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Spatial arrangement of prey affects the shape of ratio-dependent functional response in strongly antagonistic predators

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Abstract. Predators play a key role in shaping natural ecosystems, and understanding the factors that influence a predator's kill rate is central to predicting predator–prey dynamics. While prey density has a well-established effect on predation, it is increasingly apparent that predator density also can critically influence predator kill rates. The effects of both prey and predator density on the functional response will, however, be determined in part by their distribution on the landscape. To examine this complex relationship we experimentally manipulated prey density, predator density, and prey distribution using a tadpole (prey)–dragonfly nymph (predator) system. Predation was strongly ratio-dependent irrespective of prey distribution, but the shape of the functional response changed from hyperbolic to sigmoidal when prey were clumped in space. This sigmoidal functional response reflected a relatively strong negative effect of predator interference on kill rates at low prey: predator ratios when prey were clumped. Prey aggregation also appeared to promote stabilizing density-dependent intraguild predation in our system. We conclude that systems with highly antagonistic predators and patchily distributed prey are more likely to experience stable dynamics, and that our understanding of the functional response will be improved by research that examines directly the mechanisms generating interference.

Key words: *foraging; interference; intraguild predation; predator–prey; spatial heterogeneity.*

INTRODUCTION

Predators play a key role in shaping natural ecosystems, and understanding the factors that influence a predator's kill rate is central to predicting predator–prey dynamics (Hassell 1978, Turchin 2003). While prey density has a well-established effect on the predation rate (i.e., via functional and numerical responses; Holling 1959), it is increasingly apparent that predator density also critically influences per capita kill rates in many, if not most, systems (Abrams and Ginzburg 2000, Skalski and Gilliam 2001, Arditi and Ginzburg 2012). Yet, exactly how to incorporate the effect of predator density on the functional response remains somewhat controversial (e.g., Arditi and Ginzburg 2012, Abrams 2015). Ratio-dependent functional response models propose that the per capita kill rate depends on the relative abundance of prey per predator (Arditi and Ginzburg 1989). Proponents of ratio dependence argue strongly that

predation will be prey dependent (i.e., governed by prey density only) when predators are evenly distributed, but ratio dependent when predators are clumped (e.g., Arditi et al. 1991, Arditi and Saiah 1992). Even beyond proponents of ratio dependence, theoreticians have increasingly indicated that the functional response is strongly influenced by the spatial arrangement of predators and prey (e.g., Cosner et al. 1999, Fryxell et al. 2007, Fortin et al. 2015). The development of reliable predator–prey models therefore depends on our ability to resolve general relationships between prey density, predator density, and their distributions on the landscape.

Broadly speaking, the effect of prey distribution on a predator's kill rate depends on how it affects the predator's ability to encounter, detect, or capture prey (Beauchamp 2014). Theoretical work generally suggests that prey aggregation should reduce per capita kill rates because search efficiency declines as prey become more tightly aggregated (e.g., Rohlf 1969, Fryxell et al. 2007). Moreover, predators should congregate toward (or compete for) food-rich patches, meaning that prey clustering can further reduce kill rates by increasing

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the opportunity for predator–predator interactions (i.e., interference). For example, the frequency of aggressive interactions among predators should increase with spatial heterogeneity in predators or prey (Hassell 1978), and increasingly require time that would otherwise be spent searching for or handling prey. Similarly, when prey are clustered in a few high quality sites dominant individual predators can prevent subordinates from foraging effectively, creating an overall decline in per capita kill rate. For strongly antagonistic predators (e.g., those experiencing strife or intraguild predation), spatial heterogeneity of prey may compound existing effects of interference on predator kill rates, leading to further reductions in per capita rates of predation. Such additive reductions to predation efficiency should occur primarily at low prey: predator ($N:P$) ratios, when more predators are competing for fewer prey.

Herein, we manipulated prey density, predator density, and prey distribution, using a tadpole (prey)–dragonfly nymph (predator) system, and find that when prey are clumped interference plays an even stronger role in reducing predation at low $N:P$ ratios than would be predicted by hyperbolic ratio-dependent models.

METHODS

Each experimental tank received 6, 12, 24, or 60 tadpoles (*Lithobates clamitans*; wet mass 0.015 ± 0.0004 g [mean \pm SE]), and 1, 3, or 6 late-instar dragonfly nymphs (*Anax junius*), yielding 12 combinations of prey and predator densities with ratios ranging from 1:1 through 60:1. Tanks measured 50.8×25.4 cm, were filled 10 cm deep with water, and tank bottoms were lined with plastic mesh, which enabled nymphs to move naturally. Wax paper affixed to the back and sides blocked visual cues from adjacent tanks. Two lines on the tank bottoms delineated three equal-sized areas, each measuring 16.9×25.4 cm.

To manipulate the prey distribution within a tank, tadpoles were added to inverted bottomless plastic cups (9 cm diameter). For the “even” distribution treatment tadpoles were divided evenly among three cups, one placed in each section of the tank, while for the “clumped” treatment all tadpoles were placed into a single cup placed on either the right or left side of the tank (assigned randomly). To help maintain the initial prey distribution, approximately 3.7 mL of fresh-shredded, boiled, baby spinach was added to each tank as tadpole food, divided evenly among the three cups or added solely to a single cup, according to treatment. Predators were added by placing them into inverted bottomless plastic cups (7 cm diameter), which prevented physical contact with prey and among nymphs. Once all animals were arranged in tanks they were left undisturbed for a 15-min acclimation period. Nymphs were given three tadpoles 12 h before each trial to standardize hunger, and tadpoles were fed ad libitum for 24 h prior to the trials. Tadpoles are less active when well fed and when exposed to predator cues

(Fraker 2008, Bennett et al. 2013), therefore our manipulations of prey distribution should be stable over the short-term.

Following the acclimation period, all tadpoles, and then all dragonfly nymphs, were released, allowing nymphs to freely consume tadpoles and interact with other nymphs for 3 h. Every 30 min, we counted the number of tadpoles and dragonfly nymphs in each of the three sections of each tank. Once 3 h had elapsed, all nymphs were removed and the number of remaining tadpoles was recorded. This process was fully replicated three times, each using tadpoles from a separate brood (wet mass 0.0156 ± 0.0044 g, 0.0151 ± 0.0033 g, and 0.0126 ± 0.0027 g, respectively [mean \pm SD]). In addition to these full replicates sets, 12 more replicates were conducted focusing on the lower prey densities to compensate for increased variability in proportion of prey killed, as recommended by Juliano (1993). Specifically, the following six $N:P$ combinations were conducted 6:1, 6:3, 6:6, 12:3, 12:6, and 24:6 for both even and clumped distribution treatments. This gave us a final total of $n = 84$ tanks. On 17 occasions, one dragonfly nymph captured and killed another; to avoid the complexity of integrating changes in predator density over time, we immediately replaced the killed nymph. We recorded the first 20 min of a single replicate from each treatment (i.e., $n = 24$ tanks) using a top-mounted Nikon Coolpix AW110 (Nikon Inc., Melville, New York, USA). Despite the limited sample size, this provided an additional means to examine the behavioral mechanisms involved.

To evaluate our ability to manipulate prey density over the duration of our predation experiment, we calculated the Morisita’s index (I_q) for each tank at each half-hour time interval (Morisita 1959). This gave us an estimate of the spatial distribution of prey (even or clumped) in the tanks over time. A Morisita’s index value < 1 indicates a more even distribution than expected by chance, a value $= 1$ indicates a random distribution, and a value > 1 indicates a clumped population. The minimum value is 0 and the maximum value is equal to the number of sampling areas (in our case, this was 3). We used a linear mixed model to examine the effect of prey density, prey distribution treatment, time, and their interactions, on the observed prey distribution. Repeated observations were nested within tank and set as a random effect.

Next, we compared the fit of multiple competing models to determine how prey distribution influenced (1) the shape of the functional response and (2) the extent to which predation was prey or ratio dependent. Prey-dependent functional response models were fit using the theta-sigmoid model

$$F_i = \frac{aN^\theta}{1 + ahN^\theta} \quad (1)$$

where F_i is the kill rate of prey i , N is prey density, a is the attack rate, h is the handling time, and θ is a dimensionless parameter defining the shape of the curve.

To determine the shape of the functional response, we fit models where $\theta = 1$ (i.e., hyperbolic), $\theta = 2$ (i.e., sigmoidal), or where θ was estimated from the data. For the ratio-dependent models we fit both the Arditi-Ginzburg model (Eq. 2) and Arditi-Akçakaya (Eq. 3) models, as the Arditi-Akçakaya model allows for partial ratio dependence

$$F_i = \frac{aN/P}{1+ahN/P} \quad (2)$$

$$F_i = \frac{aN P^{-m}}{1+ahNP^{-m}} \quad (3)$$

where P is the predator density, and m relates the attack rate to predator density such that a value of 0 indicates pure prey dependence and a value of 1 indicates ratio dependence. Prey were not replaced as they were killed, and we account for depletion of prey over time by using the formulations of these models provided by Okuyama and Ruyle (2011). These formulations also allowed us to examine the fit of ratio-dependent models where $\theta = 1$ (i.e., hyperbolic), $\theta = 2$ (i.e., sigmoidal), or where θ was estimated from the data. We estimated parameters for all models by applying the R code provided by Okuyama and Ruyle (2011), with all parameter estimates constrained to biologically realistic values (i.e., values >0). Best-fit models were identified using Akaike's information criterion (AIC) corrected for small sample size (AIC_c; Burnham and Anderson 2002), and we considered models within 2 AIC_c values from the best-fit model as being statistically indistinguishable. To obtain bootstrap confidence intervals for our parameter estimates, we fit each model to 2000 resampled versions of our data set and calculated the 2.5 and 97.5 percentiles from the resulting distributions.

We then examined the role of prey density, predator density, and prey distribution on time to first intraguild predation event (i.e., occasions where one nymph captured and killed another). Here, we employed Cox proportional hazards regression (Cox 1972), and used a model selection approach to determine the best predictive model. Models were compared using AIC_c as above. We also fit a model using the $N:P$ ratio as a predictor to determine whether intraguild predation could be explained by ratio-dependent mechanisms. Tanks with a single predator were excluded, as intraguild predation was not possible, leaving a total of $n = 58$ tanks for the analysis. Tanks where intraguild predation was not observed were censored. From the video footage, we extracted the number of interference events among nymphs in each tank. We considered an interference event as being initiated when two nymphs directed their gaze at one another, and ending when either nymph directed their gaze and motion away from the other nymph. All analyses were conducted in R (R Development Core Team 2015).

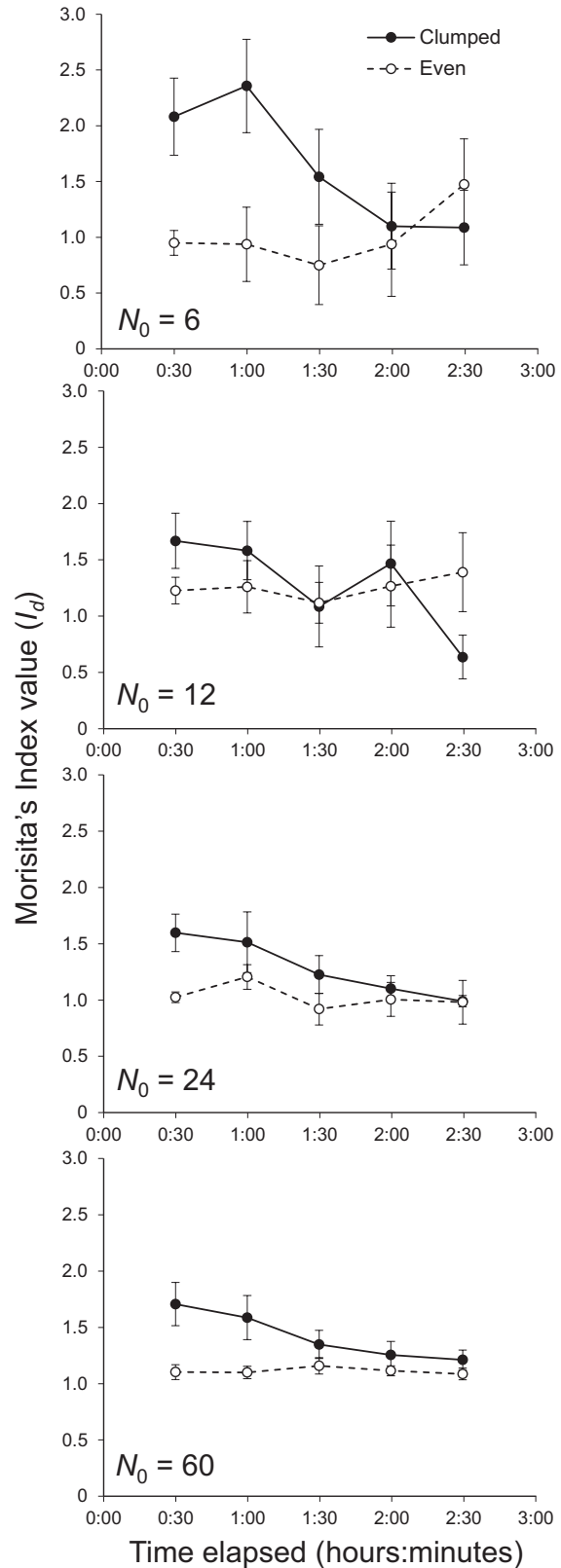


FIG. 1. The mean \pm SE dispersion of prey in experimental arenas for even and clumped treatments in tanks starting with 6, 12, 24, and 60 prey, measured at 30-min intervals over the experiment.

Table 1. Results from fitting prey-dependent, predator-dependent, and ratio-dependent functional response models for dragonfly nymphs feeding on tadpoles arranged in an even or clumped distribution.

Even distribution	<i>k</i>	AIC _c	ΔAIC	<i>w</i>	θ	<i>a</i>	<i>h</i>	<i>m</i>
Type II (hyperbolic)	2	161.49	11.87	0.0014	1	0.245 (0.148, 0.515)	0.078 (0.000, 0.191)	
Type III (sigmoidal)	2	161.53	11.91	0.0014	2	0.038 (0.009, 0.088)	0.161 (0.037, 0.237)	
Theta-sigmoid (estimated θ)	3	163.80	14.18	0.0004	1.174 (0.692, 11.726)	0.181 (0.000, 0.413)	0.106 (0.000, 0.235)	
<i>Arditi-Ginzburg</i> (hyperbolic)	2	149.62	0.00	0.5271	1	1.021 (0.718, 1.858)	0.068 (0.036, 0.149)	1
Arditi-Akçakaya (hyperbolic)	3	151.79	2.17	0.1778	1	1.312 (0.556, 13.830)	0.073 (0.038, 0.154)	1.139 (0.552, 2.474)
Arditi-Ginzburg (sigmoidal)	2	156.17	6.55	0.0199	2	0.110 (0.035, 0.269)	0.142 (0.054, 0.224)	1
Arditi-Akçakaya (sigmoidal)	3	155.59	5.97	0.0266	2	0.808 (0.130, 40.915)	0.134 (0.068, 0.218)	2.367 (1.195, 4.791)
Arditi-Ginzburg (estimated θ)	3	151.66	2.04	0.1897	0.878 (0.521, 4.525)	1.428 (0.002, 3.281)	0.060 (0.031, 0.182)	1
Arditi-Akçakaya (estimated θ)	4	154.11	4.49	0.0557	0.881 (0.423, 3.771)	1.434 (0.110, 14.216)	0.060 (0.000, 0.191)	1.008 (0.568, 4.563)
Clumped distribution								
Type II (hyperbolic)	2	141.548	8.03	0.0089	1	0.237 (0.168, 0.439)	0.022 (0.000, 0.083)	
Type III (sigmoidal)	2	140.60	7.08	0.0144	2	0.031 (0.014, 0.071)	0.105 (0.064, 0.148)	
Theta-Sigmoid (estimated θ)	3	142.91	9.39	0.0045	1.963 (0.850, 6.731)	0.034 (0.000, 0.304)	0.104 (0.000, 0.155)	
Arditi-Ginzburg (hyperbolic)	2	139.55	6.03	0.0243	1	1.574 (1.048, 2.554)	0.068 (0.048, 0.094)	1
Arditi-Akçakaya (hyperbolic)	3	139.41	5.89	0.0260	1	0.656 (0.235, 1.744)	0.051 (0.000, 0.083)	0.531 (0.000, 1.228)
<i>Arditi-Ginzburg</i> (sigmoidal)	2	133.52	0.00	0.4949	2	0.123 (0.063, 0.251)	0.101 (0.071, 0.135)	1
Arditi-Akçakaya (sigmoidal)	3	135.38	1.86	0.1949	2	0.205 (0.058, 0.767)	0.102 (0.074, 0.134)	1.328 (0.416, 2.350)
Arditi-Ginzburg (estimated θ)	3	135.60	2.08	0.1746	1.76 (1.013, 4.028)	0.220 (0.002, 1.141)	0.094 (0.055, 0.130)	1
Arditi-Akçakaya (estimated θ)	4	137.82	4.30	0.0576	1.941 (1.049, 4.905)	0.222 (0.002, 1.389)	0.100 (0.060, 0.134)	1.285 (0.401, 3.055)

Notes. Numbers in brackets are the bootstrapped 95% confidence intervals. Parameters are *k*, the number of estimated parameters in the model; AICc, Akaike’s information criterion adjusted for sample size; ΔAIC, the AICc (Akaike’s information criterion adjusted for sample size) for the model of interest minus the smallest AICc for the set of models being considered, the exponent which determines the shape of the functional response; *a*, the attack rate or equivalent parameter in predator- and ratio-dependent models; *h*, handling time; and *m*, the interference parameter. Akaike weights are indicated in the *w* column. Italicized rows indicate the best fit model for the even and clumped prey distribution scenarios, respectively.

RESULTS

Our manipulation of prey distribution was largely successful. Prey from the clumped distribution treatment had a significantly higher Morisita’s Index value than the prey in the even distribution treatment ($F_{1,62} = 10.12$, $P = 0.002$). Prey in the even distribution treatments followed a distribution close to random ($I_d \approx 1$), which remained largely unchanged throughout the trials, whereas prey in the “clumped” distribution treatment

followed a more clumped distribution ($I_d > 1$) but became less patchily distributed over time (distribution × time interaction: $F_{1,256} = 10.83$, $P = 0.001$; Fig. 1). The main effect of time was significant ($F_{1,256} = 12.83$, $P < 0.001$), but prey density and remaining terms were all nonsignificant (all $P > 0.64$).

Prey distribution significantly influenced the shape of the functional response, although both the even and clumped distribution treatments were strongly ratio dependent. Specifically, the hyperbolic ratio-dependent

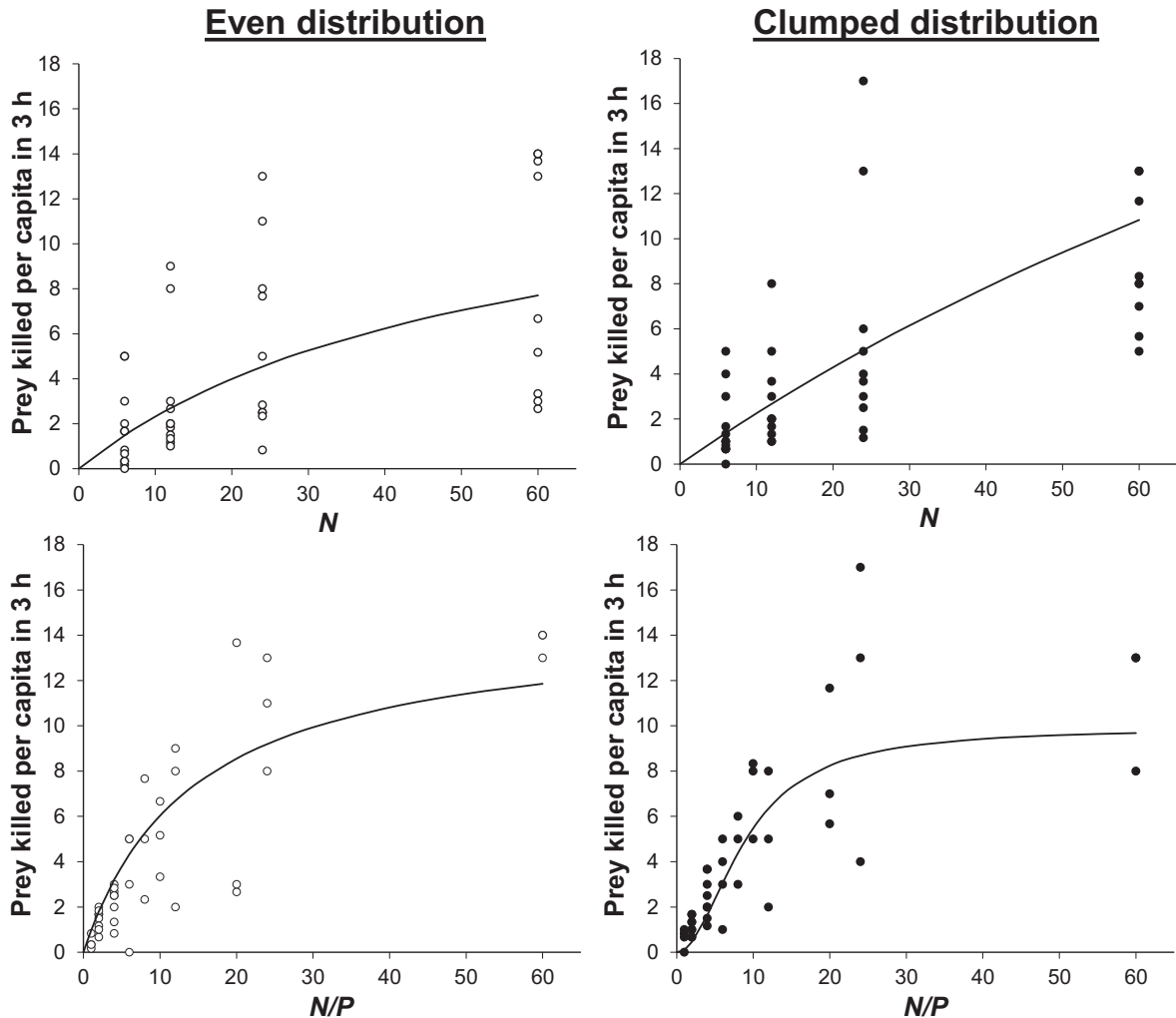


FIG. 2. The fitted functional response curves for prey-dependent (above) and ratio-dependent (below) models in the even (left) and clumped (right) prey treatments, plotted with the raw consumption data. The x-axes correspond to the initial N (or N/P).

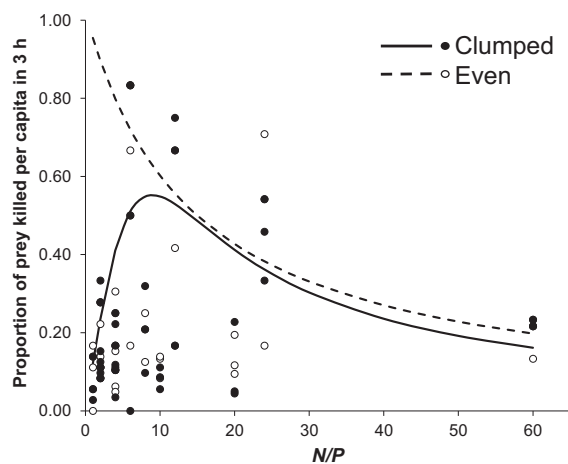


FIG. 3. The best fit functional response models (which account for depletion) and raw predation data for the even and clumped prey treatments, expressed as a proportion of prey killed.

model was strongly supported for the evenly distributed prey treatment, whereas the clumped prey treatment was clearly sigmoidal and ratio dependent (Table 1, Fig. 2). Therefore, when prey are clumped predator efficiency initially increases then declines with increasing relative abundance of prey (Fig. 3).

Intraguild predation was best explained by a model that included prey density and the predator density \times prey distribution interaction (Table 2). This reflected that the risk of intraguild predation decreased with increasing prey density, and increased with predator density more quickly when prey were clumped. The number of interference events appeared to increase with predator density only when prey are clumped (Fig. 4).

DISCUSSION

Using an experimental tadpole–dragonfly nymph system, we examined the effect of prey spatial

Table 2. Model selection based on Akaike's information criteria corrected for small sample size (AIC_c) for Cox proportional hazards models predicting time to first intraguild predation event.

Model	AIC_c	ΔAIC	w
<i>Predator</i> × <i>Distribution</i> + <i>Prey</i>	87.79	0.00	0.501
<i>Predator</i> × <i>distribution</i>	89.92	2.13	0.173
<i>Predator</i> + <i>Prey</i>	90.69	2.90	0.118
<i>Predator</i>	92.04	4.24	0.060
<i>Predator</i> × <i>Prey</i> × <i>Distribution</i>	92.15	4.36	0.057
<i>Predator</i> + <i>Prey</i> + <i>Distribution</i>	92.74	4.95	0.042
<i>Predator</i> + <i>Distribution</i>	94.18	6.39	0.021
<i>Predator</i> + <i>Prey</i> × <i>Distribution</i>	94.54	6.75	0.017
Ratio	97.42	9.62	0.004
Ratio × <i>Distribution</i>	98.81	11.02	0.002
<i>Prey</i>	99.24	11.44	0.002
Null	99.27	11.48	0.002
Ratio + <i>Distribution</i>	99.64	11.85	0.001
<i>Distribution</i>	101.39	13.59	0.001
<i>Prey</i> + <i>Distribution</i>	101.43	13.64	0.001

Note. Akaike weights are indicated in the w column.

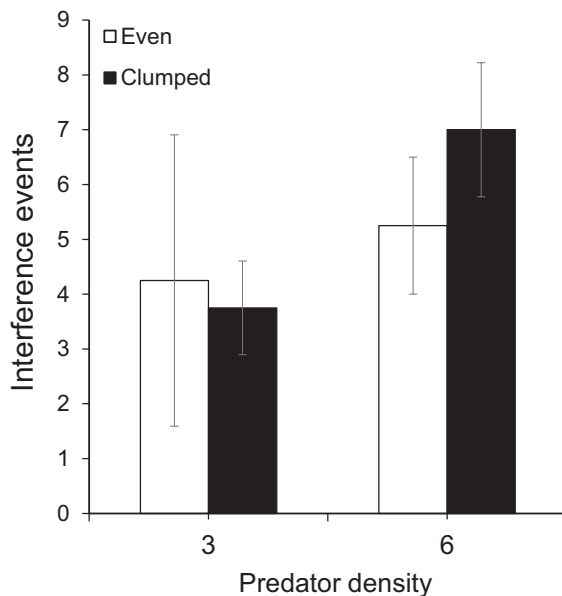


FIG. 4. The number of interference events (mean \pm SE) among three or six predators (dragonfly larvae) feeding on tadpoles that are evenly distributed or clumped within the experimental arena over a 20-min period from the onset of the trial.

distribution on the predator's per capita kill rate (i.e., the functional response). We found clear evidence for ratio-dependent predation irrespective of prey distribution,

indicating high levels of interference in both treatments. The functional response was hyperbolic when prey were evenly distributed, but shifted to sigmoidal when prey were clumped. This shift reflected a strong reduction in per capita kill rate at low $N:P$ ratios in the clumped prey treatment. Changes in the shape of the functional response can have important impacts on the dynamics of predator-prey populations, and our work suggests that sigmoidal ratio-dependent functional response models may provide better estimates of predation at low $N:P$ ratios when prey are patchily distributed.

Interference is generally thought to increase stability in predator-prey systems (Hassell and May 1973, Free et al. 1977, Freedman 1979), however, a shift from hyperbolic to sigmoidal ratio-dependent predation should further promote stability by more strongly inhibiting predators from overexploiting prey at low $N:P$ ratios (Fig. 3). The patterns of intraguild predation observed here are typical of cannibalistic and intraguild interactions (e.g., Fox 1975, Polis et al. 1989), and would have parallel effects on the dynamics of natural systems. Specifically, density-dependent intraguild predation reduces predator density when it is high and thereby diminishes the likelihood that prey populations are overexploited (Fox 1975, Freedman 1979), whereas reductions in lethal predator-predator interactions when prey are abundant leave more predators available to consume prey and should thus impede prey populations from unbounded growth. Our experiment therefore illustrates that prey distribution can influence both the shape of the functional response and the pattern of intraguild predation, such that predator-prey systems with clumped prey and highly antagonistic predators should experience elevated levels of stability.

Previous work has suggested that the functional response will shift from prey-dependent to predator-dependent as prey distribution moves from evenly distributed to clumped (Arditi and Saiah 1992, Arditi and Ginzburg 2012), however, we found the functional response to be predator-dependent irrespective of prey distribution (Table 1). Of course, predator dependence can be generated in many ways, and several mechanisms have been identified (Hassell 1978, Abrams and Ginzburg 2000). Dragonfly nymphs are incredibly aggressive toward conspecifics, and predators in both prey distribution treatments engaged in frequent and prolonged bouts of aggressive interaction (T. J. Hossie, *personal observation*; Fig. 4). Both assessments of predator-predator interaction indicate that rates of interference increase more rapidly with predator density when prey are clumped (Table 2, Fig. 4). We can therefore reasonably speculate that the time available for predators to capture and kill prey was limited by time-consuming and density-dependent aggressive interactions among predators, exacerbated in the clumped-prey treatment by the limited number of high-quality sites for prey capture.

To date, few ecologists have considered sigmoidal ratio-dependent models in empirical or theoretical

research. Important exceptions include Vucetich et al. (2002) who examined predation in a natural wolf–moose system, as well as experimental work by Kratina et al. (2009) and Spataro et al. (2012). Detecting sigmoidal functional responses (prey or predator dependent) in natural systems is inherently challenging (Marshall and Boutin 1999), and Vucetich et al. (2002) acknowledge this difficulty as well for ratio-dependent models. In contrast, experimental work is clearly well positioned to reveal conditions where sigmoidal models better represent ecological processes (Hassell 1978, Kratina et al. 2007, Hossie and Murray 2010), and therefore remains critical in the development and testing of ecological theory.

Despite the many known ways by which predator dependence can arise, the key mechanisms operating in most systems remain poorly characterized. Our understanding of interference will be improved by explicitly partitioning the effects of behavioral interference (e.g., predator–predator interactions), and interference generated by processes such as non-random search (i.e., “pseudo-interference” sensu Free et al. 1977). As with the last 50 years of functional response research, future work will benefit from collaboration between empiricists, field biologists, and theoreticians. Experimental work can better examine the mechanisms of predator dependence now that the mathematical difficulties in accounting for prey depletion have been overcome (Kratina et al. 2009, Okuyama and Ruyle 2011). Field studies of natural systems are also now well positioned to identify sources of interference using newly developed technologies (e.g., Prange et al. 2006). Finally, empiricists and theoreticians have begun developing spatially explicit functional response models (e.g., Fortin et al. 2015), and now should incorporate the undeniable effects of predator interference.

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LITERATURE CITED

- Abrams, P. A. 2014. Why ratio dependence is (still) a bad model of predation. *Biological Reviews* 90:794–814.
- Abrams, P. A., and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution* 15:337–341.
- Arditi, R., and L. R. Ginzburg. 1989. Coupling in predator–prey dynamics: ratio-dependence. *Journal of Theoretical Biology* 139:311–326.
- Arditi, R., and L. R. Ginzburg. 2012. How species interact: altering the standard view on trophic ecology. Oxford University Press, New York, New York, USA.
- Arditi, R., and H. Saiah. 1992. Empirical evidence of the role of heterogeneity in ratio-dependent consumption. *Ecology* 73:1544–1551.
- Arditi, R., L. R. Ginzburg, and H. R. Akcakaya. 1991. Functional responses and heterogeneities: an experimental test with cladocerans. *Oikos* 60:69–75.
- Beauchamp, G. 2014. Social predation: how group living benefits predators and prey. Academic Press, New York, New York, USA.
- Bennett, A. M., D. Pereira, and D. L. Murray. 2013. Investment into defensive traits by anuran prey (*Lithobates pipiens*) is mediated by the starvation-predation risk trade-off. *PLoS One* 8:e82344.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Cosner, C., D. L. DeAngelis, J. S. Ault, and D. B. Olson. 1999. Effects of spatial grouping on the functional response of predators. *Theoretical Population Biology* 56:65–75.
- Cox, D. R. 1972. Regression models and life-tables. *Journal of the Royal Statistical Society. Series B (Methodological)* 34:187–220.
- Fortin, D., et al. 2015. A spatial theory for characterizing predator–multiprey interactions in heterogeneous landscapes. *Proceedings of the Royal Society B* 282:20150973.
- Fox, L. R. 1975. Factors influencing cannibalism, a mechanism of population limitation in the predator *Notonecta hoffmanni*. *Ecology* 56:933–941.
- Fraker, M. E. 2008. The effect of hunger on the strength and duration of the antipredator behavioral response of green frog (*Rana clamitans*) tadpoles. *Behavioral Ecology and Sociobiology* 62:1201–1205.
- Free, C. A., J. R. Beddington, and J. H. Lawton. 1977. On the inadequacy of simple models of mutual interference for parasitism and predation. *Journal of Animal Ecology* 46:543–554.
- Freedman, H. I. 1979. Stability analysis of a predator–prey system with mutual interference and density-dependent death rates. *Bulletin of Mathematical Biology* 41:67–78.
- Fryxell, J. M., A. Mosser, A. R. E. Sinclair, and C. Packer. 2007. Group formation stabilizes predator–prey dynamics. *Nature* 449:1041–1043.
- Hassell, M. P. 1978. The dynamics of arthropod predator–prey systems. Princeton University Press, Princeton, New Jersey, USA.
- Hassell, M. P., and R. M. May. 1973. Stability in insect host–parasitoid models. *Journal of Animal Ecology* 42:693–726.
- Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canadian Entomologist* 91:293–320.
- Hossie, T. J., and D. L. Murray. 2010. You can't run but you can hide: refuge use in frog tadpoles elicits density-dependent predation by dragonfly larvae. *Oecologia* 163:395–404.
- Juliano, S. A. 1993. Nonlinear curve fitting: predation and functional response curves. S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman & Hall, London, UK.
- Kratina, P., M. Vos, and B. R. Anholt. 2007. Species diversity modulates predation. *Ecology* 88:1917–1923.
- Kratina, P., M. Vos, A. Bateman, and B. R. Anholt. 2009. Functional responses modified by predator density. *Oecologia* 159:425–433.
- Marshall, J. P., and S. Boutin. 1999. Power analysis of wolf–moose functional responses. *Journal of Wildlife Management* 63:396–402.
- Morisita, M. 1959. Measuring of the dispersion of individuals and analysis of the distributional patterns. *Memoires of*

- the Faculty of Science, Kyushu University, Series E. *Biology* 2:215–235.
- Okuyama, T., and R. L. Ruyle. 2011. Solutions for functional response experiments. *Acta Oecologica* 37:512–516.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297–330.
- Prange, S., T. Jordon, C. Hunter, and S. D. Gehrt. 2006. New radiocollars for the detection of proximity among individuals. *Wildlife Society Bulletin* 34:1333–1344.
- R Development Core Team. 2015. R: a language and environment for statistical computing computer program. R Development Core Team, Vienna, Austria. www.r-project.org
- Rohlf, F. J. 1969. The effect of clumped distributions in sparse populations. *Ecology* 50:716–721.
- Skalski, G. T., and J. F. Gilliam. 2001. Functional responses with predator interference: viable alternatives to the Holling Type II model. *Ecology* 82:3083–3092.
- Spataro, T., S. Bacher, L.-F. Bersier, and R. Arditi. 2012. Ratio-dependent predation in a field experiment with wasps. *Ecosphere* 3:1–12.
- Turchin, P. 2003. *Complex population dynamics: a theoretical/empirical synthesis*. Princeton University Press, Princeton, New Jersey, USA.
- Vucetich, J. A., R. O. Peterson, and C. C. Schaefer. 2002. The effect of prey and predator densities on wolf predation. *Ecology* 83:3003–3013.

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