

A meta-analysis of non-consumptive predator effects in arthropods: the influence of organismal and environmental characteristics

Amanda L. Buchanan, Sara L. Hermann, Margaret Lund and Zsófia Szendrei

A. L. Buchanan (<http://orcid.org/0000-0001-5096-5917>), S. L. Hermann (<http://orcid.org/0000-0003-2570-9027>), M. Lund (<http://orcid.org/0000-0002-3499-2357>), Z. Szendrei (<http://orcid.org/0000-0001-6893-2056>) (szendrei@msu.edu), Dept of Entomology, Michigan State University, 1129 Farm Lane, East Lansing, MI 48824, USA. SLH and ZS also at: Program in Ecology, Evolutionary Biology and Behavior, Michigan State Univ., East Lansing, MI, USA.

Non-consumptive effects (NCEs) – changes in prey behavior or physiology in response to predator threat – are common and can be as strong as consumptive effects. However, our knowledge of NCEs in arthropod systems is lacking. Factors related to study organism and environment have the potential to influence the occurrence and magnitude of NCEs in arthropod systems. While factors such as coevolutionary history of natural enemies and their prey, predator cue, predator or prey feeding mode, and refuge availability have been theoretically and empirically examined, no trends have been proposed for arthropods. We compiled 62 studies, yielding 128 predator–prey interactions, which explicitly examined NCEs in experiments where arthropods were identified to species, using a previously published database of papers from 1990 to 2005 and a new database of papers published from 2006 to 2015. Using these data, we conducted a meta-analysis to explore the influence of organismal and environmental characteristics on the magnitude of predator NCEs. Our analysis addressed the following three questions. 1) Does predator–prey coevolution give rise to stronger NCEs than when predator and prey species did not coevolve? 2) What influence does habitat type and refuge availability have on NCEs? 3) How do predator characteristics (cue type, hunting mode and life stage) and prey characteristics (mobility, life stage, specialization, gregariousness and feeding mode) influence NCEs? We found that while NCEs were similar across most measured characteristics, NCEs on prey activity were significantly stronger when predator and prey shared an evolutionary history. Our results support growing evidence that NCEs have a negative effect on prey traits and that behavioral NCEs are stronger than physiological ones. Additional studies are needed to be confident in any emerging patterns, therefore we identify key gaps in the literature on NCEs in arthropod systems and discuss ideas for moving forward.

Synthesis Non-consumptive effects of predators on prey can be influenced by characteristics of the organisms and environment. We used meta-analyses to synthesize patterns of arthropod non-consumptive effects based on 11 potentially important characteristics of the species and study environment. Our goal was to better understand the factors causing prey behavioral or physiological responses to predation risk. Our results clarify the relationship between behavior and physiology, suggesting that behavioral responses may act as a buffer against physiological costs for prey. Similar responses across the 11 characteristics suggests that we can predict non-consumptive effects of predators on prey using the examined variables.

Predator consumption of prey can alter community dynamics, but prey are not defenseless and can respond to the threat of attack (Lima 1998a, Sih and McCarthy 2002, Peckarsky et al. 2008). The non-consumptive effects (NCEs) of a predator on its prey (also known as trait-mediated interactions (TMI) or non-lethal effects, Werner and Peacor 2003) can alter prey behavioral, physiological, or morphological traits resulting in changes to prey survival, emigration, host choice or fecundity (Peckarsky et al. 2008). NCEs can be as strong as consumptive effects, contributing to over 50% of the total predator effect on prey survival and performance (Preisser et al. 2005). Conditions such as predator–prey

evolutionary relationships (Heiling and Herberstein 2004), habitat quality and structure (Lee et al. 2014), predator characteristics (Ramirez et al. 2010), and prey characteristics (Thaler and Griffin 2008), can influence NCEs.

Non-consumptive effects arise from prey perceiving and evaluating risk, which changes as the threat of predation fluctuates over time and space (risk allocation hypothesis, Lima et al. 1999). Predator and prey characteristics or environmental context may contribute to the perception of risk and thus influence the overall magnitude of NCEs. For example, naïveté to a particular predator may invoke a perception of safety (Cox and Lima 2006, Sih et al. 2010),

such that predators might impose weaker NCEs on prey with which they did not coevolve (Table 1). Similarly, refuge availability and prey proximity to a refuge are also important for perceived safety, and can influence risk perception (Lima 1998b, Sih et al. 2010). Prey using refuges may be moving into predator-free but resource-poor environments, which can increase the magnitude of NCEs. A meta-analysis examining nearly 300 observations of predator–prey pairs in aquatic systems found that NCEs on prey activity, growth, and fecundity were stronger where refuges were available (Orrock et al. 2013); thus, NCEs are likely to be stronger when predators can be avoided (Table 1).

Factors perceived as risky can increase NCEs, for example strong chemical cues emitted by sit-and-wait or sit-and-pursue predators are perceived as riskier than those of active predators (Preisser et al. 2007). Similarly, NCEs are predicted to be stronger in aquatic relative to terrestrial systems because chemical cues are more readily dispersed in water (Preisser et al. 2005). Prey characteristics such as life stage may also influence NCEs (Ramirez et al. 2010); for example adult arthropods are often more mobile than juveniles, and chewing arthropods are often more mobile than sap-feeders, leading to varying levels of risk from predators (Gullan and Cranston 2010, Hagstrum and Subramanyam 2010). Chewing arthropods may also induce the release of plant volatiles which are attractive to predators during feeding (Turlings et al. 1998), placing them at greater risk than sap-feeders. Prey that specialize on plant hosts may be better defended due to defense compound sequestration, and prey that feed gregariously may be better defended than solitary feeders (Bowers 1990, Vulinec 1990), thus weakening NCEs (Table 1). Because mechanisms of predator detection have the potential to modulate the strength of NCEs, a greater understanding of how prey species perceive and react to predator cues could aid in predicting the outcome of species interactions as well as potential cascading effects.

Prey may respond to predation threat with immediate behavioral changes such as reduction in activity or feeding to become less conspicuous to predators (Bernays 1997, Hermann and Thaler 2014), or with physiological changes such as altered development or growth (Hawlena et al. 2012, Thaler et al. 2012). For example, *Manduca sexta* larvae alter behavior (feeding rate) and physiology (assimilation efficiency and glycogen levels) in response to predation risk. However, on plants with high levels of resistance to herbivory, *M. sexta*

only altered feeding rate (Thaler et al. 2012), illustrating a tradeoff between the ability to respond to risky situations and continued survival (Sih 1987). In conditions conducive to high levels of risk, NCEs are predicted to be stronger (Sih 1987, Stankowich and Blumstein 2005).

While there is ample evidence for the prevalence of NCEs in predator–prey interactions (Lima and Dill 1990, Peckarsky et al. 2008, Hermann and Landis 2017), our knowledge of NCEs across the most diverse group of animals – arthropods – is especially lacking. Insects and other arthropods (e.g. spiders, mites) persist across natural and managed landscapes and form important predator–prey relationships. Better understanding of arthropod predator–prey relationships offers the opportunity to understand the complexities involved in responding to risk. Our review and meta-analysis aims to determine how environmental and species characteristics contribute to NCEs (Table 1). Here, we build upon a database compiled by Preisser et al. (2005) by including studies published between 2006 and 2015 to observe patterns across arthropod predator–prey systems. In this analysis, we addressed the following questions: 1) does predator–prey coevolution give rise to stronger NCEs than when predator and prey species did not coevolve? 2) What influence does habitat type and refuge availability have on NCEs? 3) How do predator characteristics (cue type, hunting mode and life stage) and prey characteristics (mobility, life stage, specialization, gregariousness and feeding mode) influence NCEs?

Methods

Database construction

We compiled a database of papers describing NCEs of arthropod predators on arthropod prey (Supplementary material Appendix 1 Fig. A1). Observations from papers published between 1990 and 2005 were obtained from a previously compiled database (Preisser et al. 2005), which were filtered to include only studies that measured arthropod predator and prey NCEs. Papers published between 2006 and 2015 were found by Web of Science search conducted on 1 March 2016 (Supplementary material Appendix 1 Fig. A1). Simultaneous search terms were: ‘nonlethal predator’ or ‘nonconsumptive’ or ‘non-consumptive’ or ‘predator

Table 1. Predicted outcomes of arthropod non-consumptive effects (NCE) comparing the strength of different traits across study and organism characteristics.

Characteristics	Stronger NCE	Weaker NCE	Citations
Evolutionary history of predator–prey pair	coevolved	non-coevolved	Cox and Lima 2006, Sih et al. 2010
Habitat type	aquatic	terrestrial	Preisser et al. 2005
Refuge availability	refuge present	refuge absent	Sih 1987, Orrock et al. 2013
Predator cues	multiple cues	single cues	Lima and Steury 2005
Predator hunting mode	sit-and-pursue, sit-and-wait	active	Schmitz 2007, Preisser et al. 2007
Predator life stage	adult	juvenile	Stankowich and Blumstein 2005, Hill and Weissburg 2013
Prey mobility	active	sedentary	Gullan and Cranston 2010, Hagstrum and Subramanyam 2010
Prey life stage	adult	juvenile	Gullan and Cranston 2010, Hagstrum and Subramanyam 2010
Prey specialization	generalist	specialist	Bowers 1990
Prey habit	solitary	gregarious	Sih 1987, Vulinec 1990
Prey feeding mode	chewing	sap-feeding	Turlings et al. 1998

avoidance' or 'predator risk' or 'trait mediated' and 'insect' and 'predator'. Because we were only interested in arthropod predator–prey interactions, simultaneously excluded terms were 'mammal', 'amphibian', 'bird', 'fish', 'marine', 'aves', 'frog' and 'intraguild'. Research areas were limited to environmental sciences, ecology, entomology, forestry, evolutionary biology, or agriculture; document type was limited to research articles. The initial search returned 210 papers; examination of title and author excluded 12 duplicate and three ineligible records. The remaining 195 full-text articles were examined for the following criteria: 1) explicitly measured NCEs, 2) sufficient information to perform a meta-analysis (e.g. sample size and variance), 3) arthropods only, 4) species names provided in order to determine coevolutionary history, and 5) available in English. Non-consumptive effects were defined as those present when predator-absent treatments were compared to non-lethal predator or predator cue treatments. To limit any potential influence of consumptive effects, we excluded experiments where a lethal predator was used, even when the experiment focused on NCEs of the lethal predator. After excluding 168 articles based on these criteria, the 28 remaining papers were combined with 34 papers from the 1990–2005 database from Preisser et al. (2005) meeting the same criteria, for a total of 62 published papers (Supplementary material Appendix 1 Fig. A1). These yielded 148 individual predator–prey interactions, for which prey responses fell into one of eight categories: activity, feeding, growth or size, fecundity, developmental time, density, longevity, survival or mortality (Supplementary material Appendix 1 Table A1). Due to insufficient sample sizes we excluded density, longevity, and survival/mortality responses, for a total of 128 predator–prey interactions used in the meta-analysis.

Effect sizes for detrimental responses (development time and detrimental activity) were multiplied by -1 . Activity was categorized as beneficial or detrimental according to the description available in the paper, for example movement away from a host resource was categorized as detrimental, while feeding attempt was categorized as beneficial (Supplementary material Appendix 1 Table A1). For each observation, mean response value, standard deviation or error, and number of replications were recorded. Values were taken from the text, tables or figures (information extracted using Image J; Schneider et al. 2012). To minimize pseudoreplication, we used only one data point from each predator–prey pair within each response category from a single publication. Although the most rigorous avoidance of pseudoreplication would eliminate multiple data points from the same research group, author, or published paper, this was not feasible due to low sample size. Where multiple responses in a single study fell into a single response category, we used the average effect size and variance across that predator–prey pair. Where studies reported responses across multiple levels of variables such as defensive chemistry of a host resource or food availability for predators, we used responses corresponding to those variables most similar to levels found in nature (e.g. intermediate levels of defensive chemistry of the host resource).

To address our question about how coevolutionary history influences strength of NCEs, predator–prey pairs were determined to have shared evolutionary histories if the

native ranges of each species overlapped and unshared evolutionary histories if they were isolated, giving a conservative estimate of predator–prey naïveté (Martin 2014). Native ranges were determined from the original paper if available, or by searching online sources including the IUCN Red List of Threatened Species (IUCN 2016) and the Catalogue of Life (2016). In addition, we characterized studies by habitat type (aquatic or terrestrial), availability of prey refuge (refuge was defined as any area where prey could avoid predators, including for example the presence of a whole plant), study type (lab, field, or greenhouse), and predator cues (chemical, visual, chemical + visual, or predator presence). Studies using the previous presence of a predator were categorized as 'chemical'; those where predators were visible but chemical or tactile cues were not available (e.g. in a neighboring glass-walled tank) were categorized as 'visual'; those with predator artifacts (eggs or spider silk, $n = 2$) or caged predators with chemical cues were categorized as 'chemical + visual'; and those with impaired but uncaged predators (e.g. non-functioning mouthparts) were categorized as 'presence'. Predators were characterized by hunting mode (active, sit-and-wait or sit-and-pursue) and life stage (adult or juvenile). Prey were characterized by mobility (active or sedentary), life stage (adult or juvenile), specialization (generalist or specialist), habit (gregarious or solitary), and feeding mode (sap-feeding or chewing).

Analysis

An appropriate effect size metric is critical for meta-analyses (Osenberg et al. 1999); commonly used metrics such as Hedge's d and log response ratio (lnRR, Hedges et al. 1999), while inappropriate for questions about population dynamics, are useful for testing qualitative predictions about the nature of species interactions (Goldberg et al. 1999). We estimated NCE effect sizes using lnRR due to its ability to detect effects when the number of available studies is low (Lajeunesse and Forbes 2003), which gives the ratio of the effect of experimental treatment (i.e. predator risk) relative to the control treatment (i.e. no predator). We estimated mean lnRR then converted the final reported values to non-logarithmic RR. An RR of 1 indicates that there is no difference between experimental and control treatments; $RR < 1$ indicates that the experimental treatment decreases the response variable (e.g. growth) relative to the control treatment; and $RR > 1$ indicates that the experimental treatment increases the response variable relative to the control treatment. Analyses were conducted in MetaWin 2.1 (Rosenberg et al. 2000).

Using random mixed-effects models for categorical data, which do not assume that all studies share a common effect size (Nakagawa and Santos 2012), we analyzed the influence of specific categorical factors, added as random effects (coevolutionary history, habitat type, prey refuge, study type, predator cues, hunting mode, life stage, prey mobility, specialization, habit and feeding mode), on NCE effect size. In addition to our primary categorical comparisons, we conducted separate analyses on several subsets of data to investigate potential interactions between organismal characteristics: prey life stage within predator life stage, prey life stage and prey feeding type within predator hunting mode, predator hunting mode within prey life stage, predator

hunting mode within predator life stage, predator hunting mode within prey refuge, and predator chemical cues within evolutionary history. We report RR values, bootstrapped (999 iterations) 95% confidence intervals, between-group heterogeneity (Q_B), and p-values for χ^2 and randomization models (p_{χ^2} and p_{rand} , respectively) for each of these comparisons for groups with a sample size of ≥ 2 (Valentine et al. 2010). We evaluated publication bias for the entire dataset and for each response variable by estimating Rosenthal's fail-safe number ($\alpha = 0.05$; MetaWin), and also by conducting a trim and fill analysis (Duval and Tweedie 2000) using the 'trimfill' function in the 'metafor' package (Viechtbauer 2010, <www.r-project.org>).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.b3k81>> (Buchanan et al. 2017).

Results

Summary of database

The database contained predators from 22 families and prey from 23 families. The majority of predators came from Aeshnidae (28% of all predators), Perlodidae (11%), Salticidae (9%), Coccinellidae (8%), Pentatomidae (7%), Formicidae (6%), Notonectidae (6%), and Phytoseiidae (4%). The majority of prey came from Lestidae (19% of all

prey), Coenagrionidae (14%), Scytodidae (9%), Aphididae (6%), Baetidae (5%), Chrysomelidae (5%), Culicidae (5%), Acrididae (5%), Heptageniidae (5%), and Sphingidae (5%).

Rosenthal's fail-safe values for the entire dataset and for separate activity, feeding, and growth responses were each > 400 . Fecundity responses ($n = 10$) had a fail-safe value of 143, and development time ($n = 10$) had a fail-safe value of 0, indicating potential publication bias for these variables. According to the funnel plots and the trim and fill method, feeding response was the most asymmetrical, with 9 missing data points on one side (Supplementary material Appendix 1 Fig. A2A–F). Average effect size was $RR = 0.7$, ranging from 0 to 2.5 (Supplementary material Appendix 1 Fig. A3, Fig. A4A–E).

Overall, NCEs decreased prey activity, feeding, growth, and fecundity, and increased development time (Fig. 1). Response ratios were generally weaker (closer to 1) for growth and development responses compared to activity, feeding, or fecundity. Prey activity was reduced on average by 50%, feeding by 40%, fecundity by 30% and growth by 10% in the presence of NCEs compared to the control. Development time increased by 10% when NCEs were present.

Do NCEs differ with coevolutionary history of predator and prey?

Non-consumptive effects on prey activity were about 30% stronger when prey and predators had a shared evolutionary history compared to when they did not coevolve, ($Q_B = 4.5$, $p_{\chi^2} = 0.03$, $p_{rand} = 0.08$, Fig. 1A), although this result should

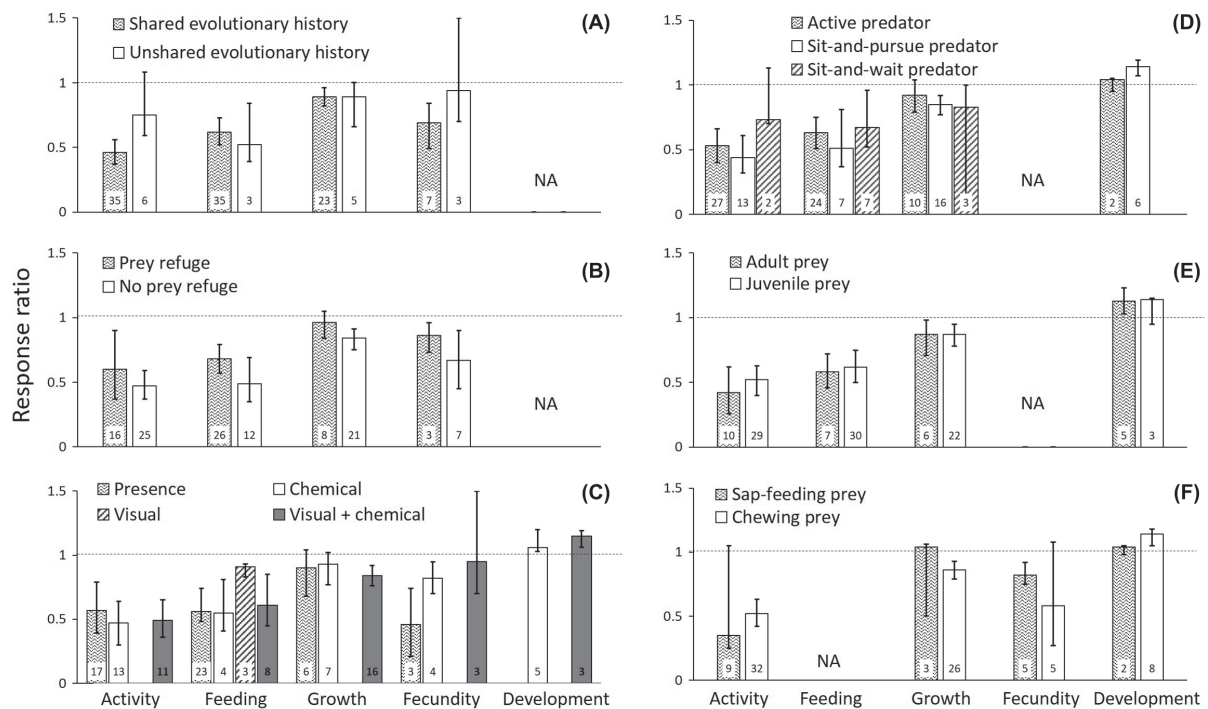


Figure 1. Response ratio (RR) of experimental treatments (i.e. predator risk) relative to control treatments (i.e. no predator) for prey responses (activity, feeding, growth, fecundity, and development time). Each set of bars represents a random-effects analysis comparing RRs across the following study or organism characteristics: (A) the presence of shared evolutionary history between the predator and prey, (B) the presence of prey refuge in the experiment, (C) the type of predator cue used in the experiment, (D) predator hunting mode, (E) prey life stage, and (F) prey feeding mode. Error bars are bootstrapped 95% confidence intervals. Numbers inside bars indicate sample size; "NA" indicates that < 2 studies were available for one or more groups in that comparison.

be treated with caution since there were only six cases where predators and prey did not coevolve. Other prey responses were not influenced by predator–prey evolutionary history ($Q_B < 0.2$, $p_{\chi^2} > 0.05$, $p_{\text{rand}} = 0.05$), but prey fecundity NCEs were present under shared (RR = 0.69, 0.49–0.84 CI) but not unshared (RR = 0.94, 0.7–1.5 CI) evolutionary history.

Do environmental factors influence NCEs?

Non-consumptive effects were slightly, but not significantly, stronger when refuge was absent ($Q_B < 3.1$, $p_{\chi^2} > 0.05$, $p_{\text{rand}} > 0.05$, Fig 1B). In addition, NCEs on prey growth were present when prey had no refuge available (RR = 0.84, 0.75–0.91 CI) but not when refuge was available (RR = 0.96, 0.84–1.04 CI). The presence of refuge had a greater impact on NCEs in aquatic habitats than in terrestrial habitats (Supplementary material Appendix 1 Table A2A–B). We found little evidence that the experimental setting influenced NCEs; there were no differences between NCE strength from terrestrial or aquatic environments ($Q_B < 2.6$, $p_{\chi^2} > 0.1$, $p_{\text{rand}} > 0.2$, Supplementary material Appendix 1 Table A2C) or between lab or field studies ($Q_B < 2.6$, $p_{\chi^2} > 0.1$, $p_{\text{rand}} > 0.1$, Supplementary material Appendix 1 Table A2D).

Do predator traits affect NCEs?

Type of predator cue influenced fecundity NCEs ($Q_B = 6.4$, $p_{\chi^2} = 0.04$, $p_{\text{rand}} = 0.09$, Fig. 1C), where the presence of an impaired predator caused the strongest NCEs and ‘visual + chemical’ cues did not lead to NCEs (RR = 0.95, 0.7–1.5 CI). Likewise, NCEs were not present for growth in response to ‘presence’ (RR = 0.9, 0.68–1.04 CI) or ‘chemical’ (RR = 0.93, 0.77–1.02, CI) cues. In studies using predator–prey pairs with shared evolutionary history, NCEs on fecundity were stronger for prey exposed to the presence of a non-lethal predator compared to a chemical cue ($Q_B = 4.6$, $p_{\chi^2} = 0.03$, $p_{\text{rand}} = 0.1$, Supplementary material Appendix 1 Table A2E).

There was no difference between NCEs for active, sit-and-pursue, and sit-and-wait predators ($Q_B < 2.0$, $p_{\chi^2} > 0.2$, $p_{\text{rand}} > 0.2$, Fig. 1D). Sit-and-wait predators did not influence prey activity (RR = 0.73, 0.70–1.13 CI) or growth (RR = 0.83, 0.05–1.0 CI) NCEs, nor did active predators influence prey growth (RR = 0.92, 0.79–1.04 CI) or development (RR = 1.04, 0.95–1.05 CI).

Prey activity NCEs were about 10% greater with adult relative to juvenile predators ($Q_B = 4.4$, $p_{\chi^2} = 0.04$, $p_{\text{rand}} = 0.07$; Supplementary material Appendix 1 Table A2F). Predator hunting mode did not influence NCEs in adult predators (Supplementary material Appendix 1 Table A2G), however juvenile sit-and-pursue predators had about 30 % greater NCEs on activity relative to active predators ($Q_B = 4.4$, $p_{\chi^2} = 0.04$, $p_{\text{rand}} = 0.09$; Supplementary material Appendix 1 Table A2H). Predator hunting mode did not influence juvenile prey’s NCEs ($Q_B < 1.9$, $p_{\chi^2} > 0.2$, $p_{\text{rand}} > 0.2$; Supplementary material Appendix 1 Table A2I), with or without prey refuge ($Q_B < 1.3$, $p_{\chi^2} > 0.5$, $p_{\text{rand}} > 0.5$; Supplementary material Appendix 1 Table A2J–K). For active predators, activity NCEs were 50% greater on

adult prey relative to juvenile prey, and on sap-feeding prey relative to chewing prey ($Q_B < 7.1$, $p_{\chi^2} < 0.05$, $p_{\text{rand}} < 0.08$, Supplementary material Appendix 1 Table A2L–M).

Do prey traits affect NCEs?

The strength of NCEs were similar for adult and juvenile prey when measuring their activity, feeding, growth and development ($Q_B < 1.5$, $p_{\chi^2} > 0.5$, $p_{\text{rand}} > 0.6$; Fig. 1E). Non-consumptive effects on development were present with adult (RR = 1.13, 1.03–1.23 CI) but not with juvenile (RR = 1.14, 0.95–1.15 CI) prey. In studies using only adult predators, NCEs on growth were present for adult (RR = 0.77, 0.57–0.86 CI) but not juvenile (RR = 0.97, 0.87–1.04 CI) prey ($Q_B = 2.5$, $p_{\chi^2} = 0.1$, $p_{\text{rand}} = 0.03$, Supplementary material Appendix 1 Table A2N). Conversely, in studies using only juvenile predators, NCEs on growth were present for juvenile (RR = 0.8, 0.74–0.93 CI) but not adult (RR = 1, 0.98–1.06 CI) prey (Supplementary material Appendix 1 Table A2O).

Non-consumptive effects did not differ between sap-feeding and chewing prey (Fig. 1F), however for some prey responses the presence of NCEs differed across feeding habit ($Q_B > 1.6$, $p_{\chi^2} > 0.08$, $p_{\text{rand}} > 0.1$; Fig. 1F). Non-consumptive effects on activity (RR = 0.35, 0.25–1.05 CI), growth (RR = 1.05, 0.50–1.06 CI) and development (RR = 1.04, 0.98–1.05 CI) were not present for sap-feeding prey. Non-consumptive effects did not differ across prey mobility, gregariousness or specialization (Supplementary material Appendix 1 Table A2P–R).

Discussion

Behavior and physiology

The results of this meta-analysis support the growing evidence in the literature that NCEs generally have a negative effect on prey traits, with a significant reduction for some prey responses relative to the control (Peckarsky et al. 2008, Reynolds and Bruno 2013). Non-consumptive effects had the largest impact on prey activity and feeding, and relatively smaller effect on growth and development. Behavioral responses encompassed a wide range of measured units possibly leading to significant variation in our data, nevertheless our results suggest that the impact of NCEs is greater on behavioral prey responses than on fitness or physiological traits (Preisser and Bolnick 2008). Although we have no direct evidence from our meta-analysis, it is possible that this effect is the result of prey adjusting their behavior to minimize the impact of NCEs on organ function (Lima and Dill 1990). Behavioral changes are often less energetically costly than physiological changes, and have shorter term reversible impacts that are metabolically preferred (Huey et al. 2003, O’Connor et al. 2006, Long et al. 2014). Therefore, when evaluating the relative impact of non-lethal effects on prey, it is important to consider the type of prey traits measured, since the magnitude of a behavioral response may not be directly proportional to a physiological one (O’Connor et al. 2006). For example, a ~50% decrease in activity relative to the control may

only cause a ~10% increase in development time, as seen on average in our meta-analysis. Therefore, behavioral defenses may be preferable not only because they can lead to the evasion of predation, but they can also buffer against physiological and ultimately fitness impacts. How behavior and physiology are connected should be the focus of future studies of NCEs (Hawlena and Schmitz 2010, Trussell et al. 2011, Zanette et al. 2014).

The ultimate test of the negative impacts of NCEs on prey is the measure of fitness or fecundity losses. Since we only had 10 cases to assess this variable, it is difficult to interpret our results, but we observed that NCEs caused a small reduction in prey fecundity. The paucity of published studies measuring fitness is likely because experiments often measure short-term effects that may not predict long-term outcomes (Okuyama and Bolker 2007). More attention should be focused on measuring long-term effects, such as prey fecundity, when evaluating NCEs.

Coevolution

Introduced predators are expected to have a greater lethal impact on prey than native ones (Palkovacs et al. 2009, Cortez and Weitz 2014). Prey failing to recognize novel predator cues suffer greater predation, thus while non-coevolved prey have lower NCEs, their mortality rate is likely higher due to direct feeding. We found some support for the naïve prey hypothesis (Cox and Lima 2006, Sih et al. 2010) in that prey that did not coevolve with predators had weaker NCEs for activity responses, relative to coevolved predator–prey pairs. Prey naïveté is likely more apparent in persistent isolation (Cox and Lima 2006) and most prey species included in our meta-analysis coevolved with predators from the same arthropod family or order as the invasive predators, therefore some cues related to predator risk may not have been particularly novel to them. Reduced responses to NCEs could also be attributed to a lack of prey experience with predators within the prey lifetime, which we did not measure in our meta-analysis. More studies are needed to resolve the role of prey experience versus coevolution in NCEs, especially with organisms that have not coevolved.

Environmental factors

The effects of predation are expected to be lower in refuge habitats where prey can reduce the risk of being noticed by predators (Lima 1998b). While refuge use can prevent consumption, the reduced quality of these habitats can increase NCEs (Sih 1987). Refuge use increased NCEs in aquatic systems in a previous meta-analysis (Orrock et al. 2013). Contrary to this, in our meta-analysis prey in refuge exhibited weaker NCEs (although not significantly) across all prey variables, in both aquatic and terrestrial studies (Supplementary material Appendix 1 Table A2A–B). The costs or benefits of refuge use is expected to depend on the quality of the resources available and competition experienced within refuge habitats. Thus it is possible that if prey are able to increase the metabolic conversion of food to energy in response to varying degrees of predation risk (McPeck et al. 2001) or if the quality or quantity of food is

similar in and out of the refuge (Kessler and Baldwin 2002), refuge use may not incur costs that increase NCEs.

Predator cue

Prey under the risk of predation need to evaluate cues from the environment that allow them to avoid being eaten (Lima and Dill 1990). General predation cues are less useful since these will easily trigger evasion responses; while specific cues might be more reliable, their detection may need to be learned or inherited (Sih et al. 2010). Relying exclusively on specialized cues can be disadvantageous because prey will not be able to respond to novel predators, thus it is likely that most arthropod prey use a mixture of cues, mediated by factors such as predator species, resource availability, prey physiological state, and predation risk (Lima and Steury 2005). Our results support this, showing that prey responded similarly to different predator cues and we found no evidence for additivity of cues (Fig. 1C); thus it is more likely that sensory systems complement each other and arthropods can compensate for the loss of a sensory modality (Lima and Steury 2005).

Arthropod characteristics

Life history traits, such as mobility and developmental stage, could play an important role in mediating NCEs. Larger and faster predators have been associated with larger NCEs (Stankowich and Blumstein 2005, Hill and Weissburg 2013). In addition, active predators' NCEs are expected to be weaker than sit-and-wait or sit-and-pursue predators' because cues from mobile predators are more dispersed across the environment (Preisser et al. 2007, Schmitz 2007). In contrast, a previous study on amphibians has found that active predators had larger NCEs due to higher encounter rates with prey, compared to sit-and-pursue predators (Davenport et al. 2014). Our results suggest sit-and-pursue type arthropod predators showed slightly stronger effects across responses (Fig. 1D). While we expected that predator body size plays a role in NCEs (Stankowich and Blumstein 2005), adult and juvenile predator NCEs were not significantly different in our analysis.

Several expectations for NCEs in response to prey characteristics were not met in our meta-analysis (Fig. 1). For example, adult and mobile prey were predicted to have stronger NCEs due to more fully developed or visually-oriented sensory modalities and an ability to respond with a greater degree of activity (Lakes-Harlan and Strauß 2006, Gullan and Cranston 2010, Hagstrum and Subramanyam 2010, Crespo 2011). Stronger NCEs were expected for solitary compared to gregarious prey due to prey aggregations conferring protection from predators (Sih 1987, Vulinec 1990), for generalists compared to specialists due to sequestration of toxic compounds by specialists to ward off enemies (Bowers 1990), and for chewing compared to sap-feeding prey due to stronger volatile cues released by chewing arthropods (Turlings et al. 1998). We did not find significant differences in NCEs across any of these comparisons, however it is difficult to assess the accuracy of our findings due to low replication.

Conclusion

While our meta-analysis suggests that NCEs are relatively consistent in arthropods across strength and direction of the different characteristics we examined, it is likely that they may be influenced by other attributes than the ones measured here, and that more studies are needed to be confident in any emerging patterns. For example, categorizing arthropod prey into slow- or fast-lifestyle groups (Sih 1987) could reveal prey traits that respond differently to predators than the ones we examined. From an evolutionary perspective, natural selection should favor behavioral over physiological prey responses, such that prey life history traits may not be important determinants for NCEs when compared to behavioral adaptations. Given our growing understanding about the role of chemical cues in mediating the responses of arthropod natural enemies to prey (Vet and Dicke 1992, Dicke and Grostal 2001, Crespo 2011, Hermann and Thaler 2014), more research should focus on how prey chemical conspicuousness influences NCEs. This is the first meta-analysis exclusively focused on NCEs in arthropod systems and in the future we should explore the relative magnitude of NCEs across arthropod taxa. It is clear that the arthropod NCE literature lacks studies on predator-prey pairs which did not co-evolve, sedentary, specialist, and gregarious prey and field based studies. We also identified a need for more studies measuring NCEs on fecundity and development, which would contribute to understanding fitness costs of prey responses to NCEs.

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Supplementary material (available online as Appendix oik-04384 at <www.oikosjournal.org/appendix/oik-04384>). Appendix 1.