0.42 to 1.20) |       |      |
|           | Carnivore      | 20 | 3 | 1536| 0.59 (0.62)      | 2.63 (0.008)  | 0.15 to 1.03 (0.16 to 1.08) |       |      |
| Familiar fish | Yes      | 41 | 15| 1350| 0.78 (0.81)      | 5.17 (<0.0001) | 0.49 to 0.98 (0.50 to 1.12) | –    | 6.94 |
|           | No             | 5  | 294|    |                  |      |                  |       |      |
| Fish in tank | 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| 0.77 (0.80)      | 7.10 (<0.001) | 0.56 to 0.99 (0.58 to 1.03) |       |      |
| Fish fed invert. | Yes | 17 | 9 | 894 | 0.75 (0.77)      | 4.99 (<0.001) | 0.46 to 1.04 (0.47 to 1.08) | 0.57  | 3.33 |
|           | No             | 33 | 8 | 2042| 0.51 (0.52)      | 3.27 (0.001)  | 0.21 to 0.82 (0.20 to 0.84) |       |      |
| Fish starved | Yes     | 12 | 5 | 280 | 0.56 (0.56)      | 2.33 (0.020)  | 0.09 to 1.02 (0.07 to 1.04) | 1.80  | 2.23 |
|           | No             | 38 | 11| 2656| 0.63 (0.65)      | 5.04 (<0.0001) | 0.39 to 0.88 (0.40 to 0.91) |       |      |
| Water type | Artificial    | 3 | 2 | 336|                  |      |                  | 5.10  | 8.86 |
|           | Dechlorinated | 34 | 7 | 1930| 0.74 (0.79)      | 3.40 (0.001)  | 0.31 to 1.17 (0.33 to 1.25) |       |      |
|           | Ground        | 10 | 2 | 288 | 1.12 (1.18)      | 2.60 (0.009)  | 0.27 to 1.96 (0.28 to 2.08) |       |      |
|           | Stream        | 11 | 5 | 470 | 0.59 (0.61)      | 2.41 (0.016)  | 0.11 to 1.08 (0.10 to 1.12) |       |      |
|           | Tap           | 8  | 7 | 70  | 1.00 (0.98)      | 1.92 (0.055)  | 0.02 to 2.02 (–0.16 to 2.11) |       |      |
| Cue addition | Single    | 26 | 8 | 1092| 0.80 (0.84)      | 4.53 (<0.0001) | 0.46 to 1.15 (0.47 to 1.20) | 1.50  | 5.45 |
|           | Constant      | 40 | 10| 2002| 0.66 (0.67)      | 3.95 (<0.001) | 0.33 to 0.98 (0.32 to 1.01) |       |      |
| Cue intensity | Yes      | 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 | Yes     | 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 (z < 0.05) are in bold.
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 P. 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 G. 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
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.

Acknowledgments

We thank Shinichi Nakagawa and Mathieu Lundy for statistical advice, and Robert Elwood and two anonymous referees for constructive comments. This manuscript was funded by NERC grant NE/G015201/1.
Rosenthal, R. 1979. The file drawer problem and tolerance for null results. *Psychological Bulletin*, 86, 636–641.

Rosenthal, R. 1994. Parametric measures of effect size. In: *The Handbook of Research Synthesis* (Ed. by H. Cooper & L. Hedges), pp. 231–244. New York: Sage.

Schmitz, O. J., Krivan, V. & Ovadia, O. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, 7, 153–163.

Scriingeour, G. J. & Culp, J. M. 1994. Foraging and evading predators: the effect of predator species on a behavioral trade-off by a lotic mayfly. *Oikos*, 69, 71–79.

Short, T. M. & Holomuzki, J. R. 1992. Indirect effects of fish on foraging behavior and leaf processing by the isopod *Lirius fontinalis*. *Freshwater Biology*, 27, 91–97.

Sih, A., Bolnick, D. I., Luttbeg, B., Orrock, J. L., Peacor, S. D., Pintor, L. M., Wudkevich, K., Wisenden, B. D., Chivers, D. P. & Smith, R. J. F. 2005. The funnel plot. In: *Publication Bias in Meta-analysis: Prevention, Assessment and Adjustments* (Ed. by H. R. Rothstein, A. J. Sutton & M. Borenstein), pp. 75–98. Chichester: Wiley.

Smrgeour, G. J. & Culp, J. M. 2006. DataThief III. http://datathief.org/.

Sommer, G., Fischer, W., Lehnert, G., Scharnagel, D. & Hillebrecht, A. 1979. The role of semiochemicals in benthic communities: responses to chemical stimuli from natural predators and injured prey. *Freshwater Biology*, 9, 51–76.

Sturdevant, A. M., Bernot, R. J. & Boes, C. M. 2003. Spatial and temporal scales of predator avoidance: experiments with fish and snails. *Ecology*, 84, 616–622.

Tiluk, Pen, M., Muotka, T. & Huhta, A. 1994. Predator detection and avoidance by lotic mayfly nymphs of different size. *Oecologia*, 99, 252–259.

Trussel, C. G., Ewanchuk, P. J. & Bertness, M. D. 2003. Trait-mediated effects in rocky intertidal food chains: predator risk cues alter prey feeding rates. *Ecology*, 84, 629–640.

Tummers, B. 2006. *DataThief III*. http://datathief.org/.

Turner, A. M. & Montgomery, S. L. 2003. Spatial and temporal scales of predator avoidance: experiments with fish and snails. *Ecology*, 84, 616–622.

Turner, A. M., Fetterolf, S. A. & Bernot, R. J. 1999. Predator identity and consumer behavior: differential effects of fish and crayfish on the habitat use of a freshwater snail. *Oecologia*, 118, 242–247.

Turner, A. M., Bernot, R. J. & Boes, C. M. 2000. Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snails. *Oikos*, 88, 148–158.

Viechtauer, W. 2010. Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48.

Vernon, J. D. & Peacock, D. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083–1100.

White, E. M., Wilson, J. C. & Clarke, A. R. 2006. Biotic indirect effects: a neglected concept in invasion biology. *Diversity and Distributions*, 12, 443–455.

Williams, D. D. & Moore, K. A. 1985. The role of semiochemicals in benthic community relationships of the lotic amphipod *Gammarus pseudolimnaeus*: a laboratory analysis. *Oikos*, 44, 280–286.

Wisenden, B. D. 2000. Qualitative assessment of predation risk in the aquatic environment. *Philosophical Transactions of the Royal Society B*, 355, 1205–1218.

Wisenden, B. D. & Millard, M. C. 2001. Aquatic flatworms use chemical cues from injured conspecifics to assess predation risk and to associate risk with novel cues. *Animal Behaviour*, 62, 761–766.

Wisenden, B. D., Chivers, D. P. & Smith, R. J. F. 1997. Learned recognition of predation risk by *Enallagma damselfly* larvae (*Odonata, Zygoptera*) on the basis of chemical cues. *Journal of Chemical Ecology*, 23, 137–151.

Wisenden, B. D., Rugg, M. L., Korp, L. N. & Feselker, L. C. 2009. Lab and field estimates of active time of chemical alarm cues of a cyprinid fish and an amphipod crustacean. *Behaviour*, 146, 1423–1442.

Wohlfehr, B., Mikolajewski, D. J., Joop, G. & Suhling, F. 2006. Are behavioural traits in prey sensitive to the risk imposed by predatory fish? *Freshwater Biology*, 51, 76–84.

Wudkevich, K., Wisenden, B. D., Chivers, D. P. & Smith, R. J. F. 1997. Reactions of *Gammarus lacustris* to chemical stimuli from natural predators and injured conspecifics. *Journal of Chemical Ecology*, 23, 1163–1173.

APPENDIX

### Table A1: Predictor variables used to investigate the influence of fish cue on invertebrate behaviour

| Variable level | Original study feature |
|----------------|------------------------|
| **Categorical variables** | |
| Invertebrate type | Amphipoda, Diptera, Odonata, Plecoptera, Gastropoda |
| Invertebrate feeding group | Shredder/grazer, Omnivore, Carnivore |
| Fish fed invertebrate | Yes, No |
| Fish starved | Yes, No |
| Fish in tank | Yes, No |
| **Water type** | Artificial |
| Tap water | Tap water with artificial additives to mimic stream water (see below) |
| Tap water | Tap water with chloride removed |
| Ground water | Water from subterranean source (e.g. spring or well) |
| Stream water body | Water from surface water body (e.g. stream, lake) |
| **Cue addition** | Single |
| Single cue addition | To experimental arena |
| Constant cue addition | To experimental arena |
| Daily | Cue added daily |
| **Continuous variables** | |
| Cue intensity | NA |
| Exposure time | NA |

Mean fish weight (g) per litre of water in experimental arena.
| Study ID | Invert. species | Invert. type | Invert. FG | Fish species | Familiar fish | Fish in tank | Fish fed invert. | Fish starved | Water type | Cue addition | Cue intensity | Exposure time | Original statistic | Control Treatment | Nc; Ni | g | Source |
|---------|----------------|-------------|-----------|-------------|--------------|-------------|----------------|--------------|-----------|--------------|--------------|---------------|------------------|-----------------|-------|---|--------|
| 1       | G. pulex       | A           | O         | S. trutta   | Yes          | No          | Yes            | No           | D         | S            | 0.024        | 10 X±SE        | -1.34±4.19; -24.77±5.60 | 8; 8              | -1.583 |       | Åbjörnsson et al. 2000 |
| 2       | G. pulex       | A           | O         | S. trutta   | Yes          | No          | No             | Yes          | D         | S            | 0.024        | 10 X±SE        | -1.34±4.19; -36.12±17.34 | 8; 7              | -1.012 |       | Åbjörnsson et al. 2000 |
| 3       | G. pulex       | A           | O         | S. trutta   | Yes          | No          | No             | No           | D         | S            | 0.024        | 10 X±SE        | -1.34±4.19; -31.15±9.11  | 8; 8              | -1.406 |       | Åbjörnsson et al. 2000 |
| 4       | G. pulex       | A           | O         | C. gobio    | Yes          | No          | No             | Yes          | D         | S            | 0.006        | 10 X±SE        | -1.34±4.19; -33.47±11.76 | 8; 7              | -1.323 |       | Åbjörnsson et al. 2000 |
| 5       | G. pulex       | A           | O         | C. gobio    | Yes          | No          | Yes            | No           | D         | S            | 0.006        | 10 X±SE        | -1.34±4.19; -21.07±8.93  | 8; 8              | -0.945 |       | Åbjörnsson et al. 2000 |
| 6       | G. pulex       | A           | O         | C. gobio    | Yes          | No          | Yes            | No           | D         | S            | 0.006        | 10 X±SE        | -1.34±4.19; -10.63±6.66  | 8; 8              | -0.559 |       | Åbjörnsson et al. 2000 |
| 7       | A. sulcatus    | Dy          | C         | P. fluviatilis | Yes        | No          | No             | Yes          | T         | C            | 0.135        | 10 X±SE        | 119.38±22.75; 60.97±11.14 | 9; 9              | 0.062  |       | Åbjörnsson et al. 1997 |
| 8       | A. sulcatus    | Dy          | C         | P. fluviatilis | Yes        | No          | No             | No           | T         | C            | 0.135        | 10 X±SE        | 73.06±20.14; 76.81±18.01 | 24; 24             | -1.510 |       | Åbjörnsson et al. 2000 |
| 9       | L. stagnalis   | G           | G         | T. tinca    | No          | No          | No             | No           | A         | S            | 0.870        | 120 X±SE       | 1.00±0.00; 0.55±0.09  | 72; 72             | -0.440 |       | Dalesman et al. 2006 |
| 10      | L. stagnalis   | G           | G         | T. tinca    | Yes         | No          | No             | No           | A         | S            | 0.870        | 120 X±SE       | 0.98±0.01; 0.76±0.08  | 72; 72             | 0.071  |       | Dalesman et al. 2007 |
| 11      | E. stammeri    | A           | O         | L. cephalus | NA          | No          | Yes            | No           | D         | C            | 2.588        | 4320 X±SE      | 20.00±0.00; 0.91±0.03  | 8; 8              | -0.492 |       | Deszul et al. 2003   |
| 12      | E. stammeri    | A           | O         | L. cephalus | NA          | No          | Yes            | No           | D         | C            | 2.588        | 4320 X±SE      | 0.67±0.09; 0.27±0.09  | 8; 8              | -0.633 |       | Deszul et al. 2003   |
| 13      | G. duebeni     | A           | O         | G. aculeatus | 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  |
| 14      | G. minus       | A           | O         | L. cyanellus | Yes         | No          | NA             | NA           | NA        | D            | 1.293        | 15 F          | 142.16          | 8; 8              | -1.311 |       | Holomuzki & Hoyle 1990 |
| 15      | G. minus       | A           | O         | L. cyanellus | Yes         | No          | NA             | NA           | D         | S            | 1.293        | 15 F          | 142.16          | 11; 11            | 0.140  |       | Holomuzki & Hoyle 1990 |
| 16      | B. rhodani     | E           | G         | P. phoxinus | 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 |
| 17      | B. rhodani     | E           | G         | P. phoxinus | 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 |
| 18      | B. rhodani     | E           | G         | P. phoxinus | 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 |
| 19      | B. rhodani     | E           | G         | P. phoxinus | 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 |
| 20      | Siphlonus spp. | E           | O         | S. fontinalis| Yes         | No          | Yes            | No           | G         | S            | 0.021        | 5 t           | -3.12            | 20; 20             | -0.72  |       | Huryn & Chivers 1999 |
| 21      | Siphlonus spp. | E           | O         | S. fontinalis| Yes         | No          | No             | No           | G         | S            | 0.021        | 5 t           | -1.40            | 20; 20             | -0.975 |       | Huryn & Chivers 1999 |
| 22      | Siphlonus spp. | E           | O         | S. fontinalis| Yes         | No          | No             | No           | G         | S            | 0.021        | 5 t           | -2.52            | 20; 20             | -0.827 |       | Huryn & Chivers 1999 |
| 23      | Siphlonus spp. | E           | O         | S. fontinalis| Yes         | No          | No             | No           | G         | S            | 0.021        | 5 t           | -0.67            | 20; 20             | -0.534 |       | Huryn & Chivers 1999 |
| 24      | Siphlonus spp. | E           | O         | S. fontinalis| Yes         | No          | No             | No           | G         | S            | 0.021        | 5 t           | -1.95            | 20; 20             | -0.206 |       | Huryn & Chivers 1999 |
| 25      | S. bicaudatus  | E           | G         | O. clarkii pleuriticus | 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)
| Study ID | Invert. type | Invert. species | 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       | E           | G              | S. fontinalis | Yes           | No           | No              | No          | S         | C           | 4.094        | 1080         | 14.98±1.64; 8.69±1.05 | 10; 10           | -1.381    |    |        |
| 10       | E           | G              | C. auratus   | No            | No           | No              | No          | S         | C           | 4.466        | 1080         | 14.58±1.64; 12.26±1.64 | 10; 10           | -0.501    |    |        |
| 11       | E           | G              | S. fontinalis| Yes           | No           | Yes             | No          | S         | C           | 0.008        | 2880         | 23.26±1.53; 11.56±1.52 | 38; 38           | -1.232    |    |        |
| 11       | E           | G              | S. fontinalis| No            | No           | Yes             | No          | S         | C           | 0.008        | 2880         | 5.23±0.86; 5.99±1.41 | 38; 38           | 0.105     |    |        |
| 12       | E           | G              | O. masou     | Yes           | No           | No              | Yes         | G         | C           | 0.032        | 1440         | 20.79±1.83; 35.76±4.73 | 6; 6             | 1.573     |    |        |
| 12       | E           | G              | C. nozawae   | Yes           | No           | Yes             | No          | G         | C           | 0.031        | 1440         | 20.04±3.51; 76.15±6.57 | 6; 6             | 4.016     |    |        |
| 12       | E           | G              | C. nozawae   | Yes           | No           | Yes             | No          | G         | C           | 0.031        | 1440         | 20.04±3.51; 77.02±5.80 | 6; 6             | 4.477     |    |        |
| 12       | E           | G              | O. masou     | Yes           | Yes          | Yes             | Yes         | G         | C           | 0.032        | 1440         | 20.79±1.83; 59.06±4.12 | 6; 6             | 4.521     |    |        |
| 13       | E           | G              | S. fontinalis| Yes           | No           | Yes             | No          | S         | C           | 0.019        | 8640         | 6.00±0.84; 2.22±0.34 | 36; 36           | -0.973    |    |        |
| 14       | E           | G              | R. cataractae| Yes           | No           | NA              | NA          | D         | S           | 3.888        | 1            | 3.00±1.30; 3.80±0.80  | 4; 4             | 0.322     |    |        |
| 14       | E           | G              | R. cataractae| Yes           | No           | NA              | NA          | D         | S           | 3.888        | 1            | 0.20±0.20; 0.50±0.50  | 4; 4             | 0.343     |    |        |
| 15       | E           | G              | E. aurivillii| Yes           | No           | NA              | NA          | D         | S           | 3.888        | 1            | 0.60±0.40; 4.20±0.70  | 4; 4             | 2.746     |    |        |
| 15       | E           | G              | L. megalotis | NA            | No           | NA              | NA          | D         | S           | NA           | 3            | 111.00±3.60; 57.40±7.80 | 6; 6             | -3.325    |    |        |
| 15       | E           | G              | S. trachanectes| Yes           | No           | NA              | NA          | D         | S           | NA           | 3            | 89.10±5.90; 57.40±2.30 | 6; 6             | -1.819    |    |        |
| 15       | E           | G              | L. fontinalis | Yes           | No           | NA              | NA          | D         | S           | NA           | 3            | 110.70±3.90; 88.00±5.80 | 6; 6             | -1.543    |    |        |
| 15       | E           | G              | L. fontinalis | Yes           | No           | NA              | NA          | D         | S           | NA           | 3            | 118.10±11.20; 83.60±11.80 | 6; 6             | -1.130    |    |        |
| 15       | E           | G              | L. cyanellus | Yes           | No           | NA              | NA          | D         | S           | NA           | 3            | 107.40±7.40; 70.00±10.10 | 6; 6             | -1.592    |    |        |
| 16       | E           | G              | P. phoxinus   | Yes           | Yes          | Yes             | Yes         | S         | C           | 0.252        | 30           | 2.22±0.52; 2.06±0.55  | 21; 21           | -0.066    |    |        |
| 17       | E           | G              | G. pseudolimnaeus| Yes           | Yes          | NA              | NA          | T         | C           | 2.326        | 5760         | 146.60±8.00; 27.10±7.40 | 3; 3             | -7.163    |    |        |
| 17       | E           | G              | G. pseudolimnaeus| Yes           | Yes          | NA              | NA          | T         | C           | 2.326        | 5760         | 217.80±13.60; 53.60±11.40 | 3; 3             | -6.044    |    |        |
| 17       | E           | G              | G. pseudolimnaeus| Yes           | Yes          | NA              | NA          | T         | C           | 2.326        | 5760         | 119.10±16.40; 10.90±6.30 | 3; 3             | -3.981    |    |        |
| 17       | E           | G              | G. pseudolimnaeus| Yes           | Yes          | NA              | NA          | T         | C           | 2.326        | 5760         | 160.90±17.20; 48.40±13.00 | 3; 3             | -3.408    |    |        |
| 17       | E           | G              | G. pseudolimnaeus| Yes           | Yes          | NA              | NA          | T         | C           | 2.326        | 5760         | 115.00±12.20; 50.00±7.60 | 3; 3             | -2.954    |    |        |
| 17       | E           | G              | G. pseudolimnaeus| Yes           | Yes          | NA              | NA          | T         | C           | 2.326        | 5760         | 198.90±25.80; 119.30±25.20 | 3; 3             | -1.442    |    |        |
| 18       | E           | G              | C. erythrophthalmus| NA            | Yes          | No              | No          | D         | C           | 2.942        | 150          | 4.66±0.43; 2.80±0.36  | 46; 48           | -0.680    |    |        |
| 18       | E           | G              | P. fluviatilis| NA            | Yes          | No              | No          | D         | C           | 2.086        | 150          | 4.66±0.43; 3.09±0.43  | 46; 48           | -0.517    |    |        |
| 18       | E           | G              | G. gobio     | NA            | Yes          | No              | No          | D         | C           | 0.810        | 150          | 4.66±0.43; 3.23±0.43  | 46; 49           | -0.478    |    |        |
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 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 | Source |
|----------|-----------------|--------------|-------------|--------------|---------------|--------------|---------------|-------------|-------------|--------------|--------------|--------------|-------------------|-------------------|--------|
| 1        | G. pulex        | AO           | C. gobio    | No           | Yes           | NA           | NA            | NA          | C           | 0.782        | 10           | X±SE         | 63.0±11.40; 15.20±1.90 | 11; 30 | −2.217 | Andersson et al. 2006 |
| 1        | G. pulex        | AO           | C. gobio    | 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        | G. pulex        | AO           | C. gobio    | 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        | G. pulex        | AO           | C. gobio    | 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        | P. integra      | GG           | L. gibbosus | Yes          | Yes           | Yes          | No            | S           | C           | 0.033        | 11,520       | X±SE         | 0.59±0.04; 0.48±0.02 | 230; 230 | −0.220 | Bernt & Turner 2001 |
| 2        | P. integra      | GG           | L. gibbosus | Yes          | Yes           | Yes          | No            | S           | C           | 0.033        | 11,520       | X±SE         | 0.65±0.03; 0.64±0.02 | 230; 230 | 1.152  | Bernt & Turner 2001 |
| 3        | P. canaliculata | GG           | A. testudine | NA           | No           | Yes          | 50% T, 50% S | S           | 0.004       | 30           | X±SE         | 1.43±2.22; 96.12±11.29 | 5; 5   | 2.716  | Carlson et al. 2004 |
| 4        | L. stagnalis    | GG           | T. tinca    | Yes          | No           | No           | No            | A           | S           | 0.870        | 120          | X±SE         | 0.01±0.004; 0.011±0.01 | 72; 72  | 0.052  | Dalesman et al. 2007 |
| 4        | L. stagnalis    | GG           | T. tinca    | 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        | C. riparius     | Di           | R. rutilus  | No           | No           | Yes          | Yes           | T           | C           | 0.0001       | 4320         | X±SD         | 6.05±0.57; 7.19±1.27 | 3; 3    | 0.928  | Hökler & Stief 2005 |
| 5        | C. riparius     | Di           | R. rutilus  | No           | No           | Yes          | Yes           | T           | C           | 0.0001       | 4320         | X±SD         | 13.32±1.38; 17.38±1.28 | 27; 27  | −0.579 | Hökler & Stief 2005 |

(continued on next page)
| 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 | N₁; N₂ | g | Source |
|----------|----------------|-------------|------------|--------------|--------------|-------------|----------------|-------------|------------|-------------|---------------|---------------|-----------------|------------------|------|---|-------|
| 5        | C. riparius    | Di          | D          | R. rutilus   | No           | No          | Yes            | Yes         | T          | C            | 0.0001        | 7200          | X±SE           | 10.27±1.88; 10.81±0.47; 17.38±1.28; 9.36±1.54 | 3; 3 | 0.352 | Hölker & Stief 2005 |
| 5        | C. riparius    | Di          | D          | R. rutilus   | No           | No          | Yes            | Yes         | T          | C            | 0.0004        | 120           | X±SE           | 6.05±0.57; 8.97±1.01 | 27; 27 | –1.077 | Hölker & Stief 2005 |
| 5        | C. riparius    | Di          | D          | R. rutilus   | No           | No          | Yes            | Yes         | T          | C            | 0.0004        | 4320          | X±SE           | 10.27±1.68; 12.19±0.74 | 3; 3 | 2.867 | Hölker & Stief 2005 |
| 5        | C. riparius    | Di          | D          | R. rutilus   | No           | No          | Yes            | Yes         | T          | C            | 0.0004        | 7200          | X±SE           | 6.05±0.57; 8.97±1.01 | 27; 27 | –1.077 | Hölker & Stief 2005 |
| 6        | G. pulex       | A            | O          | C. gobio     | Yes          | Yes         | Yes            | Yes         | D          | C            | 0.909         | 90            | X±SE           | 4.63±0.46; 0.63±0.32 | 8; 8  | –3.361 | Kaldonski et al. 2007 |
| 7        | B. bicaudatus  | E            | G          | S. fontinalis | Yes          | No          | Yes            | No          | S          | C            | 0.008         | 2880          | X±SE           | 28.42±2.27; 22.84±2.76 | 38; 38 | –0.355 | McIntosh & Peckarsky 1996 |
| 7        | B. bicaudatus  | E            | G          | S. fontinalis | Yes          | No          | Yes            | No          | S          | C            | 0.008         | 2880          | X±SE           | 16.80±1.93; 15.90±2.90 | 38; 38 | –0.059 | McIntosh & Peckarsky 1996 |
| 8        | M. signata     | P            | C          | S. fontinalis | NA           | No          | Yes            | No          | S          | C            | 0.019         | 8640          | X±SE           | 17.87±2.19; 0.095±0.05; 0.62±0.05 | 36; 36 | –0.111 | McIntosh & Peckarsky 1998 |
| 9        | G. pulex       | A            | O          | C. gobio     | Yes          | Yes         | Yes            | Yes         | D          | C            | 0.909         | 95            | X±SE           | 39.61±9.06; 18.09±5.76 | 8; 8  | –2.284 | Perrot-Minot et al. 2007 |
| 10       | P. heteromea   | E            | G          | R. cataractae | Yes          | No          | NA             | NA          | D          | S            | 3.888         | 1             | X±SE           | 9.60±1.00; 8.80±0.60 | 4; 4   | 1.100  | Scrimgeour & Culp 1994 |
| 10       | B. tricauatus  | E            | G          | R. cataractae | Yes          | No          | NA             | NA          | D          | S            | 3.888         | 1             | X±SE           | 6.80±0.70; 6.00±1.60 | 4; 4   | –0.282 | Scrimgeour & Culp 1994 |
| 10       | E. aurivillii  | E            | G          | R. cataractae | Yes          | No          | NA             | NA          | D          | S            | 3.888         | 1             | X±SE           | 5.40±0.40; 3.80±0.80 | 4; 4   | 1.100  | Scrimgeour & Culp 1994 |
| 11       | B. rhodani     | E            | G          | P. phoxinus  | Yes          | Yes         | Yes            | Yes         | S          | C            | 0.252         | 30            | X±SE           | 2.00±0.49; 1.69±0.41 | 21; 21 | –0.148 | Tikkanen et al. 1994 |
| 11       | B. rhodani     | E            | G          | P. phoxinus  | Yes          | Yes         | Yes            | Yes         | S          | C            | 0.252         | 30            | X±SE           | 2.23±0.47; 2.68±0.66 | 21; 21 | 0.166  | Tikkanen et al. 1994 |
| 11       | B. rhodani     | E            | G          | P. phoxinus  | No           | Yes          | Yes            | Yes         | S          | C            | 0.252         | 0             | X±SE           | 72.12±6.62; 65.15±4.61 | 7; 7   | –0.432 | Tikkanen et al. 1994 |
| 12       | B. rhodani     | E            | G          | P. phoxinus  | No           | Yes          | Yes            | Yes         | S          | C            | 0.252         | 0             | X±SE           | 4.42±2.10; 3.90±3.23 | 14; 14 | 0.049  | Tikkanen et al. 1994 |
| 12       | B. rhodani     | E            | G          | P. phoxinus  | No           | Yes          | Yes            | Yes         | S          | C            | 0.252         | 120           | X±SE           | 73.05±5.97; 59.93±2.54 | 7; 7   | –1.012 | Tikkanen et al. 1994 |
| 12       | B. rhodani     | E            | G          | P. phoxinus  | No           | Yes          | Yes            | Yes         | S          | C            | 0.252         | 240           | X±SE           | 76.87±5.73; 67.30±4.32 | 7; 7   | –0.668 | Tikkanen et al. 1994 |
| 12       | B. rhodani     | E            | G          | P. phoxinus  | No           | Yes          | Yes            | Yes         | S          | C            | 0.252         | 360           | X±SE           | 72.83±5.62; 66.69±3.19 | 7; 7   | –0.476 | Tikkanen et al. 1994 |
| 12       | B. rhodani     | E            | G          | P. phoxinus  | No           | Yes          | Yes            | Yes         | S          | C            | 0.252         | 1020          | X±SE           | 52.66±8.57; 47.75±5.14 | 7; 7   | –0.245 | Tikkanen et al. 1994 |
| 13       | P. acuta       | G            | G          | L. gibbosus  | Yes          | No          | Yes            | No          | G          | S            | 0.005         | 720           | X±SE           | 0.35±0.03; 0.59±0.05 | 4; 4   | 2.324  | Turner & Montgomery 2003 |
| 13       | P. acuta       | G            | G          | L. gibbosus  | Yes          | No          | Yes            | No          | G          | S            | 0.005         | 1440          | X±SE           | 0.35±0.03; 0.53±0.05 | 4; 4   | 1.882  | Turner & Montgomery 2003 |
| 13       | P. acuta       | G            | G          | L. gibbosus  | Yes          | No          | Yes            | No          | G          | S            | 0.005         | 2880          | X±SE           | 0.35±0.03; 0.48±0.04 | 4; 4   | 1.450  | Turner & Montgomery 2003 |
| 13       | P. acuta       | G            | G          | L. gibbosus  | Yes          | No          | Yes            | No          | G          | S            | 0.005         | 5760          | X±SE           | 0.35±0.03; 0.42±0.04 | 4; 4   | 0.749  | Turner & Montgomery 2003 |
| 14       | P. gyrina      | G            | G          | L. gibbosus  | Yes          | Yes         | Yes            | Yes         | No         | D            | 0.033         | 12960         | X±SE           | 7.65±1.56; 3.86±1.07 | 64; 64 | –0.352 | Turner et al. 1999 |
Invertebrate activity effect size contrast analysis results

| Variable          | Variable level | Contrast | SE  | t   | P(z)   |
|-------------------|----------------|----------|-----|-----|--------|
| Invertebrate type | Model 1        | 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    |
|                   | Model 2        | Ephemeroptera (intercept) | 0.63 | 0.14 | 4.53     | <0.0001 |
|                   |                | Odonata      | -0.37 | 0.31 | 1.21     | 0.227    |
| Prey FFG          | Model 1        | 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    |
| Fish in tank      | Model 1        | Yes (intercept) | 0.32  | 0.18 | 1.72     | 0.085    |
|                   |                | No           | 0.45  | 0.21 | 2.12     | 0.034    |
|                   | Model 2        | Yes (intercept) | 0.75  | 0.15 | 4.99     | <0.0001 |
|                   |                | No           | -0.24 | 0.19 | -1.27    | 0.205    |
|                   | Fish starved   | Yes (intercept) | 0.56  | 0.24 | 2.33     | 0.020    |
|                   |                | No           | 0.08  | 0.26 | 0.30     | 0.763    |
| Water type        | Model 1        | 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    |
|                   | Model 2        | 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    |
|                   | Model 3        | 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 (α = 0.05) are in bold.

Invertebrate refuge use effect size contrast analysis results

| Variable          | Variable level | Contrast | SE  | t   | P(z)   |
|-------------------|----------------|----------|-----|-----|--------|
| Invertebrate type | Ephemeropota (intercept) | 0.29  | 0.13 | 2.26 | 0.024  |
|                   | Gastropoda     | 0.36  | 0.18 | 2.02 | 0.004  |
| 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 (α = 0.05) are in bold.