2015

Emergent Non-Consumptive Predator Effects Alter Habitat Colonization By Dipteran Prey

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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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Richmond, Virginia
July, 2015

Acknowledgement

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Abstract

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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 (Resetarits, 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 Resetarits, 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

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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 occuring 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 14th and August 9th, 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 ± 2.8 [mean ± 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.

LITERATURE CITED

1. Alto, B. W., E. J. Muturi, and R. L. Lapman. (2012). Effects of nutrition and density on *Culex pipiens*. *Medical and Vertinary Entomology*, 26, 396-406.

2. Binckley, C. A. and W. J. Resetarits Jr. (2003). Functional equivalents of non-lethal effects: generalized fish avoidance determines distribution of gray treefrog, *Hyla chrysoscelis*, larvae. *OIKOS,* 102, 623-629.

3. Binckley. C. A and W. J. Resetarits Jr. (2008). Oviposition behavior partitions aquatic landscapes along predation and nutrient gradients. *Behavioral Ecology*, 10.1093/beheco/arm164.

4. Blaustein, L., M. Kiflawi, A. Eitam, M. Mangel, and J. E. Cohen. (2004). Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. *Oecologia,* 138, 300-305.

5. Byrnes, J., J. J. Stachowicz, K. M. Hultgren, A. R. Hughes, S. V. Olyarnik, and C. S. Thornbert. (2006). Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. *Ecology Letters*, 9, 61-71.

6. Chalcraft, D. R., C. A Binckley, and W. J. Resetarits, Jr. (2005). Experimental venues and estimation of interaction strength: comment. *Ecology*, 86(4), 1061-1067.

7. Chapman, K., J. B. Whittaker, O. W. Heal. (1988). Metabolic and faunal activity in litters of tree mixtures compared with pure stands. *Agriculture, Ecosystems and Environment*, 24, 33-40.

8. Chase, J. M. and M. A. Leibold. (2003). *Ecological niches. Linking classical and contemporary approaches*: 1-216. The University of Chicago Press, Chicago, Ill. ISBN 0 226-10180-0.

9. Cardinale, B. J., C. T. Harvey, K. Gross, and A. R. Ives. (2003). Biodiversity and biocontrol: emergent impacts of a multiple-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters*, 6, 857–865.

10. Eitam, A. and L. Bluastein. (2004). Oviposition habitat selection by mosquitoes in response to predator (*Notonecta maculata*) density. *Physiological Entomology*, 29, 188-191.

11. Fader, J. E. and S. A. Juliano. (2014). Oviposition habitat selection by container dwelling mosquitoes: responses to cues of larval and detritus abundances in the field. *Ecological Entomology*, 39, 245-252.

12. Finke, D. L. and W. E. Snyder. (2008). Niche partitioning increases resource exploitation by diverse communities. *SCIENCE*, 321, 1488-1489.

13. Finke, D. L. and W. E. Snyder. (2010). Conserving the benefits of predator biodiversity. *Biological Conservation*, 143, 2260-2269.

14. Griffin, J. N., J. E. Byrnes, and B. J. Cardinale. (2013). Effects of predator richness on Prey suppression: a meta-analysis. *Ecology*, 94(10), 2180-2187.

15. Henry, L. M., J. A. Bannerman, D. R. Gillespie, and B. D. Roitberg. (2010). Predator identity and the nature and strength of food-web interactions. *Journal of Animal Ecology*, 79, 1164-1171.

16. Kiflawi, M., L. Blaustein, and M. Mangel. (2003)a. Predation dependent oviposition habitat selection by the mosquito *Culiseta longiareolata*: a test of competing hypotheses. *Ecology Letters*, 6, 35-40.

17. Kiflawi, M., L. Blaustein, and M. Mangel. (2003)b. Oviposition habitat selection by the mosquito *Culiseta longiareolata* in response to risk of predation and conspecific larval density. *Ecological Entomology*, 28, 168-173.

18. Kraus, J. and J. R. Vonesh. (2010). Feedbacks between assembly and top predator-mediated habitat selection shape variation in local colonization. *Journal of Animal Ecology*, 79, 795-802.

19. Kraus, J. M., J. R. Vonesh, and C. Jackson. (2009). Developing a spatial framework for understanding rock pool communities: disturbance, connectivity and nutrient input. Unpublished.

20. Lawler, S. P., and P. J. Morin. (1993). Temporal overlap, competition, and priority effects in larval anurans. *Ecology*, 74(1), 174-182.

21. Letourneau, D. K., J. A. Jedlicka, S. G. Bothwell, and C. R. Moreno. (2009). Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology Evolution and Systematics*, 40, 573-592.

22. Lima, S. L., and L. M. Dill. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68, 619–640.

23. Long, E. Y. and D. L. Finke. (2014). Contribution of predator identity to the suppression of herbivores by a diverse predator assemblage. *Community and Ecosystem Ecology*, 43(3), 569-576.

24. McCoy, M. W., J. C. Touchon, T. Landberg, K. M. Warkentin, and J. R. Vonesh. (2012). Prey response to predator chemical cues: disentangling the importance of the number and biomass of prey consumed. *PLOSONE*, 7(10), e47495.

25. Miller, J. R. B., J. M. Ament, and O. J. Schhmitz. (2014). Fear on the move: Predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *Journal of Animal Ecology*, 83, 214-222.

26. Morin, P. J. (1984). Odonate guild composition: experiments with colonization history and fish predation. *Ecology*, 65(6), 1866-1873.

27. Morin, P. J. (1987). Predation, breeding asynchrony, and the outcome of competition among treefrog tadpoles. *Ecology*, 68(3), 675-683.

28. Morin, P. J. and S. P. Lawler. (1995). Food web architecture and population dynamics: theory and empirical evidence. *Annual Review of Ecology and Systematics*, 26, 505-529.

29. Otto, S. B., E. L. Berlow, N. E. Rank, J. Smiley, and U. Brose. (2008). Predator diversity and identity drive interaction strength and trophic cascades in a food web. *Ecology*, 89(1), 134-144.

30. Preisser, E. L., J. L. Orrock, and O. J. Schmitz. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology*, 88(11), 2744-2751.

31. Relyea, R. A. (2003). How prey respond to combined predators: a review and empirical test. *Ecology*, 84(7), 1827-1839

32. Resetarits, W. J. (1996). Oviposotion site choice and life history evolution. *American Zoologist*, 36, 205-215.

33. Rieger, J.F., C.A. Binkley, and W.J. Resetartis Jr. (2004). Larval performance and oviposition site preference along a predation gradient. *Ecology*, 85(8), 2094-2099.

34. Schmitz, O. J. (2007). Predator diversity and trophic interactions. *Ecology*, 88(10), 2415 -2426.

35. Schoener, T. W. (1989). Food webs from the small to the large: the Robert H. MacArthur Award lecture. *Ecology*, 70(6), 1559-1589.

36. Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Stohmeier. (1985). Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, 16, 269-311.

37. Sih, A., G. Englund, and D. Wooster. (1998). Emergent impacts of multiple predators on prey. *Tree*, 13(9), 350-355.

38. Silberbush, A. and L. Blaustein. (2011). Mosquito females quantify risk of predation to their progeny when selecting an oviposition site. *Functional Ecology*, 25, 1091-1095.

39. Silberbush, A., S. Markman, E. Lewinsohn, E. Bar, J. E. Cohen, and L. Blaustein. (2010). Predator-released hydrocarbons repel oviposition by a mosquito. *Ecology Letters*, 13, 1129-1138.

40. Snyder, W. E., G. B. Snyder, D. L. Finke, and C. S. Straub. (2006). Predator biodiversity strengthens herbivore suppression. *Ecology Letters*, 9(7), 789-796.

41. Srivastava, D. S., J. Kolasa. J. Bengtsson, A. Gonzalez, S. P. Lawler, T. E. Miller, P. Munguia, T. Romanuk, D. C. Schneider, and M. K, Trczinski. (2004). Are natural microcosms useful model systems for ecology? *TRENDS in Ecology and Evolution*, 19(7), 379-384.

42. Steffan, S. A. and W. E. Snyder. (2010). Cascading diversity effects transmitted exclusively by behavioral interaction. *Ecology*, 91(8), 2242-2252.

43. Straub, C. S., D. L. Finke, and W. E. Snyder. (2008). Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control*, 45, 225–237.

44. Vance-Chalcraft, H. D., J. A. Rosenheim, J. R. Vonesh, C. W. Osenberg, and A. Sih. (2007). The influence of intraguild predation on prey suppression and prey release: a meta-analysis (Special feature article). *Ecology*, 88(11), 2689-2696.

45. Vonesh, J. R. and L. Blaustein. (2010). Predator-induced shifts in mosquito oviposition site selection: a meta-analysis and implications for vector control. *Israel Journal of Ecology and Evolution*, 56, 263-279.

46. Vonesh, J. R., J. M. Kraus, J. S. Rosenberg, and J. M. Chase. (2009). Predator effects on aquatic community assembly: disentangling the roles of habitat selection and post-colonization processes. *Oikos*, 118, 1219-1229.

47. Walzer, A. and P. Schausberger. (2012). Integration of multiple intraguild predator cues for oviposition decisions by a predatory mite. *Animal Behaviour*, 84, 1411-1417.

48. Wasserberg, G., N. Bailes, C. Davis, and K. Yoeman. (2014). Hump-shaped density dependent regulation of mosquito oviposition site-selection by conspecific immature stages: theory, field test with *Aedes albopictus*, and a meta-analysis. *PLOSONE*, 9(3), e92658.

49. Wellborn, G. A., D. K. Skelly, and E. E. Werner. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics*, 27, 337-363.

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
Culex 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.

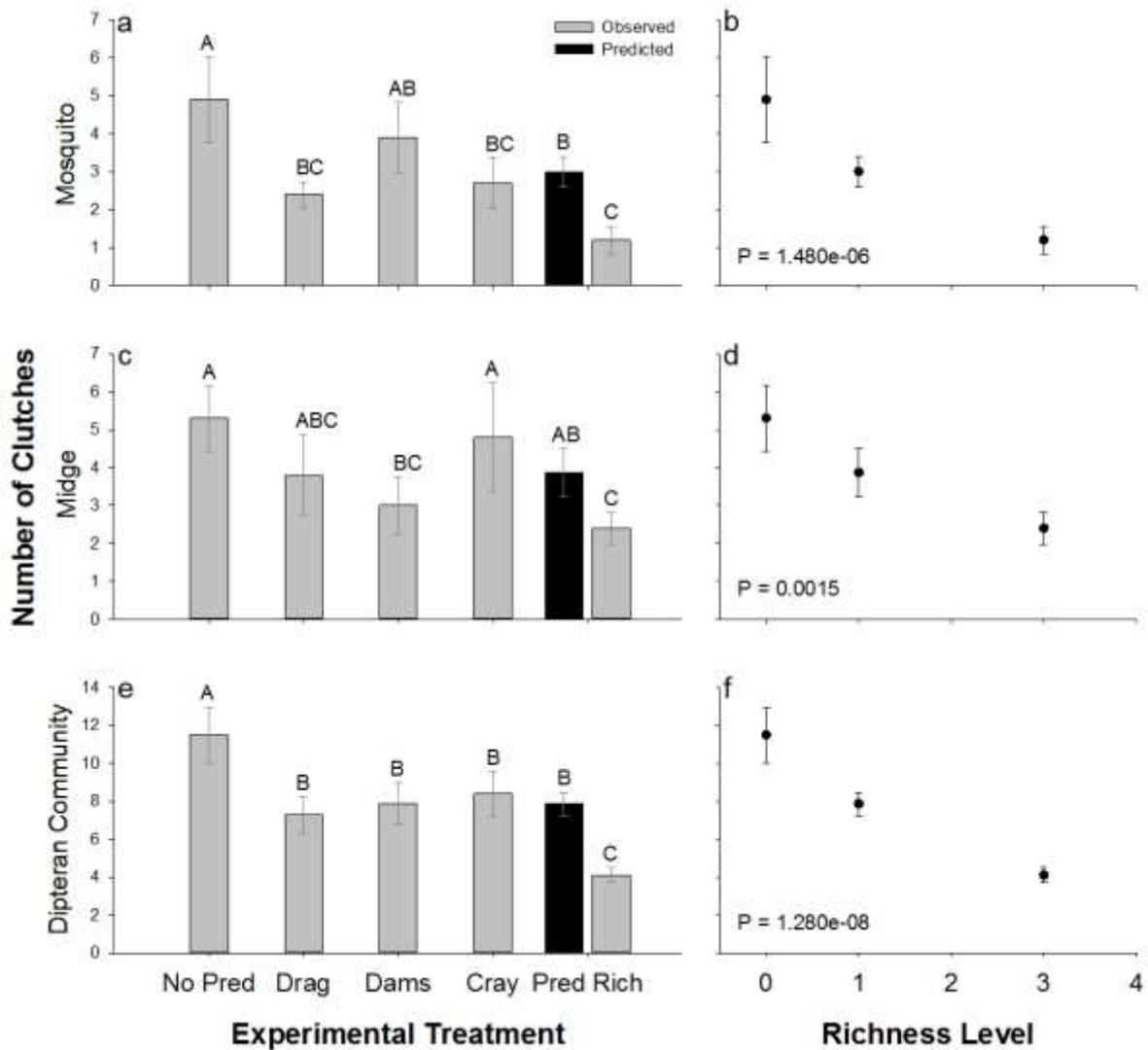| Treatment	n	Mean	SE
No-predators	10	11.5	1.47
Dragonfly-only	10	7.3	0.97
Damselfly-only	10	7.9	1.08
Crayfish-only	10	8.4	1.17
Predicted response	30	7.9	0.60
Predator-rich	10	4.1	0.41
Post-hoc Comparison	Estimate	Z value	P-value
Predator-rich to No-predators	-1.03	-5.670	< 0.0001**
Predator-rich to 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 16th, 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.