Predation risk between cannibalistic aeshnid dragonflies influences their functional response on a larval salamander prey

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Abstract

In size-structured populations of predators, the threat of cannibalism can influence behavior of prey that are attempting to avoid predation by larger conspecifics, including reducing their foraging rates. Such behavioral responses subsequently release basal prey of both cannibal and non-cannibal predators from predation risk. However, whether the non-consumptive effects of cannibalism on conspecific predators varies with basal heterospecific prey density is relatively unexplored. I conducted a laboratory study in plastic containers to test whether cannibalism risk influenced the functional response of dragonflies while foraging on three different densities of larval salamander prey. Dragonfly predators foraged with a Type II functional response, and when exposed to cannibalism cues, per capita feeding rates were lower at high prey densities. Salamander prey mortality rates declined with increasing prey densities, but the presence of cannibalism risk did not influence this pattern. Overall, this study shows that functional response curves of predators can vary in response to whether cannibalism risk is present in their environment across a small range of prey densities. Incorporating synergistic effects of multiple processes, such as non-consumptive risk factors and prey density, may help further elucidate the processes that structure both predator and prey population dynamics.

Introduction

Non-consumptive effects among predators play a critical role in regulating both predator and prey population dynamics, as well as their interactions (Sih, Englund & Wooster, 1998; Preisser, Bolnick & Benard, 2005; Schmitz, 2007; Davenport, Hossack & Lowe, 2014). A predator may limit foraging opportunities to reduce its own risk of being preyed upon, which could result in slowed individual growth or development rates. As a by-product of non-consumptive effects among predators, prey species benefit from increased survival (Vance-Chalcraft *et al.*, 2007). These non-consumptive processes have been shown to have equivalent or greater influence on prey populations as consumptive effects (Werner & Peacor, 2003; Preisser *et al.*, 2005; Preisser & Bolnick, 2008), especially in classic predator-prey studies that were previously thought to be driven by consumptive effects (Peckarsky *et al.*, 2008). Identifying and understanding the mechanisms behind non-consumptive effects among predators are therefore critical toward developing a greater understanding of predator–prey dynamics.

Many factors have been shown to influence non-consumptive effects among predators (Werner & Peacor, 2003; Preisser & Bolnick, 2008). In particular, the density of co-occurring con- or heterospecific predators that compete for the same prey can influence the per capita rate of prey consumption by an individual predator, that is its functional response (Holling, 1959; Skalski & Gilliam, 2001; Abrams, 2015). Such alterations to a predator's functional response in response to co-occurring individuals or species is often attributable to mutual interference or competitive interactions among predators that result in reduced attack rates from predators on prey (Kratina *et al.*, 2009; Schmidt *et al.*, 2014; Stier & White, 2014). Interference processes can take the form of physical interactions and/or chemical and visual cues that impact predator foraging. These latter types of interference form a typical non-consumptive effect, but whether they influence the functional response is less well developed. Such an interaction would be important, as changes to the functional response can influence predator and prey populations dynamics by inducing either equilibrium or stable limit cycles (May, 1975; Morin, 2011).

Within species, cannibalism represents a specialized type of predation that can have strong consumptive and non-consumptive effects on trophic structure and population cycles (Van Buskirk, 1992; Persson *et al.*, 2003; Rudolf, 2007; Wissinger *et al.*, 2010). Such interactions are often promoted when populations are size-structured, where larger individuals can

consume or alter behavior of smaller individuals (Rudolf, 2008b; Miller & Rudolf, 2011). The non-consumptive effects potential cannibals have on smaller conspecific individuals would have strong implications for functional response curves, but have not been evaluated for many cannibalistic systems (Crowley & Martin, 1989; Rudolf, 2008a; Long et al., 2012). Overall predation rates (i.e. attack rates) should be highly asymmetric under differing cannibalism risk scenarios: smaller individual predators may attempt to minimize exposure to cannibalism risk, and thus forage at lower rates, whereas larger individuals would not exhibit similar risk-averse behavior. Risk to foraging predators might be minimized at higher prey densities, as the likelihood of encountering and acquiring prey would be increased, offsetting the risk of consumption by a larger conspecific.

I tested the influence of cannibalism risk on the functional response of larval aeshnid dragonflies Anax feeding on larval ringed salamander Ambystoma annulatum prey. I expected that attack rates would decrease when dragonflies were in the presence of a larger cannibal (i.e. lower initial slope), and result in a lower asymptotic feeding rate. I also expected salamander prey mortality rates to be greater when the dragonfly predator foraging on them was not exposed to the threat of cannibalism.

Materials and methods

Study system

Larval dragonflies are a model system for testing non-consumptive predatory effects because of their well-studied behavioral interactions, voracious foraging abilities and size-structured populations (Wissinger, 1988; Johnson, 1991). Dragonfly larvae frequently respond to visual and chemical cues from con- and heterospecific predators with behavioral shifts such as reducing movement and foraging rates (Wissinger & McGrady, 1993; Crumrine, 2006; Ferris & Rudolf, 2007; Rudolf, 2007, 2012) and reduced survival (McCauley, Rowe & Fortin, 2011). In particular, larval dragonflies in the family Aeshnidae are voracious predators that cannibalize one another when sufficient size differences between individuals exist, as well as inducing strong consumptive and non-consumptive effects on a variety of prey species, including conspecifics (Caldwell, Thorp & Jervey, 1980; Crumrine, 2010; Kishida et al., 2011; Davenport & Chalcraft, 2013).

Both the dragonfly predator Anax and larval salamander prey A. annulatum used in this study co-occur in ponds in southern Missouri (Semlitsch et al., 2015). Ringed salamanders breed in the fall and larvae overwinter in ponds prior to undergoing metamorphosis in the spring (Semlitsch et al., 2014). Aeshnids begin breeding in late spring and complete their life cycle within several months during the summer/fall (Wissinger, 1988). Overwintering is also common in aeshnids (Wissinger, 1988), thus making semi-permanent or permanent water bodies necessary to complete each species' life cycle. Therefore, opportunities for predation from dragonflies on salamander prey are likely during the fall months when ringed salamander larvae appear in ponds but before aeshnid instars begin diapause, making this study a realistic test of potential non-consumptive effects between dragonflies on salamander prey.
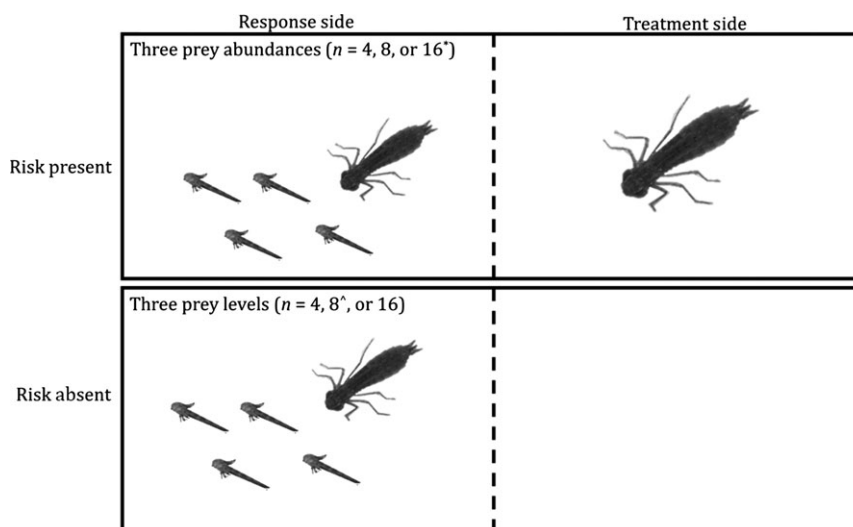
Experimental set-up

I collected larval dragonflies using dipnets from Baskett Wildlife Research Area near Ashland, MO, USA on 24 October. I transported dragonflies back to the greenhouse and kept them in individual plastic containers filled with water for 18 h to standardize hunger levels. I identified all dragonflies to species at the end of the experiment, and all predators were Anax junius, with the exception of one A. longipes (hereafter, I refer to all as Anax). I measured total length (TL) and head width of all larval dragonflies ($n = 36$) using digital calipers at the completion of the experiment.

I collected approximately 15 egg masses of ringed salamanders from Fort Leonard Wood, MO, USA on 28 September 2014, and brought them back to a greenhouse at the University of Missouri's Research Park prior to the start of the experiment. Eggs were combined in three large plastic containers until they hatched on approximately 3 October. Water was changed (50% removed and replaced) twice during the intervening weeks up to the start of the experiment, and concentrated zooplankton additions were added haphazardly (approximately twice a week) for hatchlings to feed upon. Because hatchlings were at a relatively high density, minimal growth occurred, though visible expansion of the stomach was apparent in many of the hatchlings, indicating they had eaten. I measured TL of a subset of hatchlings ($n = 107$) using ImageJ software (Rasband, 1997).

I filled 24 plastic containers ($34 \times 20 \times 12$ cm) with 4 L of aged rainwater collected in an outdoor tub. I used plastic mesh (1.6 mm openings) to divide containers in half. One half of the container (the response side) was used to quantify the functional response of a larval Anax predator, and the other half of the container (the treatment side) was used to manipulate the presence of cannibalism cues (Fig. 1). The partition limited physical interactions among organisms on the two sides, but permitted water (i.e. chemical cues) and minimal visual cues between sections. This design did not differentiate these two types of cues, and thus the results cannot be definitively attributed to either process. I also added two pieces of window screen to each side that provided both cover for salamander prey and a hunting perch for Anax predators (Drake et al., 2014). I placed containers on a shelving rack in the indoor greenhouse, with six containers per rack. The experiment occurred under daylight, from 0900 to 1200 h, and water temperature was approximately 22°C during the duration of the experiment.

I quantified the functional response of individual larval Anax by adding one individual with one of three salamander prey abundances (4, 8 or 16 hatchlings) to the response side of the experimental containers on 23 October. I crossed the prey abundances with two cannibalism risk treatments: the presence (risk-present) or absence (risk-absent) of a large Anax cannibal on the treatment side of the container (Fig. 1). All treatments had four replicates, except for one container in which the treatment Anax was erroneously added, leaving three replicates for the risk-present, salamander hatchling density = 16 and five replicates of a risk-absent, salamander hatchling density = 8. Hereafter, I will refer to the Anax on the response side as the

Figure 1 Experimental design of non-consumptive predation effects. The presence (top) or absence (bottom) of a larger *Anax* was paired with one of three densities of larval salamander *Ambystoma annulatum* prey. *(2 × 3 design, with four replicates of each treatment, except * = 3 replicates and ^ = 5 replicates).

predator, the *Anax* on the treatment side as the cannibal, and the salamander hatchlings as the prey.

The cannibal larval *Anax* was introduced into the treatment side of the container first, followed by a small dragonfly (less than half the body length of the cannibal) into the same side for it to consume. I expected that this would emit a cue into the water column that would influence the predation rate of the predator *Anax* on the response side. Within 30 min of introducing the larval *Anax* into the treatment side, I added the salamander hatchling prey and the larval *Anax* predator to the response side of the partition in all containers. I could not find enough small aeshnids to feed to the cannibal *Anax* on the treatment side of the tank due to the natural phenology in central Missouri, resulting in three cannibals being fed small libellulid dragonfly larvae instead (*Pachydiplax longipennis* or *Tramea binotata*). This difference may have influenced predation rates we observed, as dragonfly larvae can differentiate threats from con- and heterospecifics (Ferris & Rudolf, 2007). Therefore, I analyzed the results with and without these data points. Consumption of the dragonfly prey on the treatment side of the container occurred in only 50% of the trials (number consumed/total trials = 1/3 with libellulid prey; 5/9 with aeshnid prey). Whether the predator ate its prey on the treatment side did not influence the number of prey consumed by the predator on the response side (binomial generalized linear model: $t = 0.42$, df = 1, $P = 0.68$). In addition, not all prey on the treatment side were consumed immediately; subsequently, whether a strong cannibalism cue was actually emitted into the water was unclear, which should be considered when interpreting the results.

I visually searched each container every 30 min, and counted the number of remaining salamander hatchlings, recorded predation attempts if witnessed, and recorded whether the dragonfly prey was consumed on the treatment side of the tank. The experiment was terminated after 180 min, after

which a final count of surviving salamander prey was performed.

Analysis

The initial analysis followed Juliano (2001), where I tested whether survival after 180 min was predicted by linear, quadratic and cubic terms of initial prey abundances using a binomial generalized linear model; these three models approximate Type I, Type II and Type III functional responses. The cubic term was not significant and therefore removed. The quadratic term was positive but not significant, and the linear term was significant and negative, which is analogous to a Type II response. A Type I response was also supported (lack of significance in the quadratic term), but I did not use that model because I wanted to account for prey depletion throughout the experiment using the Rogers random predator equation (Juliano, 2001; Bolker, 2008).

Therefore, I fit a Type II functional response accounting for prey depletion using the following equation: $N_e \sim N_0\{1\text{-exp}(a(N_e h\text{-PT}))\}$, where a is attack rate, h is handling time, P is the number of predators, T is the temporal duration of the experiment and N_0 is initial prey density. I obtained maximum likelihood estimates for attack rate (a) and handling time (h) for the two experimental treatments separately, and compared them using the cannibalism risk treatment as an indicator variable (Juliano, 2001; Pritchard, 2016), which allowed me to assess whether a and h were significantly different between treatments. Because neither parameter was significantly different among cannibalism risk treatments, I performed a likelihood ratio test on a model that varied a and h with cannibalism risk treatment against a model where the treatment effect was absent (i.e. a functional response using all the data points together) to test whether accounting for the treatment effects had more explanatory power than the reduced model. I also

examined whether the effects of cannibalism risk treatments varied through time using the counts of surviving prey every 30 min, and estimated functional response curves at each time step. All modeling was performed using the *mle*2 function in the 'bbmle' package in R (Bolker, 2016; R Development Core Team, 2015), and the indicator analysis was performed using the 'frair' package (Pritchard, 2016), which also utilizes the *mle*2 function.

I calculated prey mortality rate (*m*) for the larval salamander prey using the equation $N_1 = N_0 e^{mt}$, where N_1 is the final prey number, N_0 is initial prey and t is time; solving for $m = -\ln(N_1/N_0)/t$ gives the mortality rate. I tested for differences in mortality rate among prey densities and risk treatment using a generalized linear model with a Gamma distribution, which fit better than normal or negative binomial error distributions based on AICc values. The covariates in this model included initial prey abundance (continuous), cannibalism risk treatment and their interaction.

Results

The average TL of the predator *Anax* on the response side of the containers did not vary between cannibalism risk treatments ($F_{1,22} = 0.10$, $P = 0.76$; mean ± SD for risk-present = 32.6 ± 3.75 mm, risk-absent = 32.2 ± 2.74 mm). The cannibal *Anax* on the treatment side of the containers were significantly larger than the *Anax* on the response side for TL (mean TL ± SD = 40.03 ± 2.89, mean HW ± SD = 7.70 ± 0.26; $F_{1,34} = 47.99$, $P < 0.001$), and the average difference in size between the response and treatment *Anax* was 7.43 mm (range 2.43–15.86) for TL and 1.15 mm (range 0.83–2.03) for HW. The mean ± SD hatchling TL for ringed salamanders was 12.733 ± 1.03 mm.

For the cannibalism risk-present treatment, attack rate was marginally different from zero ($P = 0.07$), and handling time was significantly different from zero ($P = 0.0003$). Both attack rate and handling time were significantly different from zero for the risk-absent treatment (both $P < 0.01$). Neither attack rate nor handling time was statistically different between cannibalism risk treatments ($P > 0.15$). The cannibalism risk present treatment had a slightly lower attack rate ($a = 2.69$; 95% CI: −0.267, 5.65) compared to the risk-absent treatment ($a = 2.84$; 95% CI: 0.77, 4.92; Fig. 2a). Handling time was nearly double for the risk-present treatment ($h = 0.15$; 95% CI: 0.04, 0.12) compared to the risk-absent treatment ($h = 0.08$; 95% CI: 0.07, 0.24), resulting in a lower asymptote (Fig. 2a). The likelihood ratio test was significant ($\chi^2 = 8.8$, df = 2, $P = 0.01$), indicating that the model accounting for the cannibalism treatment effects was better supported over the reduced model that did not account for cannibal effects. Finally, changes to the functional response show consistent treatment effects through time; the cannibalism risk present treatments were always resulting in lower asymptotes than the risk-absent treatments (Fig. 2b).

Excluding the data points when libellulid prey were used in place of aeshnid prey on the treatment side resulted in similar parameter estimates ($a = 2.43$, 95% CI: 0.16, 4.71; $h = 0.12$, 95% CI: 0.04, 0.020) in the cannibalism risk present treatment, and using this subset of data resulted in attack rate being
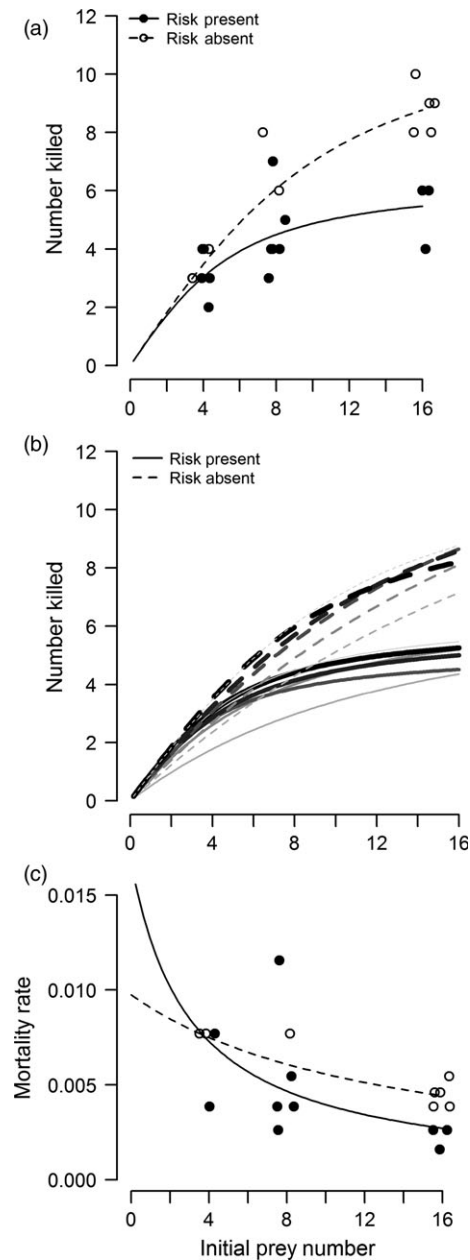
Figure 2 (a) Functional response curves for larval *Anax* predators in cannibalism risk-present and risk-absent treatments. Each line is derived from model predictions using the Rogers random predator equation and the Holling's Type II functional response. Points are raw data values, horizontally skewed to reduce overlap. (b) Predicted relationships for functional response curves as a function of time in cannibalism risk-present (dashed lines) and risk-present treatments (solid lines). Lines represent predicted relationships for surviving prey counts performed every 30 min for 180 min; later timepoints in the experiment are shown with increasing darkness and thickness of lines. (c) Mortality rate of ringed salamander prey across different initial prey abundance in the cannibalism risk-present and risk-absent treatments. Lines indicated model predictions for each treatment. The mortality rate (*m*) was calculated from an exponential mortality equation, $m = -\ln(N_1/N_0)/t$.

significantly different from zero ($P = 0.04$). Using this subset of data also resulted in an absence of significant differences between cannibalism risk treatments for either attack rate or handling time.

In general, prey mortality declined with increasing prey density (Fig. 2c). The interaction of cannibalism risk treatment and salamander prey density was not significant for prey mortality ($P = 0.23$). Upon removing the interaction term, mortality rate was significantly lower at higher salamander prey densities ($t = 2.78$, df = 1, $P = 0.012$), but the intercepts for each cannibalism risk treatment were not significantly different ($P = 0.26$; Fig. 2c).

Discussion

Non-consumptive effects among predators frequently have equal or greater impacts than consumptive effects on prey, including conspecific individuals (Werner & Peacor, 2003; Preisser et al., 2005; Davenport et al., 2014). In particular, the threat of cannibalism can strongly affect both population and community structure (Van Buskirk, 1992; Wissinger et al., 2010), especially through its influence on a predator's functional response (Crowley & Martin, 1989; Rudolf, 2008a). This study found that Anax larvae forage with a saturating (Type II) functional response, but there was not a statistically significant difference in either attack rate or handling time based on the presence or absence of a cannibalistic threat. This matches the results of Crumrine (2006), who also found that Anax larvae did not behaviorally respond to chemical cues of larger conspecifics. Yet, there was trend that the non-lethal presence of a larger cannibal resulted in a reduced maximum predation rate at higher prey densities and handling times that were nearly double, which may have been intensified had I used higher or more prey densities. Furthermore, the model that accounted for the treatment effects within the functional response was more highly supported, and the treatments showed consistent differences through time. I also observed higher prey mortality rates at low prey densities, further supporting the hypothesis that non-consumptive effects among predators on prey are density-dependent. Thus, while this small-scale study may be somewhat limited in scope, my results represent potentially important consequences for predators foraging in the presence of cannibalism.

Population size-structure is an element frequently involved in cannibalism because size differences among individuals often permit predation to occur (Woodward et al., 2005; Miller & Rudolf, 2011). I observed that the non-lethal presence of a larger cannibal had some influence on predation rates of smaller conspecifics. Similarly, Rudolf (2008a,b, 2012), and Van Buskirk (1992) found that population size-structure influenced both behavioral patterns and consumption rates among larval dragonflies, presumably because smaller individuals were avoiding predation by older, larger individuals. Furthermore, Van Buskirk (1992) showed that the consequences of such cannibalism rates also resulted in multi-year population cycles. Therefore, while the lack of statistical significance in my study could result from low replication and a subsequent lack of power, the difference in functional response curve shapes when

a non-lethal threat of cannibalism was present may signify an important biological effect in this system. Further examination of factors that determine population size structure, and/or influence interactions among different-sized individuals within a population are necessary to understand how cannibalistic threats operate. For example Kishida et al. (2011) found that predation risk from larval dragonflies reduced cannibalism rates among size-structured populations of larval salamanders, eliminating the feedback mechanism between cannibalism and size-structure. Several studies by Rudolf (2006, 2008a,b) also indicate that density-dependence within size-structured populations influence consumptive and non-consumptive effects of cannibalism and intraguild predation, including the density of intermediate predators and density ratios of heterospecific and conspecific prey.

Functional response curves can be influenced by numerous factors, of which predator interference has been a common motif. Indeed, several different functional response curve models can incorporate and test for predator (cannibal) interference effects (Skalski & Gilliam, 2001; Stier & White, 2014). I did not use these forms here as I wanted to account for prey depletion using the Rogers Random predator equation. However, qualitative comparisons of my results to those models incorporating interference support the idea that the dragonflies foraged less when the cannibalistic threat was present. In particular, the Beddington–DeAngelis functional response incorporates interference, but assumes that it dissipates at higher prey densities (Skalski & Gilliam, 2001). I observed the opposite effect, where prey consumption under the threat of cannibalism decreased at higher prey densities, fitting more with the theoretical framework of the Crowley–Martin functional response where both attack rate and handling time are influenced by predator interference (Crowley & Martin, 1989). Examination of other factors that influence attack rates and handling times beyond predator interference may reveal critical insights into what mechanisms also influence predation rates.

Elucidating whether such functional response curves exist in natural populations, given all of the potential confounding effects in more complex environments, is necessary to determine how predation rates would vary under more heterogeneous conditions (Paterson et al., 2015). For example Hossie & Murray (2010) found that the functional response curve shape of larval dragonflies changed in the presence of increased structural complexity, and Crowley & Martin (1989) found that predator (cannibalistic) interference still occurred despite alternative prey and increased physical structure. Teasing apart such context-dependent interactions are critical, especially for larval aeshnids, as they play a strong role in determining species interactions and structuring overall pond food webs (Relyea & Yurewicz, 2002; Davenport & Chalcraft, 2012, 2013). Ramos & Van Buskirk (2011) also found that predation rates saturated with two predatory aeshnids as opposed to only one, presumably through interference mechanisms, that released amphibian prey from mortality risk. Similarly, McCauley et al. (2011) found that dragonfly survival was greatly reduced in the presence of a non-lethal dragonfly. Therefore, the non-consumptive effects of cannibalism (or predation more generally) within dragonflies could be mechanisms

that promote coexistence of amphibians with larval dragonflies. This might be particularly plausible if decreased mortality occurs at high prey densities in natural populations, as I observed in this study, due to diluted predation risk for prey at the individual level.

Predation risk, especially from conspecifics, is a ubiquitous threat in ecological communities. Further studies are needed to tease apart the mechanistic components of how such non-consumptive risks are manifested in both predators and prey, especially under varying ecological conditions (e.g. increased habitat complexity). As trophic cascades (Persson *et al.*, 2003; Rudolf, 2007), population cycles (Van Buskirk, 1992; Wissinger *et al.*, 2010) or dispersal propensity (Rudolf, Kamo & Boots, 2010) have all been linked to consumptive and non-consumptive effects of cannibalism, further mechanistic tests will likely illuminate the intricacies of such processes, and their role in structuring both populations and communities.

Acknowledgments

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