

# Partitioning the non-consumptive effects of predators on prey with complex life histories

Jon M. Davenport · Blake R. Hossack · Winsor H. Lowe

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**Abstract** Non-consumptive effects (NCEs) of predators on prey can be as strong as consumptive effects (CEs) and may be driven by numerous mechanisms, including predator characteristics. Previous work has highlighted the importance of predator characteristics in predicting NCEs, but has not addressed how complex life histories of prey could mediate predator NCEs. We conducted a meta-analysis to compare the effects of predator gape limitation (gape limited or not) and hunting mode (active or sit-and-pursue) on the activity, larval period, and size at metamorphosis of larval aquatic amphibians and invertebrates. Larval prey tended to reduce their activity and require more time to reach metamorphosis in the presence of all predator functional groups, but the responses did not differ from zero. Prey metamorphosed at smaller size in response to non-gape-limited, active predators, but counter to expectations, prey metamorphosed larger when confronted by non-gape-limited, sit-and-pursue predators. These results indicate NCEs on larval prey life history can be strongly influenced by predator functional characteristics. More broadly, our results suggest that understanding predator NCEs would

benefit from greater consideration of how prey life history attributes mediate population and community-level outcomes.

**Keywords** Amphibian · Growth-predation risk · Invertebrate · Meta-analysis · Metamorphosis

## Introduction

Predators affect prey directly via consumptive effects (CEs) and indirectly via non-CEs (NCEs) that cause prey to alter their behavior, growth, or morphology (Sih et al. 1985; Abrams 1995). Recent work has revealed that NCEs of predators on prey can be as strong, and in some cases, exceed the CEs on prey (Werner and Peacor 2003; Preisser et al. 2005). Prey can assess predation risk and alter phenotypic traits to reduce mortality risk (Abrams 1995; Werner and Peacor 2003), but avoiding predation invokes trade-offs such as reduced foraging, growth, and fecundity (Werner and Gilliam 1984; Benard 2004; McPeck 2004). Likewise, prey with complex life histories (“complex lived”) can increase survival by reducing their exposure to predators via ontogenetic niche shifts [e.g., shorter larval period (Skelly and Werner 1990; McPeck et al. 2001)], but these niche shifts often impose costs that may carry over to subsequent life stages and ultimately reduce fitness (Benard and Fordyce 2003; Stamper et al. 2009).

Theory predicts that larvae of complex-lived organisms should metamorphose early from environments they perceive as risky, even if small size at metamorphosis is a trade-off (Werner 1986; Ludwig and Rowe 1990; Rowe and Ludwig 1991). Some empirical studies have supported this prediction (Skelly and Werner 1990; Benard 2004); however, recent literature reviews show that the NCEs

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J. M. Davenport (✉) · W. H. Lowe  
Division of Biological Sciences, University of Montana,  
Missoula, MT 59812, USA  
e-mail: jon.davenport@mso.umt.edu

B. R. Hossack  
Northern Rocky Mountain Science Center, Aldo Leopold  
Wilderness Research Institute, US Geological Survey, 790 E.  
Beckwith Avenue, Missoula, MT 59801, USA

of predators are inconsistent with theoretical predictions (Benard 2004; Relyea 2007). Specifically, larvae often have longer larval periods and achieve larger sizes at metamorphosis with predators than without predators (Benard 2004; Relyea 2007). Prey vary in their trait responses to predators, but some of these reported inconsistencies could result from differences in functional characteristics of predators. Predator characteristics have only recently been revealed as important for understanding the strength of NCEs (Preisser et al. 2007). Therefore, we sought to determine whether predator functional characteristics explain variation in NCEs, which may clarify observed deviations in life history responses among prey.

Predator gape limitation is one functional characteristic that could generate variation in the intensity of NCEs and trade-offs associated with prey growth and development. Many communities in nature are size structured and the relative strength of interactions within those communities is dependent on individual growth (Wilbur 1988; Polis 1991; Persson et al. 1996). The individual growth rates of predators and prey can lead to an “arms race” between predator and prey that lasts throughout development (Polis 1988; Wilbur 1988; Werner 1988). For other predators, however, limitations in the size of their mouth or feeding apparatus constrain the ability to consume prey of a certain size (Brooks and Dodson 1965; Wilson 1975). In these cases, if prey can perceive predation risk, they may escape predation through riskier foraging behavior that accelerates growth to a size refuge (Paine 1976; Wilbur 1988; Day et al. 2002; Urban 2007a). More generally, if gape limitation of a predator can influence the strength of CEs, then the strength of NCEs could also be influenced by predator gape (Higginson and Ruxton 2010).

A recent meta-analysis indicated that the strength of NCEs of predators varies based on predator hunting mode (Preisser et al. 2007). Prey confronted by sit-and-pursue predators had lower fecundity and lower growth rates than prey confronted by active predators, possibly because cues from sit-and-pursue predators suggest a greater risk of death than cues from active predator. The stronger effects of sit-and-pursue predators on prey were hypothesized to result from the potential for close proximity of these predators (Preisser et al. 2007). This work highlighted the importance of predator characteristics in predicting NCEs, but it did not address how complex life histories of prey can moderate the observed strength of predator NCEs.

We conducted a meta-analysis of published studies on amphibians and invertebrates with aquatic larvae to determine whether gape limitation and hunting mode of predators affect NCEs among prey. We identified studies that used cues from caged predators and reported larval period and size at metamorphosis, which are typically important predictors of potential fitness for species with complex life

histories (Semlitsch et al. 1988; Berven 1990; Nylin and Gotthard 1998; De Block and Stoks 2005a). In general, we expected larval prey to reduce activity in the presence of non-gape-limited predators and to increase activity in the presence of gape-limited predators. Higher activity levels are typically related to increased foraging (Relyea and Werner 1999), which can accelerate growth toward a size refuge from gape-limited predators (Higginson and Ruxton 2010). We expected prey to have greater reductions in activity with active predators relative to sit-and-pursue predators in order to lower encounter rates. This expectation is based on work showing that active predators generally have higher encounter rates with prey (Avgar et al. 2008; Sweeney et al. 2013). If these hypothesized differences in activity levels are general responses, then predator functional characteristics should strongly affect prey life history (larval period and size at metamorphosis).

## Materials and methods

### Literature survey

We limited our literature search to published studies that reported activity, larval period, or size at metamorphosis for complex-lived organisms. Amphibians and aquatic invertebrates are model organisms for understanding ontogenetic niche shifts (Werner 1986) and NCEs of predators on prey (Benard 2004; Relyea 2007) due to the wealth and legacy of relevant experimental research (Wilbur 1997; Werner 1998; Córdoba-Aguilar 2009). We only included studies that used experimental designs where predation risk (caged predators and their chemical cues) was manipulated with appropriate controls (no caged predators or cues). Because NCEs on fitness-related traits may not be evident during short-term experiments on larvae (Fauth 1990; McCauley et al. 2011), we limited our analysis to studies that carried experiments through metamorphosis. We used keyword searches in online databases (ISI Web of Knowledge, JSTOR and BIOSIS) and recent volumes of broad ecological journals (*Ecology*, *American Naturalist*, *Journal of Animal Ecology*, *Oecologia*, and *Oikos*). Keyword searches included the following terms alone or in combination: predation risk, nonlethal predation, size at metamorphosis, complex-life cycle, aquatic invertebrate, and amphibian. We also examined bibliographies of pertinent reviews for additional references (Benard 2004; Relyea 2007; Córdoba-Aguilar 2009; Higginson and Ruxton 2010).

### Data extraction

For each study, we recorded the sample size (replicates per treatment), mean treatment response, and variation in responses. If activity was measured over multiple time

periods, we used the mean across all time periods. For activity (defined as proportion active, proportion moving, or proportion feeding), we developed a 61-line data set generated from 16 publications that included 16 predator and 17 prey species (Appendix A). The 128-line data set for larval period (defined as days from the start of the experiment until metamorphosis) was generated from 38 publications and included data on 29 predator and 38 prey species (Appendix B). For analysis of size at metamorphosis, we developed a 146-line data set generated from 41 publications, including 30 predator and 40 prey species (Appendix C). “Metamorphosis” was defined by authors of amphibian studies as absorption of gills for salamanders and either absorption of the tail or emergence of forelimbs for frogs. “Metamorphosis” for invertebrates was defined by authors as emergence after final larval instar. In all three data sets, there was an approximate 2:1 bias toward studies of invertebrate predators vs. vertebrate predators (Appendices A–C). There was also a 3:1 bias towards invertebrate prey vs. vertebrate prey in the larval period and size at metamorphosis data sets (Appendices B, C).

In studies where multiple factors were manipulated (e.g., prey density, hydroperiod), we used the appropriate control for each predator treatment. For example, to assess the effects of *Gambusia holbrooki* on *Litoria aurea* at constant water levels, we constructed our response ratio with the control as *L. aurea* alone at a constant water level and the treatment as a caged *G. holbrooki* present with *L. aurea* at a constant water level (Lane and Mahony 2002). In addition, we only used treatments where either predator cues were manipulated or conspecific prey were fed to caged predators because prey responses can vary based on cues and predator diet (Schoeppner and Relyea 2009). Data were extracted directly from tables or text when available. For results presented only in graphs, we used ImageJ version 1.46r to estimate the effects (Schneider et al. 2012).

We classified each predator species into a functional group by hunting mode (active or sit-and-pursue) and gape limitation (non-gape limited or gape limited). This information was usually provided in the text or references therein (Preisser et al. 2007; Higginson and Ruxton 2010). For studies that did not provide this information, we searched published literature or contacted authors directly. Predators were considered gape limited if prey ever attained a size refuge during the study. We did not test for the independent effects of predator gape limitation and predator hunting mode on prey because functional groups were not mutually exclusive. Therefore, we combined the information on predator characteristics into three categories of predator functional groups: gape limited, active; non-gape limited, active; and gape limited, sit-and-pursue. We found only one study with a non-gape-limited, sit-and-pursue predator (Vonesh 2005), so we excluded that functional group.

## Data analysis

We used the log response ratio ( $L$ ) calculated across studies to measure relative responses of prey to the three predator functional groups. Log response ratios and their variances were calculated as the natural log of the mean experimental response divided by the mean control response [MetaWin version 2.1. (Rosenberg et al. 2000)]. The log response ratio is recommended for ecological studies and is independent of units used in the original studies (Hedges et al. 1999).

We used meta-regression to compare the NCEs of predator functional groups. To control for the non-independence of multiple effects from the same study (described above), we used hierarchical linear models with study source as a random effect and fixed the within-study error to equal the variance of each effect size [Proc Mixed in SAS 9.2 (Konstantopoulos and Hedges 2004)]. We also included prey family as a random effect to account for similarity in responses related to a shared evolutionary history. Because we suspected that the hydroperiod of the natal habitat (e.g., temporary pond or permanent pond) might affect responses to predators, we included it in all models used to test for the effect of predator functional groups on NCEs. However, most studies did not report the natal hydroperiod for experimental subjects. Therefore, we categorized prey by the hydroperiod of breeding habitats in which they typically achieve highest fitness (temporary, permanent, or no preference) based on published sources (Richardson 2001; Van Buskirk 2003; Stoks and McPeck 2006; Dodd 2013; <http://amphibiaweb.org/>). We used  $F$ -tests to assess statistical significance ( $\alpha = 0.05$ ) and least squares means to compare the effects of predator functional group on larval activity, larval period, and size at metamorphosis.

Life history theory and its predictions are primarily based on prey growth rates (Werner 1986; Ludwig and Rowe 1990; Rowe and Ludwig 1991), but the estimates of growth rates with associated variances were not available from the studies, which precluded their use in the meta-analysis (Hedges et al. 1999; Harrison 2011). However, larval activity is often assumed to be associated with larval growth rate and used as a surrogate (Skelly and Werner 1990; Anholt and Werner 1995; Lima 1998; Van Buskirk and Yurewicz 1998). To help interpret the potential fitness implications of changes in prey activity, we used the same mixed-effects model structure to measure the association between response ratios for activity and our calculations for prey growth rate. We calculated growth rates as final size at metamorphosis divided by total larval period. For these models, we limited the analysis to the subset of 14 studies (44 lines of data) that provided estimates of all three responses of larvae to predators.

Prior to the analysis, we evaluated the potential for publication bias in our data set by using Spearman

rank-correlation ( $r_s$ ) between the standardized effect size and sample size across studies (Begg and Mazumdar 1994; Rosenberg et al. 2000). We found no evidence of publication bias for larval activity ( $r_s = -0.064$ ,  $P = 0.471$ ), larval period ( $r_s = -0.22$ ,  $P = 0.089$ ), or size at metamorphosis ( $r_s = -0.099$ ,  $P = 0.238$ ) and thus used the entire data set for the analysis.

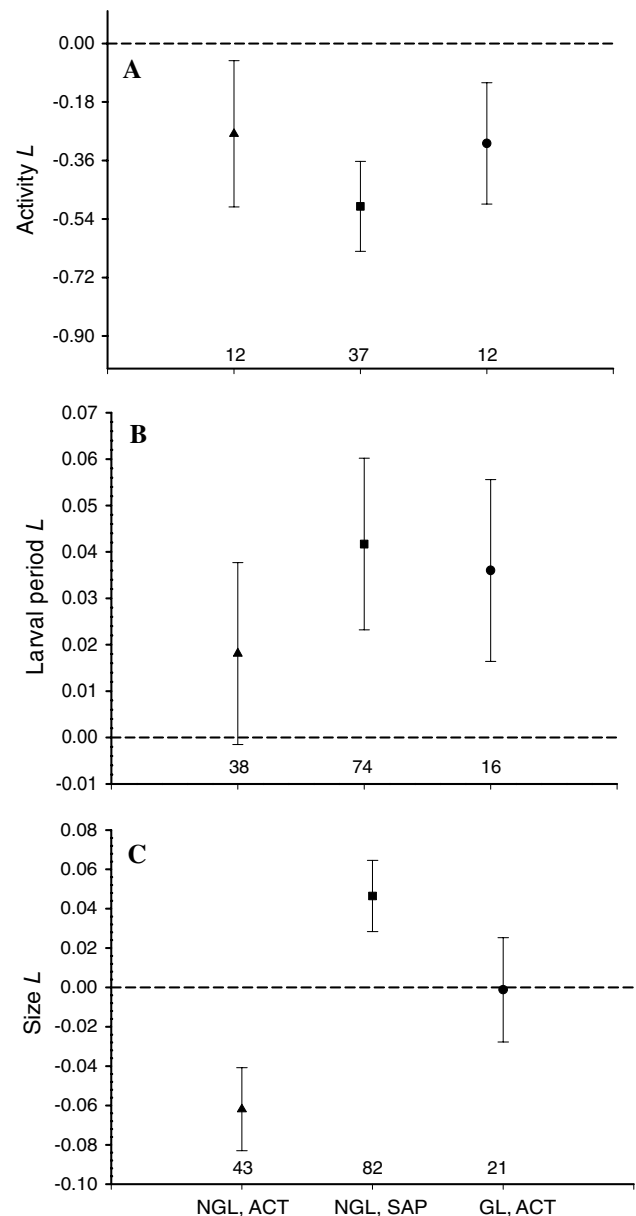
## Results

On average, larval prey reduced their activity and required more time to reach metamorphosis in the presence of all three predator functional groups, but neither response differed from zero (activity,  $F_{2,34.9} = 0.82$ ,  $P = 0.448$ ; larval period,  $F_{2,84} = 1.25$ ,  $P = 0.293$ ; Fig. 1a, b). Size at metamorphosis was affected by predator functional group ( $F_{2,67.9} = 8.30$ ,  $P < 0.001$ ; Fig. 1c). There was no difference in size at metamorphosis in response to gape-limited, active predators (mean = 0.001, 95 % CI =  $-0.052$  to  $0.054$ ), but prey metamorphosed at smaller size in response to non-gape-limited, active predators (mean =  $-0.062$ , 95 % CI =  $-0.105$  to  $-0.0194$ ). Counter to expectations, prey metamorphosed larger when confronted by non-gape-limited, sit-and-pursue predators (mean =  $0.046$ ,  $0.010$ – $0.083$ ).

The hydroperiod of breeding habitats affected how the length of larval period changed in response to predators from different functional groups ( $F_{2,84} = 4.01$ ,  $P = 0.022$ ). Prey from permanent habitats increased their larval period (mean =  $0.054$ , 95 % CI =  $0.011$ – $0.098$ ), while larval period of prey from temporary or mixed hydroperiods did not differ from zero. Habitat did not affect larval prey activity ( $F_{2,29.3} = 0.73$ ,  $P = 0.448$ ) or size at metamorphosis. Among the 14 studies that provided data to calculate growth rates, larval activity was not associated with growth rate [ $b = 0.007$  (SE =  $0.050$ ),  $F_{1,36.4} = 0.02$ ,  $P = 0.887$ ; Fig. 2].

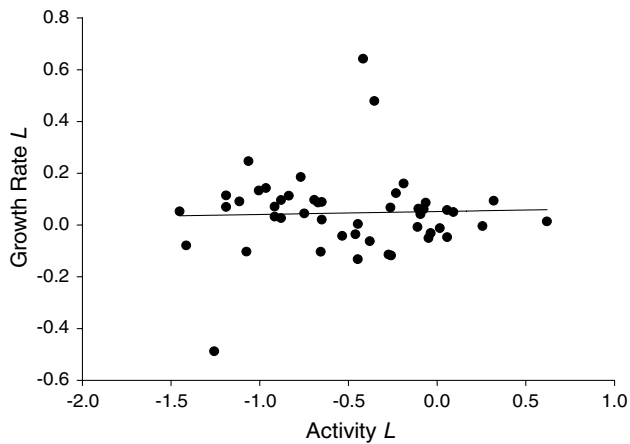
## Discussion

We found partial support for the effects of predator functional characteristics on complex-lived prey. Larval prey reduced activity and had longer larval periods in response to caged predators, but the responses were similar regardless of predator functional group. Larvae exposed to non-gape-limited, active predators tended to metamorphose at smaller size, suggesting that the NCE of these predators may reduce prey fitness. In contrast, larvae exposed to non-gape-limited, sit-and-pursue predators metamorphosed at a larger size, suggesting that these predators may indirectly increase prey fitness through NCEs.



**Fig. 1** Mean effect sizes (log response ratio;  $L$ ) of predator gape limitation and predator hunting mode on prey activity (a), larval period (b), and size at metamorphosis (c). The dashed line indicates no effect ( $0$ -value on the  $y$ -axis). Numbers at the bottom of the panels are the sample sizes for each predator functional group. Error bars are  $\pm 1$  SE. NGL, ACT Non-gape-limited active predator; NGL, SAP non-gape-limited sit-and-pursue predator; GL, ACT gape-limited active predator

We could not directly assess the independent effects of gape limitation on prey responses because nearly all gape-limited predators are active hunters. However, our results provide strong indirect evidence that NCEs of predator hunting mode are greater than that of gape limitation. Non-gape-limited, active predators produced the strongest responses by prey, with larvae metamorphosing



**Fig. 2** Within-study relationships between  $L$  of larval growth rates and activity rates. The solid line indicates the fitted relationship between the two variables

smaller compared to predator-free controls (Fig. 1c). Prey also tended to metamorphose at smaller sizes in response to gape-limited, active predators. In contrast, larvae metamorphosed larger compared to predator-free controls in response to non-gape-limited, active predators. Overall, these results suggest that, at least in combination with active hunting mode, gape limitation elicits a much weaker prey response than predator hunting mode. This result is unexpected given that the relative difference in size between predators and their prey can result in stronger CEs in predator–prey interactions (Brooks and Dodson 1965; Urban 2008).

There are several plausible explanations for the observed deviations from theory regarding size at metamorphosis (Werner 1986; Ludwig and Rowe 1990; Rowe and Ludwig 1991). First, prey may have developed a more elaborate suite of compensatory morphological defenses in response to one functional group of predators but not others [e.g., active vs. sit-and-pursue or gape limited vs. non-gape limited, respectively (Higginson and Ruxton 2010)]. Second, the trend for a smaller size at metamorphosis with non-gape-limited, active predators may be advantageous for prey to reduce detection and capture. Active predators tend to have higher encounter rates with prey than sit-and-pursue predators (Avgar et al. 2008) and smaller size is one strategy for reducing these rates (Lundvall et al. 1999). Third, differential responses of prey to predators based on sex can be important for invertebrate prey (Hechtel and Juliano 1997). For example, the magnitude and direction of mayfly (*Baetis bicaudatus*) growth to brook trout (*Salvelinus fontinalis*) cues are dependent on the sex of the prey (Pecarsky et al. 2001; Caudill and Pecarsky 2003). Unfortunately, for a large subset of our data (i.e., amphibians), the sex of prey cannot easily be determined at metamorphosis

and we thus cannot account for this effect. Fourth, deviations from theory may reflect population-specific responses of the prey, as opposed to species-level responses (Laurila et al. 2006a, b).

Although we found predator-induced effects on prey life history traits, mean differences for size at metamorphosis were small ( $\leq 4.8\%$ ; Fig. 1c). Interpreting the fitness implications of these effect sizes is difficult because while few studies carry experiments through metamorphosis, even fewer follow individuals or cohorts long enough to link larval performance with fitness correlates such as survival or fecundity (Earl and Semlitsch 2013). In wood frogs (*Lithobates sylvaticus*), a 5 % increase in size at metamorphosis resulted in an approximate 2 % (females) or 3 % (males) increase in length at first reproduction [data extracted from Fig. 7 in Berven (1990)]. Larger size at metamorphosis can confer size at maturity and thus fitness advantages (Semlitsch et al. 1988; Scott 1994). Whether larger size at metamorphosis in individuals exposed to non-gape-limited, sit-and-pursue predators translates into increased fitness depends upon relative risks and benefits of aquatic and terrestrial environments (Werner 1986; Ludwig and Rowe 1990; Rowe and Ludwig 1991).

In many organisms, the natal environment can play a large role in determining future fitness (Lindström 1999; Wilkin and Sheldon 2009). Numerous complex-lived prey breed in temporary wetlands, where even a small reduction in development time can be the difference between survival or death (Wilbur 1997; Richter-Boix et al. 2011). As a result, species or populations from temporary wetlands often have short larval periods and may be less responsive to predator cues (Wellborn et al. 1996; Wilbur 1997; De Block and Stoks 2005b). We did not find consistent effects of habitat type on any of the prey responses ( $P \geq 0.161$ ). We strongly suspect that the lack of significance is due more to the lack of information on natal environment in the literature rather than the lack of a true relationship. For most of our cases studies, authors did not provide the relevant information for an analysis, so we categorized prey according to the breeding habitat in which they tend to achieve peak potential fitness. However, many species can modify their life history strategies to maximize potential fitness in alternative environments. For example, *Rana arvalis* from different populations vary in their magnitude of induced morphological defenses and changes in larval period when exposed to a gape-limited, active predator (*Gasterosteus aculeatus*) (Laurila et al. 2006a). In addition, survival of larvae exposed to free-ranging invertebrate predators varies among *R. arvalis* populations (Laurila et al. 2006b). These population-specific responses may have prevented some mean responses from being detected in our meta-analyses. The natal environment of study organisms likely has profound effects on the outcome of

experiments and our understanding of NCEs. We encourage future studies to explore this relationship.

The theory developed for predicting time to, and size at, metamorphosis is largely based on prey growth rates (Werner 1986; Ludwig and Rowe 1990; Rowe and Ludwig 1991); however, researchers often substitute prey activity rate for growth rate. Indeed, past studies have pointed to a trade-off in prey growth that is mediated by behavior (Skelly and Werner 1990; Werner and Anholt 1993; Van Buskirk and Yurewicz 1998). Based on our calculation of growth rates from 14 studies that provided the required information, prey activity rate was not a good predictor of growth rate (Fig. 2). Therefore, our data support other recent researchers who have concluded that prey activity is a poor surrogate for predicting potential fitness of larval prey (McPeck 2004; Lind and Cresswell 2005; Stoks et al. 2005).

Our results show that NCEs of predators on prey life history traits cannot be generalized based on predator functional characteristics. The only significant effects we found were for size at metamorphosis, and these only partially supported theory that predicts prey should metamorphose at smaller size in response to predators (Werner 1986; Ludwig and Rowe 1990; Rowe and Ludwig 1991). Functional characteristics of predators are important for predator–prey interactions (Chalcraft and Resetarits 2003), but they provided little insight into variation in life history-related NCEs on complex-lived prey (Benard 2004; Relyea 2007). These same functional characteristics may still be important in mediating CEs of other prey taxa with complex life histories (Schmitz and Suttle 2001; Benard 2004; Urban 2007b). We recommend that future empirical studies should incorporate a diverse set of predators and prey from different environments to fully capture the fitness implications and community consequences of predator traits that may influence NCEs.

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