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Emergent non-consumptive predator effects alter habitat colonization by dipteran prey

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science  
in Biology at Virginia Commonwealth University.

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## Acknowledgement

We thank J. Neale, T. Price, K. Tran, and especially N. Cason and R. Lidder, for assistance with experiment setup and maintenance, data collection, encouragement, and reminders. We also thank the population-ecology lab discussion group for comments and critique on early proposal-drafts. Finally, we would like to thank the Virginia Commonwealth University's Center for Environmental Studies and Rice Center Steering Committee for funding this research, and the Rice Rivers Center for hosting.

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## Abstract

### EMERGENT NON-CONSUMPTIVE PREDATOR EFFECTS ALTER HABITAT COLONIZATION BY DIPTERAN PREY

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A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology at Virginia Commonwealth University.

Virginia Commonwealth University, 2015

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When ovipositing, prey organisms avoid habitat patches containing predator cues because predators consume, and negatively affect the fitness of their prey. Richness of predator species often enhances the strength of consumptive predator effects, but little is known about how multiple predators combined affect prey non-consumptively. We quantified dipteran colonization in aquatic mesocosms in response to varied predator richness. Multiple predator species combined reduced oviposition by *Culex* mosquitoes, chironomid midges, and the general colonizing dipteran community more than predicted by the effects of the independent predator species. Previous research which quantifies effects of multiple predators on prey as prey abundance, but does not measure consumption by predators, may be underestimating or overestimating the strength of effect by assuming equal colonization. Our findings enhance understanding of the ways predators influence abundances and distributions of their prey, and yields insight into the ways predators may non-consumptively affect prey by changing prey behavior.

## INTRODUCTION

Research on drivers of aquatic community structure has historically focused on the roles of colonization sequence, and post-colonization competition and predation (Morin, 1984; Morin, 1987; Lawler and Morin, 1993; Wellborn et al., 1996). This work has demonstrated that predators can change prey distributions and abundances (Sih et al., 1985; Morin and Lawler, 1995; Wellborn et al., 1996) by more effectively consuming prey species which are good competitors than cryptic and well defended prey (Chase and Leibold, 2003). Further, consumption of prey by predators often increases with both predator abundance and species richness (e.g., reviewed in Sih et al., 1985; Sih et al., 1998; Schmitz, 2007; Vance-Chalcraft et al., 2007; Griffin et al., 2013).

By focusing on post-colonization processes without exclusively considering whether or not prey choose to colonize, previous research has implicitly assumed that habitat colonization by prey is random with respect to predation risk. However, prey colonization can be non-random, and organisms often preferentially colonize lower-risk habitat (Binckley and Resetarits, 2003; Kiflawi et al., 2003a&b; Eitam and Blaustein, 2004; Silberbush and Blaustein, 2011). Thus, in addition to consumptive effects, predators can shape prey populations and communities non-consumptively by affecting behavior and life-history traits related to habitat colonization (Vonesh et al., 2009; Kraus and Vonesh, 2010). One way that organisms colonize habitat patches is by choosing to deposit fertilized eggs. Previous studies have demonstrated adaptive oviposition habitat selection (OHS) in response to variation in resource availability (Binckley and Resetarits, 2008; Fader and Juliano, 2014), competition (Kiflawi et al., 2003b; Fader and Juliano, 2014), and predation risk (Kiflawi et al., 2003b; Rieger et al., 2004; Silberbush and Blaustein, 2011). By sensing physical or chemical cues in the environment, prey can avoid



habitat which is likely more risky due to greater predator density (Kiflawi et al., 2003b; Eitam and Blaustein, 2004; Rieger et al., 2004; Silberbush et al., 2010; Silberbush and Blaustein, 2011; Walzer and Schausberger, 2012). While studies have shown that prey habitat selection influenced by presence and changes in abundance of predators can impact prey community structure (Kraus and Vonesh, 2010), how the effects of multiple predators combined may shape prey habitat colonization is unclear and has important implications for understanding the relationships among predator diversity, community structure, and ecosystem function.

Oviposition habitat selection theory predicts that predation risk sensitive oviposition should evolve with respect to the abiotic and biotic environment by favoring organisms that oviposit where offspring performance will be greatest (Resetarits, 1996). OHS theory also predicts that sensitivity of OHS to any particular variable should relate positively with the strength of influence that variable has on offspring performance, which has been suggested and shown to be strong in the case of predation (Resetarits, 1996, Rieger et al., 2004). Indeed, evidence shows that prey are highly sensitive to predators when making OHS decisions (Kiflawi et al., 2003a; Wasserberg et al., 2014). However, adaptive responses to predation risk require that prey can accurately assess risk. In natural communities where there are typically more than a single predator species (Schoener, 1989) adaptive OHS may represent a challenge as the consumptive effects of multiple predator species combined are often difficult to predict from the independent effects of individual species (Sih et al., 1998; Schmitz, 2007; Finke and Snyder, 2010; Griffin et al., 2013). Such emergent multiple-predator effects may result in risk enhancement, where prey suppression by combined predators is greater than predicted from their independent effects, or risk reduction, where combined predators consume fewer prey than expected. Because prey typically experience risk from multiple predators in natural communities,

theory which predicts that colonizing organisms should evolve high sensitivity to predation risk (Resetaarits, 1996) by extension also predicts that organisms should be able to assess and appropriately respond to predation risk from combined predators.

A limited number of studies have demonstrated the existence of emergent non-consumptive predator effects by showing that prey species (Steffan and Snyder, 2010) and communities (Byrnes et al., 2006) can detect and respond to multiple predators differently than would be predicted from the independent predator effects. However, despite evidence that prey suppression often increases with increasing predator diversity (Sih et al., 1998; Finke and Snyder, 2010; Griffin et al., 2013), that non-consumptive predator effects can be a large component of predator effects on prey (Binckley and Resetaarits, 2008), and that risk sensitive habitat selection is wide spread across prey taxa (Eitam and Blaustein, 2004; Rieger et al., 2004) the role of aquatic-predator richness in shaping prey OHS is yet unexplored. To elucidate how aquatic predator richness changes prey OHS we measure non-consumptive oviposition responses by prey to independent and combined predators.

## **METHODS**

### *Study System*

Our study focused on the system of temporary riverine rock pools found along the fall zone of the James River. These pools are habitat patches for many invertebrate organisms including flies, odonates, beetles, true-bugs, crayfish, snails, and worms but are often numerically dominated by culicid mosquito (up to 51%) and chironomid midge (up to 96%) larvae where they occur (Vonesh, unpubl. data). Predator assemblages in these pools can be species rich and abundant, containing from one to eight predator taxa, and from one to 57 individual predators per pool (Vonesh, unpubl. data). Odonate larvae are numerically dominant

predators in the pools, with dragonfly larvae (up to 96% of the predator assemblage) and damselfly larvae (up to 47% of the predator assemblage) often occurring together (37% of pools) (Vonesh, Unpubl. Data). Rock pools are from six to 1500 L in volume (Vonesh, unpubl. data), and occur 0.3 - 25 m apart from one another (Kraus et al., unpubl.).

### *Experimental Design*

Our experiment took place between July 14<sup>th</sup> and August 9<sup>th</sup>, 2014, in open old-field habitat at the edge of secondary oak- and pine-forests at Virginia Commonwealth University's Rice Rivers Center for Environmental Life Sciences in Charles City County, Virginia. To test for emergent non-consumptive predator effects on prey OHS we quantified oviposition by female *Culex* mosquitoes (Diptera: Culicidae), non-biting midges (Diptera: Chironomidae), and colonizing dipterans in general. As predators we used larval Halloween Pennant dragonflies (Odonata: Libellulidae: *Celithemis eponina*), larval Bluet damselflies (Odonata: Coenagrionidae: *Enallagma spp.*), and first-year *Procambarus* crayfish (Decapoda: Cambaridae: *Procambarus spp.*). We selected crayfish from 1.3 - 5.1 cm, and all odonates were between the second and last instars. Predators that died or emerged during trials were replaced.

Larval odonates are generalist predators in aquatic systems, whereas crayfish are generalist omnivores which will prey on smaller organisms. We chose these particular predators because they are abundant, and readily collected from local rock pool and stream systems, and because they all occur in rock pools, sometimes together (2% of pools) (Vonesh, Unpubl. Data). This combination makes use of predators which together utilize multiple hunting modes and foraging habitats, which is thought to contribute to the potential for synergistic or antagonistic interactions among organisms (Finke and Snyder, 2008).

We simulated rock pools using aquatic-mesocosms (37.9 L Sterilite® plastic tote-boxes) arrayed three meters apart. We filled each mesocosm with water from the James river and three L of loosely packed leaf-litter from the floor of the nearby forest stand. Mesocosms were allowed to age for one day before establishing treatments. Mesocosm experiments are a useful substitute for natural experiments because mesocosms are more easily manipulated than the natural systems they approximate, and the implications of mesocosm experiments are generally applicable so long as they are conducted at appropriate scales and under appropriate context (Srivastava et al., 2004; Chalcraft et al., 2005). Our experimental design set mesocosms within one standard deviation of the mean size, spatial proximity, predator abundance, and predator richness of rock pools in our simulated system. All three of our experimental predators are co-inhabitants of these rock pools.

For two separate experimental trials we counted and removed egg-masses of colonizing dipterans floating on the water-surface every other day for seven days (four counts per mesocosm per trial) beginning the day after treatment establishment. We focused on the initial week of colonization because we were specifically interested in OHS response to predator assemblages, and previous research has shown that patterns of OHS can change as aquatic communities assemble (Kraus and Vonesh, 2010). We removed all visible colonizers immediately before establishing treatments. The experiment involved five treatments. A no predator treatment, treatments with three individuals of one predator group, for each group independently, and a treatment with one individual from each predator group. Treatments were replicated five times in two temporal blocks for a total of 50 experimental units. We caged predators individually to separate non-consumptive effects on OHS from possible consumption of egg-rafts. Cages were made from red-plastic 16 ounce SOLO® cups with bottoms removed

and screening sealed to the open-bottom, and partially sealed to the open top to control food-supply to predators. Because prey response to chemical cues of predator presence is driven most strongly by number of prey consumed (McCoy et al., 2012) we fed predators equal numbers of mosquito larvae ( $6 \pm 2.8$  [mean  $\pm$  SD], depending upon availability) five times per trial.

### *Statistical Analysis*

We utilized generalized linear models (GLM) assuming a Poisson distribution to test both the effects of experimental treatment as well as the overall effects of predator richness on prey oviposition. We included time-block and position from the forest edge as covariates where appropriate. We considered experimental treatment and time-block as categorical variables, and predator richness and position as continuous variables. To test for non-linear predator effects on OHS we developed an *a priori* contrast between the observed response for the predator-rich treatment and the constituent single-species treatments using a Fisher's LSD linear-hypothesis test. This test compared the observed response from the multi-species treatment to a predicted response based on the proportional contributions of the observed responses in the constituent single-species treatments assuming no emergent properties (e.g. Chapman et al., 1988), hereafter the predicted response. Because we utilized a substitutive design, a linear, i.e., non-emergent, oviposition response is evidenced when the observed result is not significantly different from the predicted result. We tested the null-hypotheses that mosquitoes, non-biting midges, and general aquatic-colonizing dipteran communities do not avoid rich predator assemblages more strongly than would be predicted based on their responses to single predator treatments. Alternatively, increasing predator richness may show either increased or decreased oviposition relative to the predicted response, demonstrating an emergent OHS response.

## **RESULTS**

Both *Culex* mosquitoes ( $n = 151$  egg-rafts) and chironomid midges ( $n = 193$  egg-masses) oviposited frequently enough to be analyzed individually. *Anopheles* mosquitoes ( $n = 37$  egg-rafts) and an unidentified fourth colonizer ( $n = 11$  egg-masses) did not oviposit frequently enough to be analyzed individually, but were included in combined dipteran community oviposition analyses. There was no significant effect of position from forest edge ( $Z = -0.107$ ,  $P = 0.9150$ ) or time-block ( $Z = -1.614$ ,  $P = 0.1060$ ) on general dipteran oviposition. Chironomids did not favor pools with respect to position ( $Z = 1.170$ ,  $P = 0.2420$ ) but oviposited more frequently in August ( $Z = -4.986$ ,  $P < 0.0001$ ). Mosquitoes favored pools near the forest edge ( $Z = -2.008$ ,  $P = 0.0446$ ) and oviposited more frequently in July ( $Z = 6.417$ ,  $P < 0.0001$ ).

Predators had strong effects on dipteran colonization. Accounting for position and time-block where appropriate, *Culex* mosquito ( $F = 28.150$ ,  $df = 5$ ,  $P < 0.0001$ ; Fig. 1a), chironomid midge ( $F = 15.406$ ,  $df = 5$ ,  $P = 0.0088$ ; Fig. 1c), and general dipteran oviposition ( $F = 37.336$ ,  $df = 5$ ,  $P < 0.0001$ ; Fig. 1e) differed across predator treatments. Furthermore, mosquito ( $F = -4.332$ ,  $P < 0.0001$ ; Fig. 1b), midge ( $F = -3.183$ ,  $P = 0.0015$ ; Fig. 1d), and general dipteran oviposition ( $F = -5.688$ ,  $P < 0.0001$ ; Fig. 1f) all decreased with increasing predator richness.

Mosquito oviposition was reduced 51% by dragonflies ( $Z = 2.773$ ,  $df = 18$ ,  $P = 0.0056$ ) and 45% by crayfish ( $Z = -2.761$ ,  $df = 18$ ,  $P = 0.0058$ ), but was not altered by damselflies, relative to the predator-free control. The predator-rich treatment received 76% fewer egg-rafts than the predator-free control ( $Z = -4.073$ ,  $df = 18$ ,  $P < 0.0001$ ), 60% fewer than the single-species average ( $Z = -2.473$ ,  $df = 18$ ,  $P = 0.0134$ ), but did not reduce oviposition when compared to dragonfly larvae, the single predator eliciting the strongest avoidance response by mosquitoes.

Midge oviposition was reduced 43% by damselflies ( $Z = 2.491$ ,  $df = 18$ ,  $P = 0.0127$ ), but not by other single predators, relative to the predator-free control. The predator-rich treatment

received 55% fewer egg-masses than the predator-free control ( $Z = -3.220$ ,  $df = 18$ ,  $P = 0.0013$ ) and 38% fewer than the single-species average ( $Z = -2.127$ ,  $df = 18$ ,  $P = 0.0334$ ), but did not reduce oviposition when compared to damselflies, which elicited the strongest avoidance by midges.

Oviposition by the dipteran community was reduced 37% by dragonflies ( $Z = 3.037$ ,  $df = 18$ ,  $P = 0.0024$ ), 31% by damselflies ( $Z = 2.570$ ,  $df = 18$ ,  $P = 0.0102$ ), and 27% by crayfish ( $Z = -2.189$ ,  $df = 18$ ,  $P = 0.0286$ ), relative to the predator-free control. The predator-rich treatment received 64% fewer ovipositions than the predator-free control ( $Z = -5.670$ ,  $df = 18$ ,  $P < 0.0001$ ), 48% fewer than the single-species average ( $Z = -3.851$ ,  $df = 18$ ,  $P = 0.0001$ ), and 43% fewer ovipositions than dragonfly-only mesocosms, which yielded the strongest community response ( $Z = -2.956$ ,  $df = 18$ ,  $P = 0.0031$ ).

## DISCUSSION

Here we show that OHS responses by *Culex* mosquitoes, chironomid midges, and the general dipteran community were reduced in predator-rich mesocosms. We also show that the dipteran community reduced oviposition beyond what would be predicted based on the effects of the independent constituent predator species. This is both the first evidence for predator richness changing prey habitat colonization, and for emergence in prey habitat colonization response. All three groups responded as if anticipating consumptive synergism among the rich predator assemblage. However, because we have not quantified this particular predator combination as consumptively synergistic, simple, or antagonistic we cannot conclude whether prey response was to only potential synergism among multiple predator species or to actual consumptive synergism. Synergism, non-interaction, or antagonism among this particular assemblage would all allow that prey are responding generally to a rich predator assemblage. Avoiding predator

richness generally makes sense as a bet-hedging life-history strategy because richness of predator species often enhances prey consumption (Finke and Snyder, 2010; Griffin et al., 2013). If this is true then predator richness may be a constant apparent threat, rather than a true threat. And in combination with the strength of the responses we observed, general avoidance of predator richness would suggest that emergent non-consumptive predator effects can be highly influential on prey communities even before actual consumption takes place. This insight may warrant reinterpretation of field-studies and meta-analyses which consider prey abundances in response to varied predator richness, rather than considering consumption by predators directly (e.g., Snyder et al., 2006; Griffin et al., 2013), if they fail to address possible reduced colonization and overestimate the strength of consumptive control.

It is also possible that this particular predator combination represents an actual synergistic assemblage. This opens interpretation to the possibility that dipterans were responding to the specific predators' identities and the specific combination of them to avoid consumptive synergism. Prey can be capable of species specific (Otto et al., 2008; Henry et al., 2010) or functional-identity specific (Preisser et al., 2007; Miller et al., 2014) responses to predators, as well as integration of multiple predator cues when making colonization decisions (Walzer and Schausberger, 2012). Together these findings support the possibility of assemblage-specific responses. In this case previous work may be overestimating the strength of consumption as previously noted, or underestimating by assuming random colonization where antagonistic predator assemblages might be attractive to colonizers. Research attempting to determine if emergence in OHS, or responses to predators in general, is general to predator richness or assemblage specific should quantify consumption by individual and combined predators before measuring OHS.



*Culex* mosquito and Chironomid midge oviposition were both reduced in predator-rich mesocosms when compared with the predicted response, suggesting an emergent response. However, both mosquito and midge responses to predator richness were not different from two of the three constituent-species treatments and may therefore be examples of sampling- or identity-effect, where prey respond to multiple predators only as strongly as they would to the most dangerous predator (e.g., Long and Finke, 2014). Although, this would indicate that mosquitoes and midges were responding similarly to the only one or two dangerous predators in the predator-rich treatments as they were to all three individuals in the respective single-species mesocosms. This seems unlikely as aquatic macroinvertebrates avoid higher predator density while ovipositing (Eitam and Blaustein, 2004; Silberbush and Blaustein, 2011).

The results of this research may be important socio-economically. Biocontrol by natural enemies represents an effective means of reducing agronomic losses by herbivorous pests (Straub et al., 2008; Letourneau et al., 2009). While the effects of predator biodiversity on agro-pest suppression have been examined (Cardinale et al., 2003) this has not yet been considered from the perspective of agro-pest habitat colonization. Likewise, mosquitoes are vectors for many human diseases for which facilitation of effective predator assemblages may represent an effective means of control (Vonesh and Blaustein, 2010). Our finding of emergent OHS is relevant if prey colonization and production are directly related. This relationship seems likely as female mosquitoes which choose to not oviposit in predator-rich pools must oviposit somewhere, and if habitats lacking predator richness are densely populated due to prey redirecting oviposition, then density effects may reduce survivorship to adulthood (Alto et al., 2012). Potential pest biocontrol programs may wish to evaluate the facilitation of predator-rich habitat as a strategy.

Colonization history can interact with post-colonization processes to yield unique communities (Vonesh et al., 2009; Kraus and Vonesh, 2010), and we now know that richness of predator species can influence both colonization and post-colonization consumption. We do not know, however, how emergence in both pre- and post-colonization processes may interact to influence total prey suppression. Emergence in pre- and post-colonization processes may be independent of each other if predator effectiveness at prey capture is independent of prey abundance, or they may interact to yield further non-additivity (i.e., a meta-emergence) if predator efficiency is related to prey abundance. Future research should examine the possibility of interactions among pre- and post-colonization emergent predator effects by quantifying consumption by, prey colonization in response to, and total prey emergence from simple- and multiple-predator assemblages.

Previous studies that have examined non-consumptive effects of combined predator species have revealed mixed results. In some cases combined effects of predators on prey can be predicted from constituent predator species effects (Relyea, 2003), in other cases not (Byrnes et al., 2006; Steffan and Snyder, 2010). The lack of consistency may reflect taxonomic, or behavioral versus developmental response differences as Relyea (2003) quantified development in vertebrate prey, whereas Byrnes et al. (2006), Steffan and Snyder (2010), as well as our study quantified behavior in invertebrate prey. Further, in all three examples of emergent non-consumptive predator effects, the responses indicated a perception of enhanced predation risk. A response which anticipates reduced predation risk has yet to be observed. Future research may consider taxa-specific differences, the nature of prey responses, or if prey can anticipate predator antagonism in order to further our understanding of how multiple predators come together to affect shared prey.

Non-consumptive interactions between predators and their prey are appreciated as a key factor shaping aquatic communities and their functions (Lima and Dill, 1990; Vonesh et al., 2009; Kraus and Vonesh 2010). We now know that richness of predator species can strongly influence colonization by prey at species and community levels. This may influence total prey suppression by redirecting oviposition from predator-rich habitat and concentrating it in predator-free habitat or habitat with simpler predator assemblages. Likewise, emergent non-consumptive predator effects in combination with emergent consumptive effects may further alter total prey suppression if pre- and post-colonization emergences interact. It is still unclear how specific and how taxonomically widespread emergent non-consumptive effects are. This research represents another step in understanding how predator assemblages affect prey organisms.

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## Appendix

### TABLES AND FIGURES

Table 1. Total oviposition responses by *Culex* mosquitoes, chironomid midges, and general colonizing dipterans to our treatments; numbers are summed across both trials.

	No -predators	Dragonfly -only	Damselfly -only	Crayfish -only	Predator -rich	Total
<i>Culex</i> egg-rafts	49	24	39	27	12	151
Chironomid egg-masses	53	38	30	48	24	193
Dipteran oviposition	117	73	79	84	41	394



Table 2. Summary statistics for, and *post-hoc* Fisher's LSD linear hypothesis comparisons among the *Culex* mosquito oviposition responses to our experimental treatments.

Treatment	n	Mean	SE
No-predators	10	4.9	1.13
Dragonfly-only	10	2.4	0.34
Damselfly-only	10	3.9	0.92
Crayfish-only	10	2.7	0.67
Predicted response	30	3.0	0.40
Predator-rich	10	1.2	0.36
Post-hoc Comparison	Estimate	Z value	P-value
Predator-rich to No-predators	-1.33	-.073	< 0.0001**
Predator-rich to Damselfly-only	-1.05	-3.098	0.0020**
No-predators to Predicted response	0.54	2.875	0.0040**
No-predators to Dragonfly-only	0.73	2.773	0.0056**
Crayfish-only to No-predators	-0.68	-2.761	0.0058**
Predator-rich to Predicted response	-0.79	-2.473	0.0134*
Crayfish-only to Predator-rich	0.65	1.806	0.0710
Damselfly-only to Dragonfly-only	0.45	1.712	0.0869
Predator-rich to Dragonfly-only	-0.60	-1.640	0.1010
Crayfish-only to Damselfly-only	-0.40	-1.608	0.1079
Damselfly-only to Predicted response	0.26	1.372	0.1701
No-predators to Damselfly-only	0.28	1.249	0.2116
Dragonfly-only to Predicted response	-0.19	-0.808	0.4190
Crayfish-only to Predicted response	-0.14	-0.637	0.5238
Crayfish-only to Dragonfly-only	0.05	0.164	0.8696

Table 3. Summary statistics for, and *post-hoc* Fisher's LSD linear hypothesis comparisons among the chironomid midge oviposition responses to our experimental treatments.

Treatment	n	Mean	SE
No-predators	10	5.3	0.87
Dragonfly-only	10	3.8	1.06
Damselfly-only	10	3.0	0.76
Crayfish-only	10	4.8	1.43
Predicted response	30	3.9	0.64
Predator-rich	10	2.4	0.43
Post-hoc Comparison	Estimate	Z value	P-value
Predator-rich to No-predators	-0.79	-3.220	0.0013**
Crayfish-only to Predator-rich	0.69	2.773	0.0056**
No-predators to Damselfly-only	0.57	2.491	0.0127*
Predator-rich to Predicted response	-0.48	-2.127	0.0334*
Crayfish-only to Damselfly-only	0.47	2.019	0.0434*
No-predators to Predicted response	0.32	1.902	0.0572
Predator-rich to Dragonfly-only	-0.46	-1.762	0.0779
No-predators to Dragonfly-only	0.33	1.565	0.1175
Crayfish-only to Predicted response	0.22	1.260	0.2077
Damselfly-only to Predicted response	-0.25	-1.239	0.2154
Crayfish-only to Dragonfly-only	0.23	1.076	0.2820
Damselfly-only to Dragonfly-only	-0.24	-0.968	0.3331
Predator-rich to Damselfly-only	-0.22	-0.815	0.4152
Crayfish-only to No-predators	-0.10	-0.497	0.6190
Dragonfly-only to Predicted response	-0.02	-0.093	0.9259

Table 4. Summary statistics for, and *post-hoc* Fisher's LSD linear hypothesis comparisons among general dipteran oviposition responses to our experimental treatments.

Treatment	n	Mean	SE
No-predators	10	11.5	1.47
Dragonfly-only	10	7.3	0.97
Damselfly-only	10	7.9	1.08
Crayfish-only	10	8.4	1.17
Predicted response	30	7.9	0.60
Predator-rich	10	4.1	0.41
Post-hoc Comparison	Estimate	Z value	P-value
Predator-rich to No-predators	-1.03	-5.670	< 0.0001**
Predator-rich to Predicted response	-0.65	-3.851	0.0001**
Crayfish-only to Predator-rich	0.72	3.765	0.0002**
Predator-rich to Damselfly-only	-0.66	-3.408	0.0007**
No-predators to Predicted response	0.38	3.339	0.0008**
No-predators to Dragonfly-only	0.45	3.037	0.0024**
Predator-rich to Dragonfly-only	-0.58	-2.956	0.0031**
No-predators to Damselfly-only	0.38	2.570	0.0102*
Crayfish-only to No-predators	-0.31	-2.189	0.0286*
Crayfish-only to Dragonfly-only	0.14	0.877	0.3804
Dragonfly-only to Predicted response	-0.07	-0.558	0.5767
Crayfish-only to Predicted response	0.07	0.516	0.6056
Damselfly-only to Dragonfly-only	0.08	0.487	0.6266
Crayfish-only to Damselfly-only	0.06	0.392	0.6954
Damselfly-only to Predicted response	0.00	0.033	0.9740

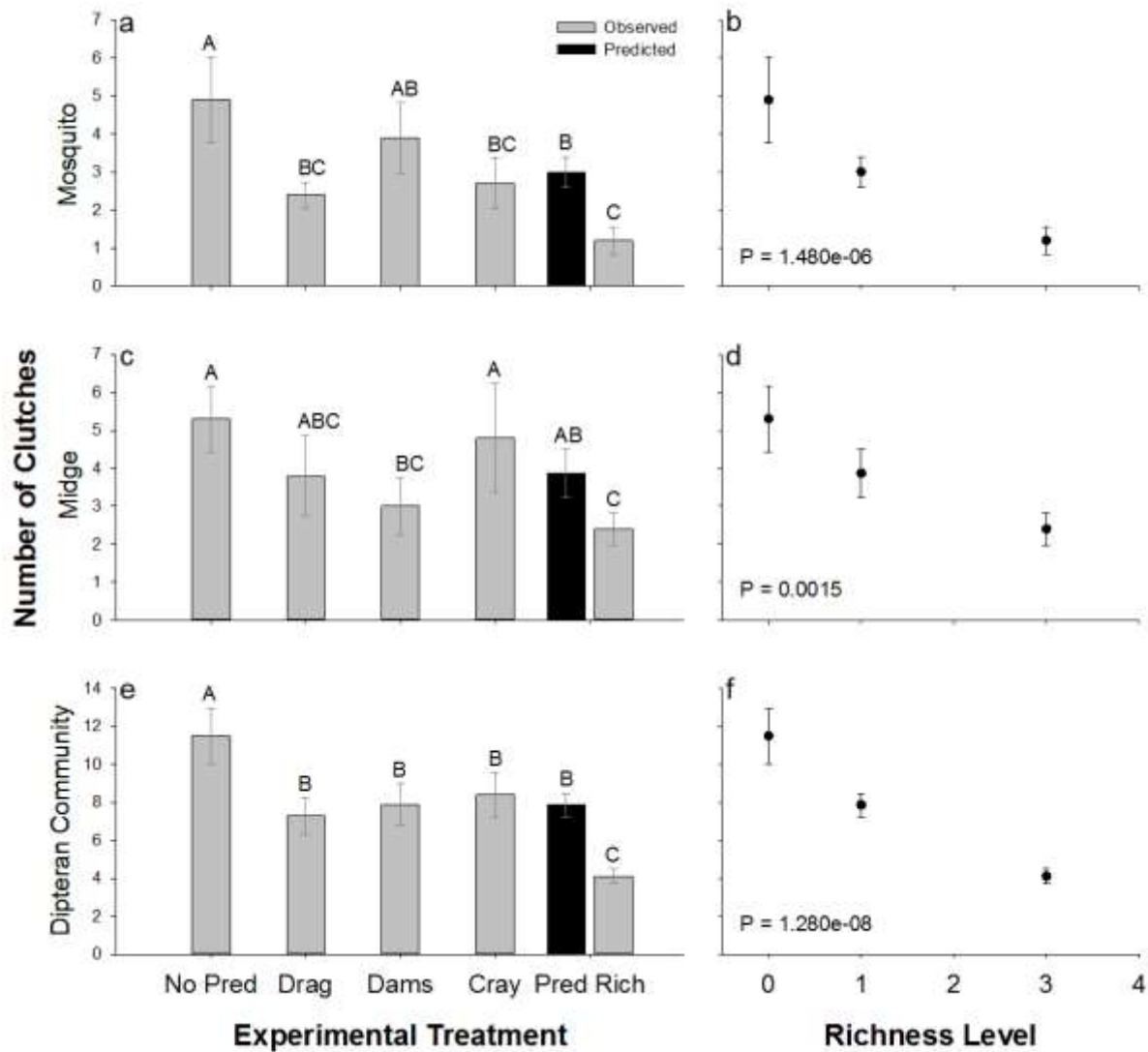


Figure 1. Means and standard errors for mosquito (a), midge (c), and general dipteran (e) oviposition responses among experimental treatments (No Pred = No-predator, Drag = Dragonfly-only, Dams = Damselfly-only, Cray = Crayfish-only, Pred Rich = Predator-rich), and point-and-whisker plots showing the overall effect of richness on oviposition by mosquitoes (b), midges (d), and dipterans in general (f).

## Vita

Ethan Garrett Staats was born June 16<sup>th</sup>, 1991, in Albany County, New York, and is an American citizen. He graduated from Columbia High School, Rensselaer, New York in 2009. He received his Bachelor of Arts in Biology from Hartwick College, Oneonta, New York in May 2013 and subsequently moved directly to work on his M.Sc. at Virginia Commonwealth University.