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Habitat selection and consumption across a landscape of multiple predators

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Abstract

Predator community composition can alter habitat quality for prey by changing the strength and direction of consumptive effects. Whether predator community composition also alters prey density via nonconsumptive effects during habitat selection is not well known, but is important for understanding how changes to predator communities will alter prey populations. We tested the hypothesis that predator community composition (presence of caged trout, caged dragonflies, or caged trout + dragonflies) alters colonization of aquatic mesocosms by ovipositing aquatic insects. In a previous experiment in this system, we found a spatial contagion effect, in which insects avoided pools with predators, but only when predator-free pools were isolated (~5 m away from predator pools). Here, we removed the isolated predator-free pools, allowing us to test whether insects would make fine-scale (~1 m) oviposition decisions in the absence of preferred isolated pools. We also estimated consumptive effects by allowing predators to feed on colonists for 5 days following colonization. All insects collected after 21 days were dipterans, dominated by Chironomidae. Total colonization, measured as the number of developing larvae after 21 days, was not affected by either predator presence or composition. Consumption was significant in the trout only treatment, reducing larval insect density by 46 ± 37% (mean ± SE). No other predator treatment significantly reduced prey density, although the proportion of chironomid larvae in protective cases increased in response to direct predation from dragonflies, indicating an anti-predatory behavioral response. Taken together, these results reveal that predator community composition altered larval survival and behavior, but colonizing females either did not or could not assess these risks across small scales during oviposition.

Introduction

Habitat selection is a critical process in community assembly (Resetarits 2005; Kraus and Vonesh 2010). The ability to distinguish high-quality from low-quality habitats during habitat selection, or colonization, is crucial to survival and therefore fitness (Spencer et al. 2002). For this reason, it is generally assumed that organisms will select habitats based on their intrinsic quality to maximize fitness (Fretwell and Lucas 1970; Morris 2003). One measure of habitat quality is the presence of predators, and when given the choice, colonizers typically choose predator-free habitats over habitats with predators (Grostal and Dicke 1999; Resetarits 2001, 2005).

Differential habitat selection in response to predators reveals the importance of indirect predator effects on prey populations (Preisser et al. 2005; Resetarits 2005). Such indirect effects of predators are common (Preisser et al. 2005), yet most of our knowledge of these effects comes from studies that estimate the effect of single predator species. While these studies reveal important insight, they abstract a reality of nature that most habitats are not only distinguished by predator presence/absence, but also by predator community composition (Schmitz 2007). The composition of predator communities can enhance,

weaken, or have no effect on direct prey consumption, depending on the traits of the predator and prey species (Schmitz 2007, 2010; Wesner 2012). Predator community composition can therefore be an indicator of habitat quality, but distinguishing among predator communities during colonization may require a more refined perception of threat than simple presence/absence. Colonizers have demonstrated such refinement by differentially selecting habitats in which single predator species vary in the intensity of predation risk (McCauley and Rowe 2010) and density (Silberbush and Blaustein 2011).

In a previous experiment, we estimated the combined effects of predator composition and spatial contagion on colonization of aquatic mesocosms by aquatic insects (Wesner et al. 2012) As predicted, insects avoided predator-free patches that were adjacent (1 m away) to patches with predators in favor of isolated (2 m away), predator-free patches, confirming a spatial contagion effect of predators (sensu Resetarits and Binckley 2009). They made no distinction among patches with different predator communities, revealing that habitat context and predator presence trumped predator community composition as important factors determining colonization (Wesner et al. 2012). It is possible that this lack of distinction was caused by the presence of the isolated pools. In other words, colonizers may have chosen isolated, predator-free pools above all else, obviating the need to make finer scale distinctions among pools with different predator communities.

In this experiment, we created a landscape of aquatic habitat patches that was identical to those from our previous experiment (Wesner et al. 2012), but without the isolated predator-free habitats. In other words, predator and predator-free habitats were only separated by 1 m here, as opposed to both 1 m and 5 m in (Wesner et al. 2012). This tested the hypothesis that predator community composition alters colonization when isolated, predator-free patches are not available. Following colonization, we also allowed predators to feed on developing larvae. This tested the hypothesis that colonizing insects accurately assess the risk to offspring among predator communities. In other words, patches with low colonization rates should have correspondingly high per capita predation rates. Alternatively, if colonization does not differ across predator communities, but predation rates do, then that indicates that colonizers either cannot (McPeek 1989) or do not distinguish among predator communities. Finally, it is possible that a spatial contagion effect remains, regardless of whether there are isolated pools available. In that case, we would expect qualitatively similar colonization patterns and colonization rates to the same treatments as in the previous experiment.

Materials and Methods

We conducted a 21-day experiment using 30 oval plastic outdoor aquatic mesocosms (135 cm length × 91 cm width × 60 cm depth) on the campus of Brigham Young University (BYU) in Provo, Utah, USA. (40°15′40.85″ N, 111°39′36.74″ W, 1417 m elevation). The Provo River is located 0.3 km from the study site and likely served as the primary source of insect colonists, although we did not measure this. We added approximately 5 cm of sand and 0.25 kg of grass clippings to each mesocosm to provide habitat for colonizing insects. Using grass instead of aquatic plants avoids accidental introduction of aquatic organisms (Resetarits 2001; Wesner et al. 2012). We then added 380 L of well water to each mesocosm and covered them immediately with plastic tarps to prevent early oviposition. Mesocosms were inoculated on the same day with approximately 10 zooplankton (*Daphnia* spp.) from a laboratory culture. Zooplankton populations reproduced quickly, providing a potential food base for developing insects and caged predators. We aerated each mesocosm using an air pump and air stones and kept them covered for 23 days prior to the experiment to allow the water to age and the zooplankton populations to reproduce and establish.

Predators

We used non-native brown trout (*Salmo trutta*), an active water column forager, and a native dragonfly (*Ophiogomphus severus*), an ambush predator that burrows in the sand, as the predators in this experiment. On 16 May 2012, we obtained brown trout from the Glenwood State Hatchery (Glenwood, Utah, USA.) and transported them in aerated holding tanks to the BYU campus. Dragonflies were collected from Soldier Creek, a nearby natural stream that also contains brown trout. We did not measure individual sizes of predators, although both brown trout and dragonflies were visually similar in size and mass to individuals collected in the same way the previous year (brown trout: total length = 92.7 ± 7 mm, wet mass = 8.5 ± 1.5 g; dragonflies: length = 25 ± 2 mm, wet mass = 0.32 ± 0.14 g, (Wesner et al. 2012). Both prior to and during the experiment, brown trout and dragonflies were fed twice weekly with freshly killed, chopped aquatic insects (mayflies and stoneflies from Soldier Creek). Using freshly killed insects avoided accidental introduction of prey into the mesocosms, and also mimicked the chemical signature of actual predation, even though live colonizers were not being consumed.

Design

Colonization

We created a landscape of paired mesocosms where each mesocosm in a pair was separated by 0.5 m and each pair of mesocosms was separated by 5 m. One mesocosm in each pair was randomly assigned to one of three predator treatments: brown trout only (T), dragonfly only (D), or brown trout + dragonfly (TD). The other mesocosm in the pair was predator-free, and we refer to these as predator-associated controls: brown trout associated (TA), dragonfly associated (DA), and brown trout + dragonfly associated (TDA). Thus, our experiment contained six treatments replicated five times. However, if there was no variation among "associated" treatments, then they were pooled and treated as a single control to simplify the models (see Analysis). We added predators to the mesocosms on 24 May 2012, marking the start of the experiment. Predators were placed in screened cages to ensure that differences in larval abundance were driven by oviposition avoidance and not direct predation. Cages were constructed using a 5-gallon plastic bucket with mesh windows for trout and small plastic cups with drilled holes (3 mm) for dragonflies (Wesner et al. 2012). The design of these cages allowed predator chemical cues to permeate the mesocosms while preventing the predators from consuming prey. We placed predator containers at one end of the oval mesocosm and covered that end with a tarp to prevent visual cues of the buckets or cups. Tarps covered approximately 10% of the mesocosm surface, providing partial shade. Additionally, tarps and cages without predators were placed in predator-free mesocosms to ensure the containers themselves did not prevent oviposition. We added predators in the following densities, following: brown trout only (two fish), dragonfly only (12 dragonflies), and brown trout + dragonfly (one fish + six dragonflies). We did not attempt to equalize biomass among predator treatments, because to do so would have required an unnaturally large number of dragonflies (≈25 dragonflies for each fish, above the natural density for *O. severus*; J. Wesner, personal observation). Thus, our experiment replicates the natural predator densities likely to be experienced by ovipositing female insects.

To ensure mixing of chemical cues throughout the mesocosm, we lifted predator cages out of the water three times per week and allowed them to drain directly into the mesocosm. We also did this in the predator-free mesocosms. Predators were checked daily, and dead individuals (~15% of dragonflies and ~25% of trout over the entire experiment) were replaced immediately. On the final day of the experiment, 13 June, we used a dip net (15 × 10 cm, 1 mm mesh) to sample aquatic organisms at the surface, middle, and bottom of each mesocosm. At each level, we made a single scoop with the dip net from the center to the long side of the oval mesocosms. Samples were pooled and preserved in 70% ethanol for identification in the laboratory.

Consumption

After samples were taken on 13 June, we removed the predators from their enclosures marking the start of the consumption experiment. We allowed predators to feed for 5 days. A small number of dragonflies attempted to emerge during the consumption trial and were replaced immediately. After 5 days, on June 18, we resampled each mesocosm identical to the above methods. All taxa were identified to family. At the end of the experiment, all trout were euthanized with an overdose of tricaine methanesulfonate (MS-222).

Analysis

Colonization

We tested whether predator community composition or presence affected colonization using a mixed model ANOVA (Proc MIXED; SAS version 9.2; SAS Institute, Cary, NC), where number of larvae on June 13 was the response variable, treatment was a fixed effect, and mesocosm was a random effect. We initially intended to compare each predator treatment to its associated control (i.e., D vs. DA, T vs. TA, TD, vs. TDA). However, larval abundance in the associated controls (DA, TA, TDA) was similar across treatments ($F_{2,12} = 0.69$, $P = 0.52$; mean ± SE, DA: 182 ± 21, TA: 189 ± 88, TDA: 105 ± 34), and there was no relationship between a given treatment replicate and its paired control ($r^2 = 0.14$, $P = 0.47$). Therefore, we pooled the control treatments so that all predator treatments were compared to a single group of control replicates. This simplified the model and reduced the number of pairwise comparisons. Data from the control were slightly non-normal (Shapiro-Wilk, $W = 0.87$, $P = 0.04$). A natural-log transformation removed the violation of normality, but did not change the outcome of the mixed model. Therefore, results below are based on raw abundance totals.

Consumption

We estimated consumption effects by measuring the change in larval insect densities after 5 days of consumption. However, mesocosms were open to colonization during the consumption trial, meaning that prey

populations could have increased even in the presence of strong predation. As a result, measuring the absolute change in prey density would not have given an accurate measure of consumption. Instead, what is needed is a measure of change relative to the control. To achieve this, we divided prey density in each predator replicate by mean prey density of the controls and transformed the result using the natural log. The resulting metric is the log response ratio (LRR):

$$\mathrm{LRR}_i = \ln(X_{e,j}/X_{c,j}) \quad (1)$$

where $X_{e,j}$ is the density of insects in experimental replicate e on date j, and $X_{c,j}$ is the mean of the control replicates on date j. Log response ratios are a common metric of effect size in meta-analysis (Hedges et al. 1999), which can also be applied within individual studies (Osenberg et al. 1997). A key difference in our approach versus meta-analytic approaches is that we estimated LRR using individual experimental replicates, rather than experimental means.

To determine the consumption effect after correcting for continuous colonization, we subtracted LRR on 18 June from LRR on 13 June. The resulting metric is the log odds ratio (LOR), which represents the change over time in the proportional relationship between a treatment and control. An LOR = 0 indicates no consumption effect, LOR < 0 indicates a consumption effect, and LOR > 0 indicates higher survival in a consumption treatment than the control. Significance of LOR relative to zero was determined with a *t*-test. To test whether consumption effect sizes differed among predator treatments, we compared LOR among predator treatments using a mixed model ANOVA (Proc MIXED), where LOR was the response variable, treatment was a fixed effect, and tank was a random effect.

As mentioned above, our predator treatments were confounded by differences in predator mass. To determine whether there were mass-specific differences in consumption among predator treatments, we divided consumption effects (LOR) by the mass of predators in each treatment. Mass was assumed to be similar to direct mass measurements from a previous experiment using the same species (Wesner et al. 2012). We then reran the mixed ANOVA as above.

In addition to direct consumption, we measured an indirect effect of predator communities by asking whether prey altered their behavior in the presence of feeding predators. We did this by measuring the proportion of cased chironomids before and after the onset of direct consumption. The prey community was dominated by larval chironomids (*Tanytarsus* spp., and *Chironomus* spp.), which often build tubular cases of sand. Chironomids may retreat to cases (or build them more often) in response to predation (Hershey 1987). We compared the change in the proportion of cased chironomids over time among treatments using a mixed model repeated measures ANOVA (Proc MIXED), where proportion of cased chironomids was the response variable, treatment was the fixed variable, time was the repeated measure, and mesocosms were the subjects. We ran analyses on raw proportions, rather than logit-transformed proportions (Warton and Hui 2011), because the logit-transformation worsened normality; 3/12 cases were non-normal after transformation versus 1/12 before. Treatment associated controls (DA, TA, TDA) varied significantly both before and after the onset of direct consumption (before – 13 June: $F_{2,12} = 5.3$, $P = 0.02$; after – 18 June: $F_{2,12} = 8.63$, $P = 0.0048$). Therefore, we retained the associated controls in the model. Using planned comparison post hoc tests, we compared the change between dates within each treatment. If a predator treatment showed a change in proportion of cased chironomids, but its associated control did not, we took this as evidence of a behavioral shift in case-building caused by predation risk.

Results

Colonization

After 21 days of colonization, we collected a total of 5223 larval insects, dominated by chironomids (>95%; Fig. 1), and followed by mosquitoes (Culicidae) and biting midges (Ceratopogonidae). No other insect taxa were found. The number of larvae collected per sample ranged from 36 to 405 individuals, but did not vary across treatments ($F_{3,26} = 1.07$, $P = 0.38$; Fig. 2; see Appendix 1 for raw data).

Figure 1. An adult chironomid male. Chironomids and other dipterans colonized mesocosms containing brown trout, dragonflies, both, or neither. Photograph Credit: C. Riley Nelson.

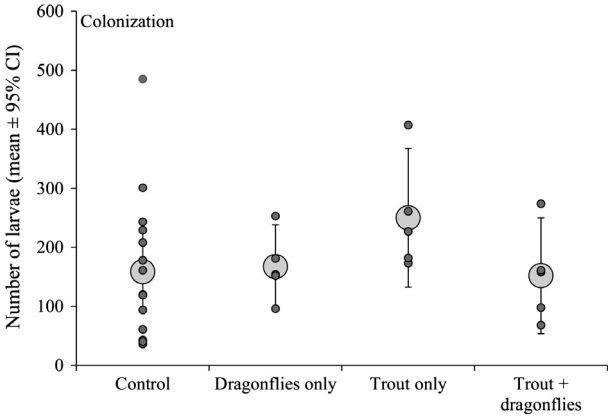

Figure 2. Colonization effect of each predator community treatment. Large circles are the mean number of larvae (mean ± 95% CI) collected after 21 days of colonization (13 June). Small circles are data points from individual replicates. Overall mixed ANOVA: $F_{3,26} = 1.07$, $P = 0.38$.

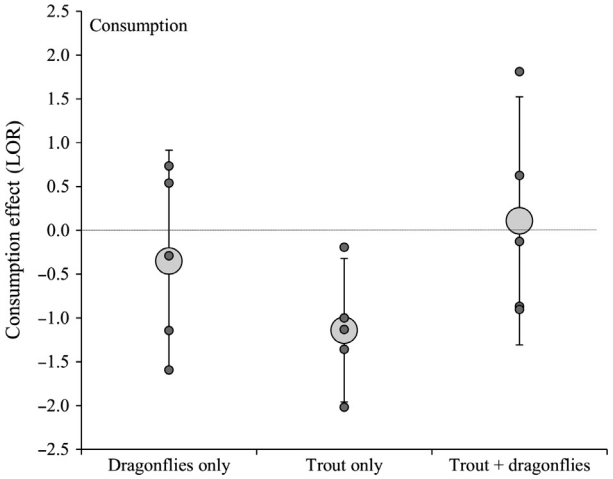

Figure 3. Consumption effect of each predator community, measured as the log odds ratio ($LRR_{13June} - LRR_{18June}$). An log odds ratio (LOR) = 0 indicates no consumption effect, LOR < 0 indicates a consumption effect, and LOR > 0 indicates higher survival in the predator treatment than the nonpredator treatment. Large circles are means ± 95% CI. Small circles are data points from individual replicates. The trout only treatment was significantly different from zero: *t*-test, $t = -2.65$, $P = 0.03$. No other treatment was significantly different from zero. Overall mixed ANOVA: $F_{2,9} = 2.16$, $P = 0.17$.

Consumption

There was a significant consumption effect (LOR) in the trout only treatment (Fig. 3; $t = -2.65$, $P = 0.03$). Larval density in this treatment declined on average by 46 ± 37% (mean ± SE; range: −81 to 17). By comparison, larval densities in the control pools increased on average by 58 ± 26% (mean ± SE; range: −92 to 281%).

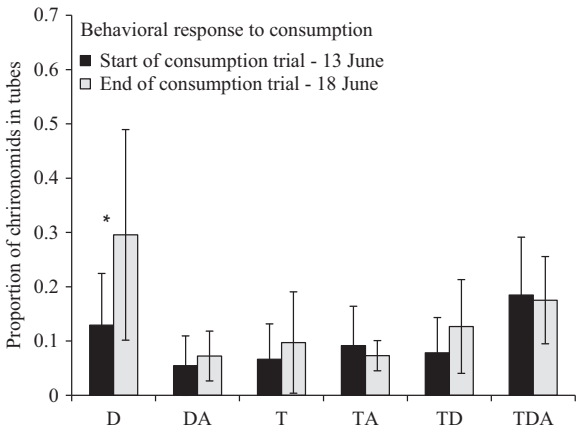

Figure 4. Behavioral response of chironomids to direct consumption, measured as the proportion of chironomids in cases (means ± 95% CI). D, dragonflies only; DA, dragonfly associated control; T, trout only; TA, trout associated control; TD, trout + dragonflies; TDA, trout + dragonflies associated control. Treatment × time interaction: $F_{5,24} = 3.78$, $P = 0.01$; * = planned comparison for dragonfly only treatment before vs. after: $t = -4.82$, $P < 0.0001$). No other treatment changed significantly.

Consumption effects in the dragonfly only and trout + dragonfly treatments were not different from zero (Fig. 3). Consumption did not differ significantly among any predator treatment, despite the apparent trend of a stronger effect in the trout only treatments (Fig. 3; *t*-test for T vs. TD: $t = -2.05$, $P = 0.07$; for T vs. D: $t = 1.3$, $P = 0.23$). This trend disappeared when consumption effects were corrected for predator mass ($P \geq 0.36$ for all pairwise comparisons).

The overall proportion of cased chironomids increased slightly during the consumption phase (0.10 ± 0.01 on 13 June vs. 0.14 ± 0.01 on 18 June; $F_{1,24} = 7.75$, $P = 0.01$), but this was driven almost entirely by the dragonfly only treatment, in which the proportion of cased chironomids more than doubled (Fig. 4; treatment x time: $F_{5,24} = 3.78$, $P = 0.01$; planned comparison for dragonfly only treatment: $t = -4.82$, $P < 0.0001$). No other treatment changed significantly (Fig. 4). As a result, the proportion of cased chironomids in the dragonfly only treatment was nearly twofold higher than any other predator treatment at the end of the consumption phase (Fig. 4; planned comparisons between D vs. T: $t = 4.27$, $P = 0.0003$; D vs. TD: $t = 3.63$, $P = 0.0013$). This difference was not present at the start of the consumption phase (D vs. T: $t = 1.35$, $P = 0.19$; D vs. TD, $t = 1.1$, $P = 0.28$).

Discussion

We found no evidence of differential habitat selection in response to changes in predator composition despite clear

fitness costs to ovipositing dipterans. This contrasts with previous studies showing that predators elicit strong avoidance by colonizing insects, including egg-laying adults (Resetarits and Wilbur 1989; Petranka and Fakhoury 1991; Blaustein 1999; Grostal and Dicke 1999; Vonesh et al. 2009). Taken alone, our result suggests that colonizers (ovipositing dipterans) simply did not or could not perceive risks to offspring.

One explanation for a lack of differential colonization in this experiment is that the habitats did not differ in quality from the perspective of ovipositing females. Habitat quality is ultimately determined by offspring survival, and predators do not always reduce prey survival (e.g., Thorp and Bergey 1981), particularly for prey that have antipredator defenses. Sufficient antipredator defenses can obviate the need to discriminate among predator/predator-free habitats. For example, larvae of the midge, *Chironomus riparius*, are not susceptible to predation from an aquatic predator, *Notonecta maculata*, but larvae of the mosquito, *Culiseta longiareolata*, are. As a result, female mosquitoes avoid ovipositing in pools with *Nototecta*, but female midges do not (Blaustein et al. 2004). But our consumption trial refutes this explanation by demonstrating a difference in offspring success when predators are present. Trout ate larval insects, reducing density by nearly 50%. Dragonflies had minimal effects on density, perhaps because they had lower biomass than the trout only treatment, but caused chironomid larvae to retreat to protective cases. This is consistent with laboratory observational studies that show chironomids spend more time in cases when predators are present (Hershey 1987; Macchiusi and Baker 1992), a behavior that enhances survival, but at a potential cost to fitness through reduced feeding and growth (Hershey 1987). Thus, antipredator defenses in larvae were not sufficient to erase fitness differences among habitats, particularly those with trout only.

Interestingly, in a previous experiment in our system, the same group of colonizers (chironomids, culicids, ceratopogonids) displayed predator avoidance, indicating that these taxa (at least at the family level) were able to perceive risks to offspring (Wesner et al. 2012). However, the experiment in Wesner et al. (2012) only found predator avoidance when control mesocosms were isolated from (5 m away), rather than adjacent to, predator mesocosms, indicating predator spatial contagion (Resetarits and Binckley 2009). When control mesocosms were adjacent to predator mesocosms, the results of Wesner et al. (2012) were qualitatively similar to our current results (i.e., no effect). The current experiment did not have isolated, predator-free controls, and we expected that the absence of these habitats would elicit a finer scale response in insects between predator and predator-free pools. That we did not find such a response suggests the possibility that spatial contagion occurred even in the absence of isolated controls. In other words, it is possible that most insects avoided our array all together, because they did not perceive "high-quality" habitat (i.e., isolated, predator-free tanks). For insects that did oviposit, both predator habitats and predator-free habitats may have appeared similar due to spatial contagion.

While predator community composition did not affect final insect densities via colonization, we cannot rule out the possibility of differential timing of colonization, triggered by avoidance of conspecifics as mesocosms were colonized. This could have occurred in the following sequence: (1) insects choose predator-free habitats initially; (2) predator-free habitats become saturated with conspecifics; and (3) insects avoid conspecifics, choosing instead to colonize predator habitats. To test this would have required multiple samples during colonization, which we did not have. However, we find this explanation unlikely, because larval densities in the current experiment were almost an order of magnitude lower than densities in the isolated, predator-free pools in the previous study, which were preferred by the same taxa of colonizers as the current experiment (Wesner et al. 2012). Because high conspecific densities did not trigger avoidance in the previous study, it seems unlikely that conspecific density in the current experiment was high enough to trigger strong avoidance.

Predators affect prey communities through a combination of differential colonization and postcolonization consumption, yet the effects of each of these processes have rarely been considered together (Vonesh et al. 2009). Our experiment sheds light on the importance of these two processes by revealing that, at least at the local scale, predator effects on prey were dominated by consumption rather than differential habitat selection. A previous study also found that consumption had stronger effects on prey density than avoidance during colonization, but that colonization was nevertheless higher in predator-free pools versus pools with predatory green sunfish (*Lepomis cyanellus*; Vonesh et al. 2009). This indicated that colonization had lasting effects on the prey community that persisted in the face of direct consumption (Vonesh et al. 2009). However, because our consumption experiment was not run simultaneously to the colonization experiment, our comparisons of the two responses (consumption/colonization) are potentially confounded with time.

Until recently, ecologists have largely defined habitat quality based on intrinsic properties of the habitat (Fretwell and Lucas 1970; Morris 2003). But intrinsic habitat quality alone may be insufficient to predict habitat selection in some species (Resetarits and Binckley 2009; Wesner et al. 2012); Resetarits and Binckley 2013. Our

results indicate that aquatic dipterans do not always perceive fine-scale differences in intrinsic habitat quality, even when those differences have potentially strong fitness costs.

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Conflict of Interest

None declared.

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Appendix 1. Raw data of total number of insects collected from each mesocosm.

Collection date	Tank	Treatment	Total Larvae	Chiro Larvae	Chiro Pupae	Chiro Tubed	Other
6/13/12	6	DA	243	223	5	10	5
6/13/12	10	DA	161	151	0	1	9
6/13/12	12	DA	178	150	6	15	7
6/13/12	19	DA	208	196	3	5	4
6/13/12	25	DA	120	94	9	13	4
6/13/12	5	D	181	142	5	27	7
6/13/12	9	D	96	61	1	5	29
6/13/12	11	D	154	121	10	22	1
6/13/12	20	D	152	103	1	32	16
6/13/12	26	D	253	225	5	9	14
6/13/12	1	TA	301	286	2	10	3
6/13/12	8	TA	36	26	2	4	4
6/13/12	14	TA	60	49	1	10	0
6/13/12	24	TA	485	457	8	16	4
6/13/12	29	TA	61	54	0	6	1
6/13/12	4	TDA	43	32	0	2	9
6/13/12	16	TDA	40	23	3	7	7
6/13/12	17	TDA	229	151	11	63	4
6/13/12	21	TDA	119	94	2	16	7
6/13/12	28	TDA	94	61	6	20	7
6/13/12	3	TD	158	127	6	21	4
6/13/12	15	TD	274	236	8	23	7
6/13/12	18	TD	161	155	2	3	1
6/13/12	22	TD	98	76	5	11	6
6/13/12	27	TD	68	63	0	2	3
6/13/12	2	T	173	156	3	1	13
6/13/12	7	T	261	197	2	35	27
6/13/12	13	T	182	166	5	8	3
6/13/12	23	T	407	370	5	26	6
6/13/12	30	T	227	192	5	14	16
6/18/12	6	DA	123	116	1	6	0
6/18/12	10	DA	160	148	2	10	0
6/18/12	12	DA	230	208	4	12	6
6/18/12	19	DA	178	150	0	24	4
6/18/12	25	DA	457	430	0	27	0
6/18/12	5	D	52	33	2	13	4
6/18/12	9	D	283	224	1	19	39
6/18/12	11	D	163	107	4	50	2
6/18/12	20	D	369	177	1	191	0
6/18/12	26	D	114	77	2	34	1
6/18/12	1	TA	322	291	2	15	14
6/18/12	8	TA	55	48	1	5	1
6/18/12	14	TA	40	36	0	4	0
6/18/12	24	TA	1034	965	3	58	8
6/18/12	29	TA	165	153	0	11	1
6/18/12	4	TDA	91	68	5	16	2
6/18/12	16	TDA	93	69	3	18	3
6/18/12	17	TDA	18	13	0	4	1

Appendix 1. Continued.

Collection date	Tank	Treatment	Total Larvae	Chiro Larvae	Chiro Pupae	Chiro Tubed	Other
6/18/12	21	TDA	306	271	1	19	15
6/18/12	28	TDA	99	77	1	19	2
6/18/12	3	TD	94	72	3	18	1
6/18/12	15	TD	157	128	1	27	1
6/18/12	18	TD	1393	1363	4	22	4
6/18/12	22	TD	122	101	3	17	1
6/18/12	27	TD	180	158	2	20	0
6/18/12	2	T	90	84	0	3	3
6/18/12	7	T	49	44	2	2	1
6/18/12	13	T	83	66	2	11	4
6/18/12	23	T	148	134	3	9	2
6/18/12	30	T	265	206	2	55	2

D, dragonfly only; T, trout only; TD, trout plus dragonfly; DA, dragonfly associated; TA, trout associated; TDA, trout plus dragonfly associated; Total Larvae, the sum of all larvae; Chiro Larvae, number of chironomids that were not cased and were not pupae; Other, Culicidae plus Ceratopogonidae.