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THE IMPACT OF CANNIBALISM IN THE PREY ON PREDATOR–PREY SYSTEMS

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Abstract. Cannibalism is ubiquitous in natural communities and has the potential to alter the functional relationship of predator–prey interactions. Although cannibalistic species are frequently subject to predation, the consequences of cannibalism in the prey for predator–prey interactions are poorly understood. Using a dragonfly larvae system, I provide the first experimental evidence that cannibalism in the prey creates behavior- and density-mediated indirect effects that result in nonlinear predator–prey interactions. As a consequence, cannibalism in the prey altered the functional relationship of the predator and its prey and reduced the impact of the predator on prey mortality by 47%. By parameterizing a mechanistic predation model, I show that the nonlethal interaction between cannibals and predators reduced cannibalism rates, which explained almost two times more of the observed mortality reduction than the consumption of cannibals. However, only a model that accounted for both behavioral interactions and the consumption of cannibals could predict ∼100% of the observed mortality. Using the mechanistic model, I discuss the long-term effects of cannibalism on community dynamics and how they can differ from effects of simple density-dependent mortality. In general, these results demonstrate the importance of accounting for the trophic structure in cannibalistic populations and the resulting nonlinear interactions to predict predator–prey dynamics.

Key words: community dynamics; competition; density-dependent mortality; intraguild predation; multiple predators; ontogenetic niche shift; predator–prey dynamics; risk reduction; stage- or size-structured interactions; trait-mediated indirect interactions; trophic structure.

Introduction

Predator–prey systems are key features of natural communities, and thus have been of central interest to community ecologists. Theoreticians recognized early on that density-dependent, intraspecific processes in the prey can strongly alter the dynamics of predator–prey systems (Leslie 1947, May 1973); this has been demonstrated by numerous studies of the effect of intraspecific competition on predator–prey dynamics (e.g., Chase et al. 2002, De Roos and Persson 2003, Hixon and Jones 2005). Cannibalism is a common intraspecific interaction that is ubiquitous in aquatic and terrestrial communities (Fox 1975*a*, Polis 1981, Woodward and Hildrew 2002, Woodward et al. 2005), but unlike other intraspecific processes it is a trophic interaction. Yet despite its known importance for population dynamics, the general impact of cannibalism on community dynamics is still poorly understood (Claessen et al. 2004).

Food web theory usually assumes that cannibalism is some form of density-dependent mortality that does not alter the functional relationship between interacting species (e.g., Hart 2002, Williams and Martinez 2004, and references in Claessen et al. 2004). This assumption, however, is often erroneous, because cannibalism introduces trophic structure and feedback loops within populations. When interacting with other species, the added trophic structure and feedback loops allow for indirect interactions even in two-species systems (Rudolf 2006, 2007*a*). Such indirect interactions alter the functional relationships between species and can lead to nonlinear community dynamics that are impossible with simple density-dependent mortality. For example, cannibalism in the predator can lead to size-structured behavior (trait, TMII) and density (DMII) mediated indirect interactions that can strongly reduce the per capita impact of the predator on prey mortality (i.e., that can result in nonlinear predator–prey interactions) (Sih 1982, Crumrine 2005, Rudolf 2006, 2008), stabilize predator–prey systems, and alter the strength of trophic cascades (Rudolf 2007*a*). The impact of cannibalism in the prey on predator–prey interactions, however, is virtually unknown despite its importance for community dynamics (Rudolf 2007*b*).

If we want to integrate cannibalism into food web theory it is imperative to understand its impact across trophic levels. While the way nonlinear interactions resulting from cannibalism in the predator alter predator–prey interactions has recently been explored (Rudolf 2006, 2007*a*, 2008), the observed underlying mechanism cannot be applied to cannibalism in the prey. The reason

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for this is that the indirect interaction pathways differ depending on the specific trophic level at which cannibalism occurs. Although cannibalism is equally common in herbivores, detritivores, and intermediate predators that are all prone to predation themselves (Fox 1975*a*, Woodward and Hildrew 2002, Woodward et al. 2005), most theoretical studies (e.g., Gabriel 1985, Van den Bosch et al. 1988, Van den Bosch and Gabriel 1997, Claessen et al. 2004, but see Rudolf 2007*b*) and previous empirical studies (e.g., Fox 1975*b*, Leonardsson 1991, Schellhorn and Andow 1999, Buddle et al. 2003, Leon-Beck and Coll 2007) (but see Claus-Walker et al. 1997) have focused only on cannibalism in the top predator, even though the focal species were often intermediate predators that are consumed themselves by top predators (C and P in Fig. 1, respectively). Thus, we still lack the basic knowledge of when and how cannibalism in the prey affects the functional relationship between predator and prey.

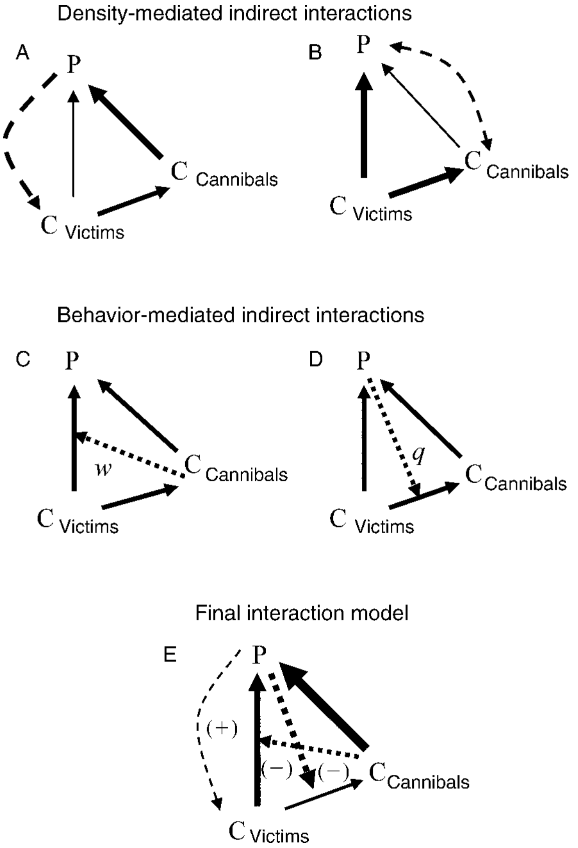

FIG. 1. (A–D) Possible and (E) observed direct and indirect interactions within a system with a stage-structured cannibalistic prey (C) and a top predator (P). (A) The preferred consumption of cannibals results in a positive density-mediated indirect interaction between top predator and small prey. (B) Preference for small prey stages results in a negative density-mediated (competitive) indirect interaction between the predator and the large cannibalistic prey stage. The nonlethal presence of the large cannibalistic stage or the predator can alter (C) the predation rate of the top predator or (D) the cannibalism rate, respectively. (E) Observed direct and important indirect interactions in this study. Solid arrows indicate feeding relationships from resource to consumer, dashed arrows indicate density-mediated indirect interactions, and dotted arrows indicate behavior-mediated indirect interactions. The thickness of the lines indicates the relative interaction strength. The double-headed arrow in panel (B) indicates a reciprocal interaction. Positive or negative signs indicate if the indirect interaction has a positive or negative effect on the recipient/interaction. The symbols q and w in panels (C) and (D) indicate estimated behavior-mediated interaction modifications.

To predict the dynamics of predator–prey systems with cannibalism requires that we understand when nonlinear species interactions result from cannibalism, what the underlying mechanisms are, and which components are affected (e.g., functional response of predators or cannibals). With cannibalism in the prey several density- and behavior-mediated indirect interactions are possible that can result in nonlinear interactions (Fig. 1). A density-mediated indirect interaction can arise when predators consume cannibals, thus reducing prey mortality due to cannibalism (Fig. 1A), or when predators consume noncannibalistic prey, which results in competition between predator and cannibals that could increase prey mortality (Fig. 1B). These indirect interactions arise due to changes in the density of interacting functional groups, but they have no effect on the per capita interaction coefficients. This, however, would be the case with behavioral interactions between heterospecific predators, cannibalistic or noncannibalistic prey (Fig. 1C, D). For example, in dragonfly larvae (Crowley et al. 1987, McPeek and Crowley 1987, Van Buskirk 1992), salamanders (Rudolf 2006), isopods (Leonardsson 1991), backswimmers (Sih 1982), fish (Persson and Eklov 1995, Greenberg et al. 1997, Biro et al. 2003), and reptiles (Keren-Rotem et al. 2006) small individuals reduce their activity, change their activity schedule or habitat, and hide more often in response to the presence of larger cannibalistic conspecifics. Such general antipredator behaviors are also likely to reduce the per capita predation rates of heterospecific predators (i.e., result in a TMII) (Fig. 1C). In turn, predators could also induce behavioral responses that could then reduce per capita cannibalism rates (Fig. 1D). Such TMII are often highly nonlinear, and recent empirical and theoretical work indicates that they can significantly alter the dynamics of size-structured predator–prey systems (Rudolf 2006, 2007*a*). The different TMII, however, affect different species (predator or prey), and will therefore have different long-term consequences for both populations and ultimately for the community.

The objective of this study was to experimentally test the hypothesis that cannibalism in the prey creates different behavior- and density-mediated indirect interactions and thus alters the impact of a predator on prey population dynamics. In particular, the goals of the study were: (1) to estimate how the impact of a predator differs between cannibalistic and noncannibalistic populations, (2) to determine if cannibalism results in

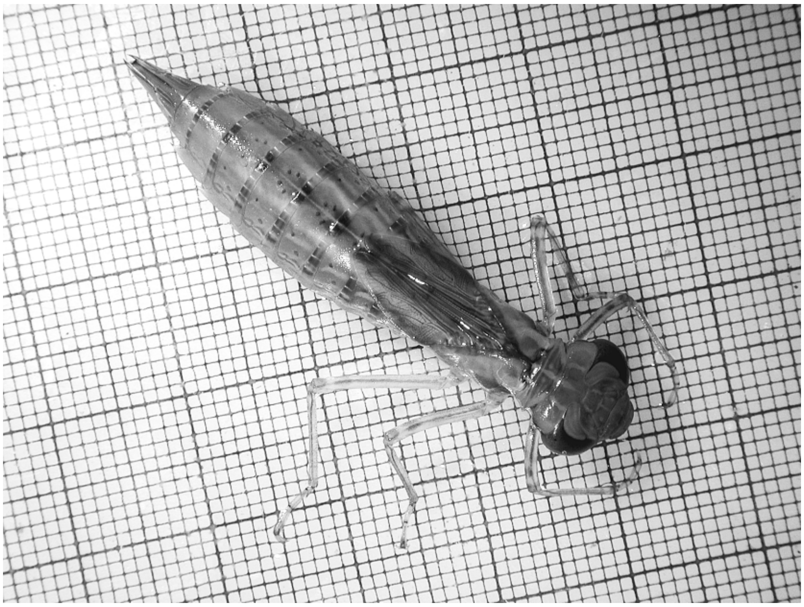

PLATE 1. Larvae of *Anax junius* are often top predators in fishless ponds and strongly impact the structure of pond communities. These voracious predators can have strong impacts on the survival and behavior of smaller odonate species such as *Plathemis lydia*. Photo credit: V. Rudolf.

nonlinear predator–prey interactions, (3) to identify the specific underlying mechanisms of these nonlinear interactions, and (4) to create a mechanistic model that accounts for these indirect interactions. Results show that cannibalism results in nonlinear interactions due to different TMII and DMII that strongly reduced the impact of a predator on the mortality of its prey.

METHODS

Field experiment

The species used in this study are the dragonflies *Anax junius* and *Plathemis lydia* (see Plate 1). Larvae of both species commonly co-occur in ponds through North America. *A. junius* larvae are large (~5 cm body length in final instar) active predators and are known to prey on smaller larvae (~2.5 cm body length in final instar) of *P. lydia* (Crumrine and Crowley 2003; V. H. W. Rudolf, *unpublished data*). *P. lydia* can reach very high densities (~380 individuals/m^2) during peak summer months (Wissinger 1989). They reproduce nearly all summer, and overwinter in the pond as larvae. As a consequence, cohorts that can differ fourfold in size commonly coexist throughout the year (Wissinger 1989; V. H. W. Rudolf, *unpublished data*). Cannibalism is uncommon within an instar, but increases with increasing instar differences (Wissinger 1988*a*; V. H. W. Rudolf, *unpublished data*). Recent studies have shown that larvae of *P. lydia* use chemical and visual cues to detect large cannibalistic conspecifics, and they alter their behavior in the presence of conspecifics or *A. junius* (Ferris and Rudolf 2007). All larvae were collected on 17–21 August 2006 from two ponds close to Mountain Lake Biological Station (MLBS), Giles County,Virginia, USA.

The experiment was carried out in cylindrical field enclosures (diameter 40 cm, height 60 cm) that were set up in the Station Pond at MLBS, where both species naturally coexist. Each cage was constructed of mosquito netting (1-mm mesh width) within a stable frame of plastic fencing. The bottom of each cage was sealed, while the top remained open to allow colonization by invertebrates. Larvae of the two study species will never leave the water unless they metamorphose. Each cage contained a removable plastic dish 40 cm in bottom diameter holding 2 cm of sediment and leaf litter from the pond. Each cage received four rinsed *Isoetes* plants obtained from the local pond, approximating the natural density found in the habitat where both species overlap. Ten days before the start of the experiment, cages were set up at a water depth of 30 cm in a line along the edge of the pond to allow natural colonization by invertebrates. At the beginning of the experiment, a variety of species (including mostly zooplankton, and small mayfly and zygopteran larvae, but also some tadpoles, beetle larvae and adults) had colonized the cages, providing ample alternative prey for *P. lydia* and to a smaller extent for *A. junius*. Predatory invertebrates that were large enough to consume small *P. lydia* were removed from the cages.

The experiment consisted of seven treatments, each replicated six times, that were used to examine direct and indirect interactions within the system and to create and parameterize a predation model that accounts for each indirect effect. Each cage received 40 small *P. lydia* (a density of 318.3 individuals/m^2), all within instars F-4–

F-5 (body length 0.68 ± 0.06 cm [mean ± SD], $N = 200$). Four treatments represented a 2 × 2 factorial design, in which the presence (6 *P. lydia* to give a density of 48 individuals/m^2) and absence of large cannibalistic *P. lydia* (L) was crossed with the presence (1 *A. junius* to give a density of 8 individuals /m^2) and absence of the predator *A. junius* (A). These treatments were used to determine if the effects of cannibals and predators were independent or if they led to any indirect interactions altering the survival of small prey (Wilbur and Fauth 1990). Because those indirect interactions could result from TMII, DMII, or both, the remaining three treatments were used to separate the individual TMII between cannibals and predator from the DMII (Schmitz et al. 1997, Crumrine and Crowley 2003). Predator and cannibals were always present together, but either the cannibals (Lg + A) or the predator (L + Ag) or both (Lg + Ag) had glued mouth parts (g) to prevent consumption of small *P. lydia* by cannibals or predators, respectively. The last treatment (Lg + Ag) served as control for the effectiveness of the mouthpart manipulation. Due to the morphological difference, *A. junius* mouth parts were tied shut and glued (see Appendix A for detailed gluing procedure). Behavioral observations showed that glued individuals still attempted to attack prey (see Appendix A and results below). Additional laboratory experiments showed that this treatment completely prevented cannibalism and strongly reduced predation rates (by 97%) of the predator in the laboratory (Appendix A). In the field experiment, predation rates of glued predators were not significantly different from zero (see *Results*). To control for handling effects, larvae in cannibalism and predation treatments underwent a "sham procedure," in which they were handled in exactly the same way, except that they were not glued. Large *P. lydia* were all F-2 instar (~1.4 cm body length) and *A. junius* all F-2 instar (~4.0 cm body length). The densities for *A. junius*, and for small and large *P. lydia*, represented the natural frequency and relative abundance of both stages and the predator found at this time of the year (Wissinger 1988*b*; V. H. W. Rudolf, *unpublished data*). The experiment ran from 23 to 27 August 2006, and the duration was based on pilot studies to ensure that some large *P. lydia* survived the experiment. At the end of the experiment, cage contents were removed and I recorded the number of surviving individuals for each species and stage.

Cannibal activity.—I carried out three night (24–26 August) surveys to monitor the activity of large *P. lydia*. Because of their coloration, *P. lydia* larvae were well camouflaged during the day, but could easily be detected with a flashlight at night. Thus, surveys were carried out at night from 21:00 to 22:00 hours. Each cage was carefully checked with a flashlight and the number of large *P. lydia* that were visible (on top of the substrate, plants, or on the side of the cages) was recorded. Small *P. lydia* were too small to be observed, and *A. junius* do not hide in the substrate and thus were always visible. Activity was defined as the proportion of visible individuals per observation. To correct activity for the variation in survival of large *P. lydia* between replicates, I calculated proportional activity for each census period (t) as (number of larvae observed at census period t) ÷ (number of larvae present at census period t). The number of larvae present in each cage at time t (N_t) was calculated using the survival model $N_t = N_0 e^{-mt}$, with $t =$ days since start of the experiment and the cage-specific mortality rate, m, which was calculated based on the final number of survivors in the respective cage. For each cage all three observation nights were pooled to calculate the mean cage activity for the analysis. The gluing treatment of *A. junius* did not affect the behavior of large *P. lydia* ($Z = 0.45$, $P > 0.4$). Thus, I only analyzed treatments where *A. junius* had glued mouth parts (Ag + L and Ag + Lg) to maintain similar numbers of surviving large *P. lydia* per cage between treatments to avoid potential confounding effects due to changes in the behavioral interactions between cannibals. There was also no difference in the activity between treatments with *A. junius* where large *P. lydia* had glued or normal mouthparts (Mann Whitney U test, $Z = -0.9$, $P = 0.4$). Thus, to maximize statistical power the two treatments were pooled to test for the overall effect of *A. junius* on activity of *P. lydia*.

Prey size structure.—To gain additional insight into the interaction of cannibals and predators, I also examined if predators or cannibals have different and independent effects on the prey size structure of the small-prey stage. Prior to the experiment, 200 small *P. lydia* from five randomly selected cages were photographed and their head width and body length were measured using the program ImageJ as a reference for initial mean body size (program *available online*).[2] At the end of the experiment, all surviving small *P. lydia* of each cage were photographed to determine the final size structure within a cage. Body growth was calculated as the difference between initial estimated cage mean and the respective cage mean at the end of the experiment. Body length varies with food intake and is variable within instar, while head width varies across the instar, but varies little within the instar. Due to low molting rates there was no significant change in head width during the experiment, which was thus excluded from the growth analysis, and final head size was used to test for size-selective survival. To test how large *P. lydia*, *A. junius*, and their interactions affect the size structure of the population of small *P. lydia*, I carried out a two-way MANOVA analysis, with *A. junius* and *P. lydia* as fixed factors, and the standard deviation, skewness, and the maximum and minimum body size within a cage at the end of the experiment, and the mean growth in body length within a cage as dependent variables. If the MANOVA was significant, I used individual ANOVAs

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[2] ⟨http://rsb.info.nih.gov/ij/⟩

to test for treatment effects on the individual statistics. The preference of *A. junius* for the different prey stages (small victims or cannibalistic stage) was calculated using Manly's preference index, α (without prey replacement), where α lies between 0 and 1 (Manly et al. 1972). This index corrects for differences in the densities of prey types. With two groups, $\alpha > 0.5$ indicates a preference.

Building a mechanistic model with indirect interactions

The seven treatments were used to determine which interaction modifications were significant and to parameterize five mortality models to identify the relative strength of TMII and DMII in systems where both predator and cannibals are present. In the following section m refers to the *observed* mortality rate of small *P. lydia* within a treatment, with the subscript indicating the respective *A. junius* (A) and *P. lydia* (L) treatment, and m^* indicates an *estimated* mortality rate for the scenario where both predator and cannibals are present. The mortality rate, m, within a cage was calculated assuming the survival model $N_t = N_0 e^{-mt}$, with N_t = final prey density, N_0 = initial prey density, and t = duration of the experiment, and solving for $m = -\ln(N_t/N_0)/t$.

If μ_p is the predation rate, μ_c the cannibalism rate, and μ_0 the background mortality rate in the absence of the predators and/or cannibals, then the expected mortality rate (m^*_{NoInt}) of the null hypothesis (i.e., no interaction effects between cannibals and predator) is

$$m^*_{\mathrm{NoInt}} = \mu_p + \mu_c + \mu_0.$$

Note that this is the log version of a multiplicative risk model, which accounts for prey depletion, i.e., prey eaten by a predator cannot be eaten by cannibals later and vice versa (Soluk and Collins 1988, Wilbur and Fauth 1990). A significant interaction in the two-way ANOVA of the mortality effects of large *P. lydia* and *A. junius* would indicate that this null model must be rejected, and that the interaction between cannibals and predators reduces ($m^*_{\mathrm{NoInt}} > m_{\mathrm{A+L}}$) or increases ($m^*_{\mathrm{NoInt}} < m_{\mathrm{A+L}}$) the mortality rate of the prey (Wilbur and Fauth 1990, Billick and Case 1994). For the parameterization of the model, the predator/cannibal independent mortality μ_0 was calculated as the average of the control treatments (m_{none}). The mortality due to predation (μ_p) and its 95% CI was calculated from the difference between the mortality observed in treatments with *A. junius* alone (m_{A}) minus mortality in the control (m_{none}). The same process was used to estimate the cannibalism rate (μ_c). (See Appendix B for a summary of models and parameters.)

If the null model is rejected, three possible indirect interactions could be responsible for this discrepancy (Fig. 1). First, because μ_c is a function of the density of the cannibals, it will be indirectly reduced if the predator consumes cannibals. We can account for this consumption effect by adjusting μ_c by the factor k. The expected mortality of the adjusted model is given by

$$m^*_{\mathrm{Cons}} = \mu_p + \mu_c k + \mu_0$$

with $k = 1 -$ (the mean proportional reduction in the density of large *P. lydia* by *A. junius* across all A + L/Lg replicates integrated over the duration of the experiment [and assuming a constant predation rate]).

The nonlethal presence of the predator can alter the cannibalism rate μ_c by some factor q (Fig. 1D). This change is given by $q = (m_{\mathrm{Ag+L}} - m_{\mathrm{Ag+Lg}})/(m_{\mathrm{L}} - m_{\mathrm{None}})$, i.e., the proportional change in cannibalism rates. This calculation uses the respective glued control ($m_{\mathrm{Ag+Lg}}$) instead of the no-predator control (m_{None}) in the nominator to correct for the slightly higher mortality rate in the glued control and thus represents a conservative estimate of the behavioral effect. I calculated q using bootstrap procedures (10 000 replications). Note that in principle my approach is similar to Peacor and Werner's (2004) change in interaction coefficient Δ_{RC}, except that the estimation used here also corrects for density-independent prey mortality. To calculate if q was significantly different from 0, I used a randomization test with 10 000 runs to calculate the absolute P value (Edgington 1995). The expected mortality accounting for this behavior-mediated predator effect is given by

$$m^*_{\mathrm{BehP}} = \mu_p + q\mu_c + \mu_0.$$

Similarly, the nonlethal presence of cannibals can alter the predation rate of the predator by the factor w (Fig. 1C), which is given by $(m_{\mathrm{A+Lg}} - m_{\mathrm{Ag+Lg}})/(m_{\mathrm{A}} - m_{\mathrm{None}})$. The value of w, and if it is significantly different from 0, were calculated as above for q. The expected mortality of the prey is then

$$m^*_{\mathrm{BehP}} = w\mu_p + \mu_c + \mu_0.$$

Finally, I calculated a full model that accounts for all three indirect interactions with the expected mortality

$$m^*_{\mathrm{Full}} = w\mu_p + q\mu_c k + \mu_0.$$

Note that the mortality model naturally corrects for the potential confounding effect of altering the predator density in the combined treatment by measuring the net per capita effect of cannibals and predators (Finke and Denno 2005). This approach allowed me to individually test which indirect interactions (i.e., k, w, q) in the predator + cannibals scenario are significant and need to be included in the final mortality model.

I compared the effect of each parameter on prey mortality in the combined predator–cannibal scenario by calculating the relative contribution of each indirect interaction to the difference in the expected prey mortality from the null model vs. observed prey mortality (e.g., $[m^*_{\mathrm{NoInt}} - m^*_{\mathrm{Cons}}]/[m^*_{\mathrm{NoInt}} - m_{\mathrm{A+L}}]$; Crumrine and Crowley 2003). To compare how well each of the models predicted the actual/observed mortality in the A + L treatment, I calculated the relative difference between the predicted and observed mortality for each model, e.g., $(m^*_{\text{Cons}} - m_{\text{A+L}})/(m_{\text{A+L}})$. The results of these calculations are represented as percentages. Note that all model parameters are estimated independently from $m_{\text{A+L}}$, allowing for an independent comparison between predicted and observed mortalities.

Prey activity experiment

I carried out a laboratory experiment to (1) determine the separate and combined behavioral effects of cannibals and predators on the activity of the small prey stage, and (2) to gain more detailed information on what specific components of the foraging behavior of the cannibalistic prey stage are altered in the presence of the predator. The experiment consisted of a 2 × 2 factorial randomized complete block design manipulating the presence/absence of a nonlethal cannibal (one large glued *P. lydia* per box) and presence/absence of a nonlethal predator (one *A. junius* per box) with eight replicates per treatment. Each box received 10 small *P. lydia* and 40 mosquito larvae that served as food for small and large *P. lydia*. The cannibal was allowed to move freely through the box, while the predator was confined to a transparent and perforated plastic cylinder in the center of the cage (see Appendix C for the detailed setup). This setup allowed me to simultaneously monitor small prey and cannibal activity and to detect cannibalistic but nonlethal encounters using video recordings. Using this setup I tested for treatment effects of the cannibal and/or predator on the activity and consumption rate of small *P. lydia* and for predator effects on (1) the corrected foraging movement activity of cannibals, (2) the number of total attacks on conspecific and heterospecific prey, and (3) the probability of cannibalism (i.e., number of cannibalistic attacks/number of cannibalistic encounters). (See Appendix C for experimental and statistical details.)

RESULTS

Interactions between cannibals and predators

The mortality of small *P. lydia* differed significantly between treatments (one-way ANOVA, $F_{6,30} = 11.59$, $P < 0.0001$). The presence of only large cannibalistic *P. lydia* or only *A. junius* led to a 7.4 times and 12.5 times increase in the mortality of small *P. lydia*, respectively (Fig. 2A). Their effect, however, was altered in the presence of the other species, as indicated by the significant interaction term (two-way ANOVA, L × A: $F_{1,15} = 9.56$, $P < 0.01$). As a consequence, the interaction between cannibals and predators led to a 47% lower mortality rate (86.7% proportional reduction) than expected from their independent effects (Fig. 3). The nonlethal presence of *A. junius* significantly ($P = 0.02$) reduced the cannibalism rate by 59.4% ($q = 0.406$) (Fig. 2B). The predation rate of *A. junius* was on average reduced by 32.6% in the presence of noncannibalistic large *P. lydia* ($w = 0.674$) (Fig. 2B), but this was not significant ($P > 0.15$).

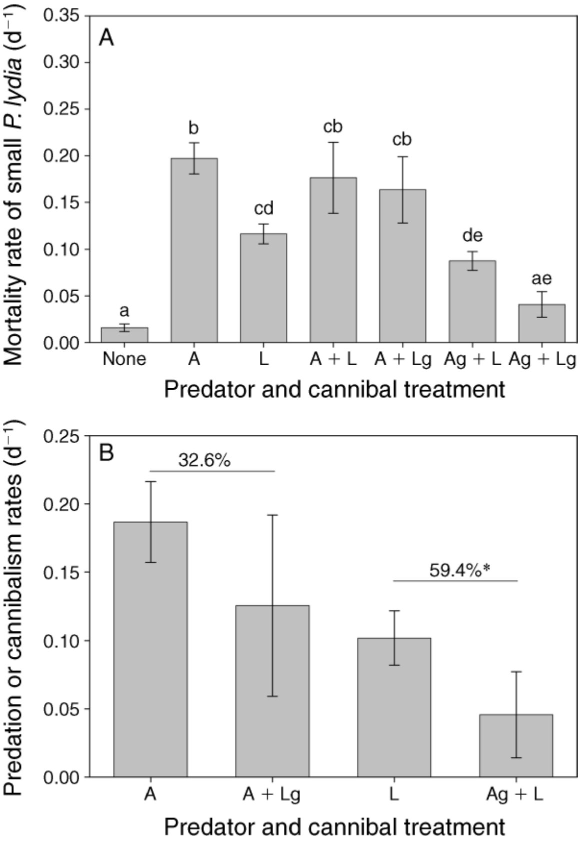

FIG. 2. (A) Mortality rate, m (mean ± SE), observed in all treatments manipulating the presence/absence of the top predator *Anax junius* (A) and the large cannibalistic prey stage of *Plathemis lydia* (L) and their feeding ability ("g" indicates glued mouth parts). Multiple comparisons were carried out after a significant one-way ANOVA. Treatments with different letters are significantly different at $P = 0.05$ after correcting for the false discovery rate (FDR) to control for the Type I error due to the multiple comparisons (Benjamini and Hochberg 1995). (B) Mean and 95% confidence intervals estimated for predator (A) and cannibalism rates in the absence or presence of nonlethal predators or cannibals (Ag and Lg, respectively). Parameters were estimated by subtracting the appropriate no-predation or cannibalism control from the observed mortality using a bootstrap procedure (see *Methods* for details). The mean proportional reduction in predation or cannibalism rates in the presence of nonlethal predators or cannibals is indicated, and the significance of each reduction was calculated with a randomization test (see *Methods*).

$^*P = 0.02$.

The mortality rate of large *P. lydia* was significantly affected by the treatments (one-way ANOVA, $F_{4,25} = 5.63$, $P = 0.002$). The presence of *A. junius* resulted, on average, in a significant 5.5 times increase in the mean mortality rate of large *P. lydia* (Fig. 4A), reducing the cannibalism rate by 37.5% ($k = 0.625$). *A. junius* strongly preferred large *P. lydia* (Manly's $\alpha = 0.71$, t test, $t = -2.824$, $P = 0.017$, df $= 11$) to the small *P. lydia* stage. There was no significant correlation between mortality rates of small and large *P. lydia* (Pearson's $r = 0.716$, P

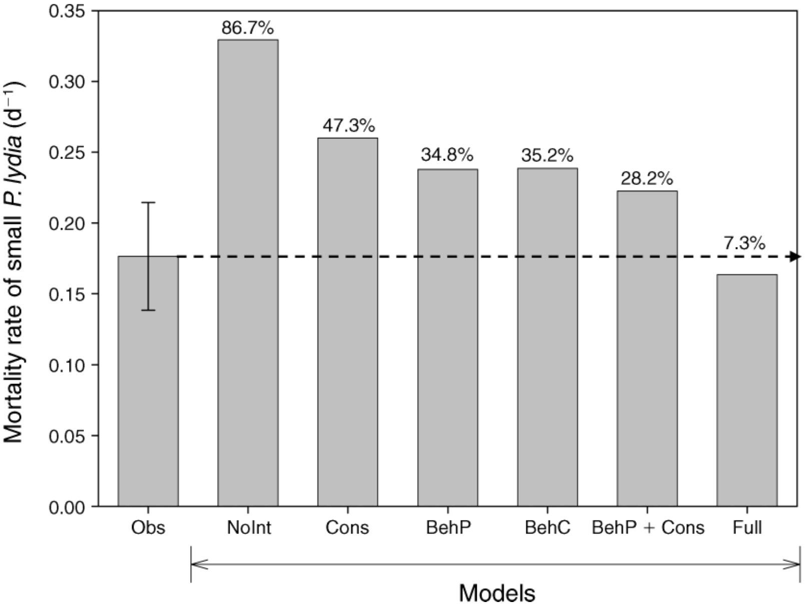

FIG. 3. Mean (±SE) total mortality rates of the small-prey stage observed (Obs) and predicted by the different predation models assuming no interaction effect (NoInt), accounting for the consumption of cannibals (Cons), accounting for the behavioral effect of the predator on the cannibalism rate (BehP), accounting for the behavioral effect of cannibals on the predation rate (BehC), accounting for the consumption of cannibals and the behavioral effects of predators on cannibalism rates (BehP+Cons), and accounting for all three possible indirect interactions (Full). Values above the bars show the average percentage differences between the mortality predicted by the model and the mean observed mortality (indicated by the dashed line)

> 0.1, $N = 6$) in *A. junius* treatments in which large *P. lydia* were prevented from cannibalizing small conspecifics (i.e., A + Lg). The median of the proportional night activity of large *P. lydia* was significantly reduced in the presence of *A. junius* by 78.7% (Mann-Whitney *U* test: $Z_{6,12} = -3.01$, $P = 0.001$) (Fig. 4B).

Indirect interactions models

The proportional difference between the prediction of the null model assuming no indirect interactions (m^*_{NoInt}) and the observed mortality was 86.7% (Fig. 3). The model accounting for the consumption of the cannibals (m^*_{Cons}) overestimated the mortality on average by 47.3%, while the model accounting for the nonlethal effect of the predator on the cannibals (m^*_{BehP}) overestimated the mortality by 34.8%, and the nonsignificant model accounting for the nonlethal effect of cannibals on the predator (m^*_{BehC}) differed by 35.2% (Fig. 3). The consumption of cannibals by the predator (i.e., k) explained only 34.3% of the reduction in prey mortality, while the behavioral effect of the predator on cannibals (i.e., q) and the behavioral effect of cannibals on the predator (i.e., w) explained 59.8% and 59.4%, respectively (Fig. 3). (Note that these individual percentages reflect their relative importance and are not expected to sum to 100%.) The final significant model accounting for the behavioral effects on cannibals and their consumption explained 69.8% (Fig. 3). The full model accounting for all three interactions slightly overestimated the mortality on average by only 7.3%, explaining >100% of the mortality reduction (Fig. 3), but this was not the most parsimonious model and included one nonsignificant factor (i.e., w). A summary of all model parameters and performances is given in Appendix B.

Prey size structure

The MANOVA analysis showed that *A. junius* had a significant effect on the size structure of small *P. lydia* (Appendix D). Large *P. lydia* and the interaction between large *P. lydia* and *A. junius* had no effect (Appendix D). The individual analysis showed that the increase in mean body length of small *P. lydia* was significantly lower when *A. junius* was present (Appendix D). However, the significant increase in the positive skew of body length (i.e., relatively more small and fewer large individuals) from 0.15 without *A. junius* to 0.55 with *A. junius* (Appendix D) suggests that this could be due to size-selective predation on large prey individuals. This was supported by the significant reduction in head size in *A. junius* treatments (Appendix D).

Prey activity experiment

The laboratory experiment showed that the activity of small *P. lydia* was significantly affected by the interaction of *A. junius* and large *P. lydia* (interaction term: $F_{1,26} = 5.29$, $P < 0.03$). A post hoc multi-comparison showed that all treatments with the predator and/or cannibal were significantly different from the control ($P < 0.05$), but there was no difference between treatments with predator, cannibal, or both ($P > 0.05$) (Fig. 5A). Similarly, the survival of mosquito larvae only significantly increased in the presence of *A. junius* by 3% ($F_{1,26} = 9.54$, $P < 0.005$), but was not affected by the presence of cannibals ($F_{1,26} = 1.80$, $P > 0.19$) or the interaction of cannibals and predators ($F_{1,26} = 0.75$, $P = 0.4$) (Fig. 5A). The presence of predators significantly reduced the median of the probability of a cannibalistic attack on average by 81% ($Z_{4,7} = 2.133$, $P < 0.03$) (Fig. 5B), it reduced the foraging activity of cannibals by 61% ($F_{1,13} = 12.47$, $P < 0.004$), and reduced their total attack rates by 53% ($F_{1,13} = 5.90$, $P = 0.03$) (Fig. 5C).

DISCUSSION

To predict the impact of cannibalism on community dynamics we need to understand when and how cannibalism alters species interactions and what the underlying mechanisms are. This study shows for the first time that cannibalism in the prey can strongly alter the functional relationship between predator and prey and lead to nonlinear interactions. The nonlinear interactions resulted from different behavior- and density-mediated indirect effects that are not possible without cannibalism (Fig. 1E).

Indirect interactions resulting from cannibalism and consequences for community dynamics

Theory predicts that cannibalism in the prey has important long-term consequences for community dynamics because it can alter the strength and direction of trophic cascades (Rudolf 2007*b*). When the prey and the predator compete for a shared resource (i.e., intraguild predation), increasing the predator density should lead to a decrease in the bottom resource if cannibalism in the prey is stronger than predation, while the resource will increase if predation is stronger than cannibalism. In this study, the indirect interaction resulting from the consumption of cannibals did not alter the predation rate but instead reduced cannibalism rates, which indirectly compensated for the added mortality due to predation. Per capita predation rates were generally much higher than cannibalism rates, which suggests that the direction of trophic cascades would not be altered by this interaction, but the observed cannibalism would still considerably reduce the strength of the top-down control due to the dampened effects on prey survival.

The study revealed that besides considering the density-mediated indirect effects resulting from cannibalism, it is also important to account for the concurrent behavior-mediated indirect effects. Indeed, results showed that the indirect effects of behavioral interactions were even stronger than the effects of lethal interactions, although this difference is likely to be density dependent if the functional response for the consumption of cannibals is not linear. However, the important difference between density- and behavior-mediated indirect interactions is that the latter alter the per capita interaction strength between functional groups.

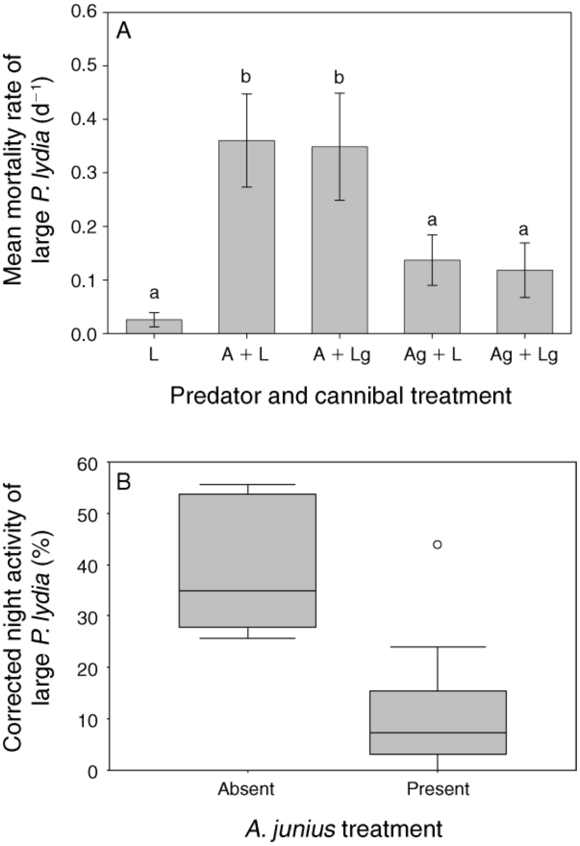

FIG. 4. (A) Mortality rate (mean ± SE) of large cannibalistic *P. lydia* in different predator (A) and cannibal (L) treatments; g = glued (i.e., nonlethal). Treatments with different letters are significantly different at $P = 0.05$ after correcting for the false discovery rate to control for Type I error due to the multiple comparisons (Benjamini and Hochberg 1995). (B) Reduction in corrected night activity of cannibalistic large *P. lydia* in response to the nonlethal presence of *A. junius*, averaged across three consecutive night observations. The gray box indicates the 50% quartile, the black line within the box indicates the median, and the whiskers give the range excluding one significant outlier (shown by the small circle) in the treatment where *A. junius* was present.

Based on current theory, a behavior-mediated reduction in the per capita predation rate would reduce the strength of top-down cascades (Rudolf 2007*a*, *b*). Although predation rates were on average reduced by 32.6% in the presence of cannibals, this difference was not significant. However, to estimate the difference, it was necessary to sum the variance of four treatments resulting in a large variation in predation rates. Furthermore, accounting for this behavioral effect in the full model improved the model fit by >20% and allowed it to predict most of the observed mortality. Thus, the absence of significance might reflect a lack of statistical power rather than the lack of biological

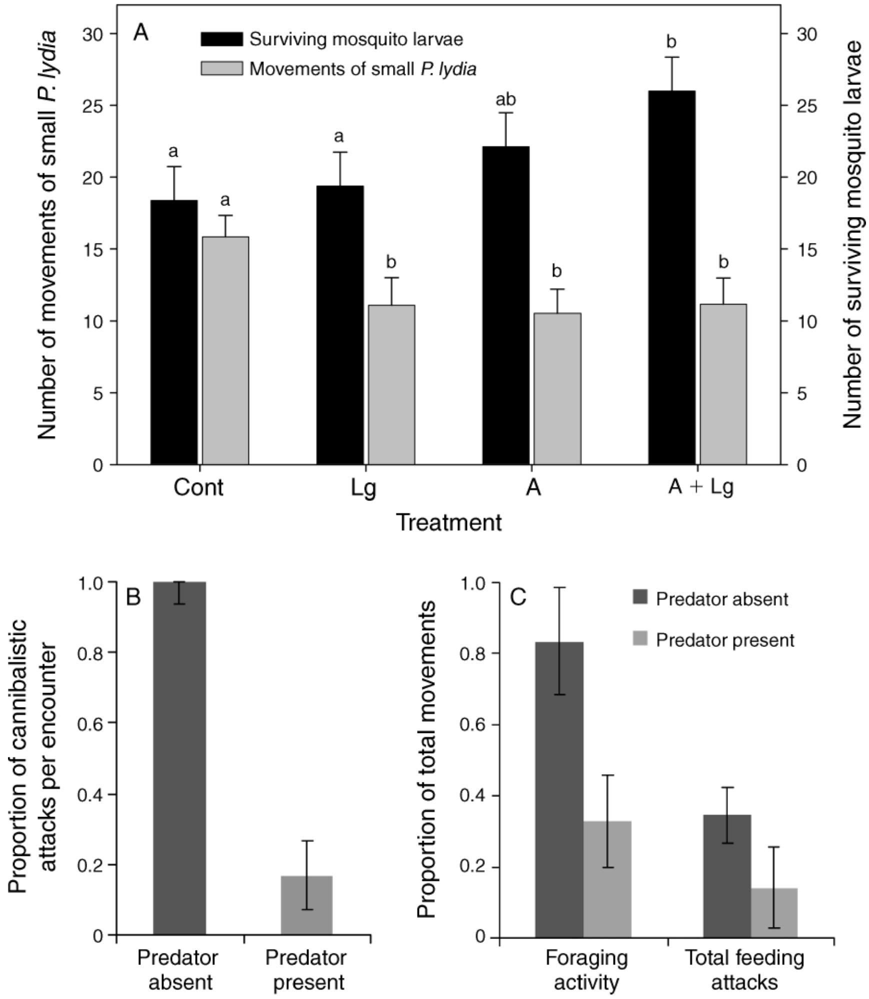

FIG. 5. Movement and foraging activities of (A) small and (B, C) large *P. lydia* in the respective treatments in the laboratory behavioral experiment. (A) Number of movements of small *P. lydia* and surviving mosquito larvae (mean ± SE) in all treatments manipulating the nonlethal presence or absence of cannibalistic large *P. lydia* (Lg) and the predator *A. junius* (A). Within each response variable, treatments with different letters are significantly different at $P = 0.05$ after correcting for the false discovery rate to control for the Type I error due to the multiple comparisons (Benjamini and Hochberg 1995). (B) Median (±25% quartile) of the proportion of physical encounters between large and small *P. lydia* resulting in a cannibalistic attack. (C) The proportion of the foraging activity (excluding attacks) and proportion of attacks on mosquito larvae plus small conspecifics (mean ± SE) relative to the total number of movements (which include fleeing movements; see Appendix B for details).

importance and the absence of an indirect effect. Although the full model slightly overestimated the mortality on average, this was largely driven by one replicate with the lowest observed mortality, and the model slightly overestimated the mortality as often as it slightly underestimated it.

On the other hand, behavior-mediated indirect interactions clearly reduced the per capita cannibalism rates in the presence of the predator. Both field and laboratory experiments suggest that the reduced cannibalism rate in the presence of the predator was largely due to changes in the behavior of the cannibals rather than changes in the behavior of small conspecifics. Predators and cannibals had similar and nonadditive effects on the activity of small prey, but both field and laboratory experiments showed that cannibals decreased their activity and were less likely to engage in cannibalism. This reduction in the cannibalism rate reduced the net impact of the predator on prey mortality. As a consequence it could reduce the strength of top-down cascades further than expected from mere consumptive interactions. In systems where cannibalism and predation rates are similar, such behavioral effects could even lead to the reversal of the direction of trophic cascades (i.e., decrease in bottom resource) depending on the relative competitiveness of predator and prey for a shared resource (Rudolf 2007*b*). This indicates the crucial importance of accounting not only for density-mediated but also for behavior-mediated indirect interactions to predict the consequences of cannibalism for community dynamics, especially given that most species reduce their foraging rates in response to the risk of predation (Lima 1998). Thus, while the long-term effects of behavioral interactions could also be affected by trade-offs in growth rates (Bolker et al. 2003), these results nevertheless clearly demonstrate how the density- and behavior-mediated indirect interactions resulting from cannibalism can substantially alter the functional relationship of predator–prey systems and the dynamics of communities.

Mortality risk reduction through cannibalism in the prey

The results clearly showed that the cannibalistic prey had a substantially lower mortality rate than expected without cannibalism, indicating that cannibalism can strongly decrease the per capita impact of a predator on its prey. Previous studies have shown a similar mortality risk reduction in the prey due to the indirect effects resulting from the interaction of predation and cannibalism in the predator, but this was due to a reduction in the predation rates of the predator itself (Sih 1982, Crumrine 2005, Rudolf 2006, 2007*a*, 2008). In contrast, I found that the indirect effects resulting from the interaction of predation and cannibalism in the prey mostly reduced cannibalism rates, which increased prey survival and thus indirectly compensated for the added mortality due to predation. This indicates that although cannibalism had a similar effect on prey survival irrespective of the trophic position at which it occurred, the specific underlying mechanisms differ. These differences have important effects on long-term community dynamics (Rudolf 2007*b*) and emphasize the need to account for the trophic position at which cannibalism occurs when integrating it into community models.

In three-species systems, multi-predator interactions can result in higher than expected mortalities (risk enhancement) (Soluk and Collins 1988, Losey and Denno 1998, Eklöv and VanKooten 2001) and lower than expected mortalities (risk reduction) (Wissinger and McGrady 1993, Crumrine and Crowley 2003, Vance-Chalcraft and Soluk 2005), although the latter seems to be more common. In general, the outcome will depend on the specific ecology of the predators involved (Vance-Chalcraft and Soluk 2005). If one predator is able to consume the other predator (or cannibal), risk reduction is likely, as observed in the present study. However, if both predators differ in their foraging modes and habitat use, their interaction can lead to a higher than expected mortality risk. In the present study, cannibals and their victims are very similar in their ecology (i.e., mostly burrowing in substrate, less active foragers), while both differ considerably from the heterospecific predator (i.e., mostly in vegetation, very active forager). However, both cannibals and predators share the same prey, and this overlap in the feeding niche might be enough to explain why the observed risk reduction was very high, despite this disparity in ecology. Mortality risk enhancement might be more likely in systems where cannibals are not subject to predation. This might reduce the behavioral interference between cannibals and predators and emphasize the differences in the ecology of predator and prey. Future studies that examine the effects of cannibalism in the prey in such systems will provide important new insight into the general effects of cannibalism on the functional relationship in predator–prey systems.

Consequences of cannibalism vs. competition for predator–prey interactions

Both cannibalism and competition can result in density-dependent mortality, but besides the obvious energy gain with cannibalism, the consequences for the dynamics of species interactions are often not differentiated in food web models (e.g., Hart 2002, Williams and Martinez 2004, and references in Claessen et al. 2004). The present study clearly demonstrates that cannibalism can introduce several indirect interactions (Fig. 1E) that alter the functional relationship between a predator and its prey. These indirect interactions are not possible with simple density-dependent mortality, such as competitive interactions. For example, with cannibalism, changes in the behavior of cannibals in response to the predator strongly increased prey survival due to reduced cannibalism rates. With intraspecific competition in the prey, the effect of changing the behavior would not necessarily reduce or alter resource competition, and the behavioral response has either no consequence on prey survival (Altwegg 2002), or can even reduce survival in the long term if competition is increased and foraging decreased among vulnerable prey (Peacor and Werner 2001, Turner 2004).

With resource competition in the prey, the effect of the predator on prey mortality often decreases with increasing food resources for the prey (Bolnick and Preisser 2005). Cannibalism is usually dependent on the relative abundance of alternative prey and conspecific prey (Fox 1975*b*, Polis 1981, Leonardsson 1991, Rudolf 2008): if the abundance of heterospecific prey is relatively high, cannibalism rates are low. The mechanistic model developed in this study suggests that under these conditions the indirect interaction effect of predators on cannibalism rates would be reduced, which in turn would increase the impact of the predator on prey mortality. Thus, the effect of increasing the productivity of the prey resource is likely to result in opposite outcomes for cannibalism and competition.

With interference competition, the change in behavior or prey mortality can increase the survival of the prey if it reduces the interference and increases the resource intake per individual (Morin et al. 1983, Wilbur 1987). In that case, the effect of interference competition would be similar to the effect of cannibalism in the prey. With cannibalism, however, small prey individuals can show antipredator behaviors toward cannibalistic conspecifics (e.g., Leonardsson 1991, Van Buskirk 1992, Rudolf 2006) that are likely to reduce the heterospecific predation risk if the antipredator response is general. This behavior and the resulting indirect interactions are not expected with interference competition, emphasizing the importance of differentiating between factors that cause intraspecific density dependence.

In conclusion, this study suggests that if the prey are cannibalistic, we cannot predict the community dynamics by simply assuming unstructured density-dependent mortality, because cannibalism alters the functional relationship between a predator and its prey. Instead, it is important to account for the trophic structure resulting from cannibalism within the prey population with all the resulting nonlinear dynamics. This indicates the need to simultaneously integrate inter- and intraspecific size-structured interactions into food web theory to reliably predict the dynamics and functioning of communities.

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APPENDIX A

Details of gluing procedure and experimental test of effectiveness (*Ecological Archives* E089-179-A1).

APPENDIX B

Summary table of interaction coefficients, interaction modifications, model parameters, and model performance (*Ecological Archives* E089-179-A2).

APPENDIX C

Detailed methods of laboratory prey activity experiment (*Ecological Archives* E089-179-A3).

APPENDIX D

MANOVA and ANOVA analysis of the treatment effects on the size structure of small *Plathemis lydia* (*Ecological Archives* E089-179-A4).