The effects of lake-derived midges on terrestrial ecosystems and arthropod communities

By

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“I would just like to remind all of us that ecology is not a luxury science. It is not about pleasant appearances. It *is* about survival. About whether we are all going to make it. Period.”

- Benjamin Horne

TABLE OF CONTENTS

Inspirational Quote....................i

Table of Contents....................ii

Acknowledgments....................v

Thesis Abstract....................vii

Thesis Introduction....................ix

Literature Cited....................xi

Chapter 1: Aquatic insect deposition to land: an example from a subarctic lake with consequences for terrestrial primary production

Abstract....................1

Introduction....................2

Material and Methods....................5

Results....................12

Discussion....................14

Literature Cited....................18

Tables....................23

Figures....................25

Appendix....................33

Chapter 2: Lake-derived midges increase abundance of shoreline terrestrial arthropods via multiple trophic pathways

Abstract.. 38

Introduction..39

Material and Methods..41

Results..46

Discussion..47

Literature Cited..51

Tables...55

Figures..57

Appendix..61

Chapter 3: Positive indirect effect of aquatic insects on terrestrial prey even at elevated predator density

Abstract..63

Introduction..64

Material and Methods..67

Results..76

Discussion..79

Literature Cited..81

Figures..84

Appendix..88

Thesis Conclusions..91

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THESIS ABSTRACT

The movement of organisms and material across ecosystem boundaries is fundamental to many ecological processes. Bodies of water regularly produce large numbers of aquatic insects that swarm on their shorelines. On the shorelines of lakes numerous aquatic insects may influence terrestrial arthropods by feeding detritivores and predators alike. Because midges are so abundant at Lake Mývatn, Iceland it is an ideal place to examine how aquatic insects influence bottom-up and top-down forces on land. First, to determine the amount and spatial distribution of midge deposition on land I measured the density of midges that emerged from Lake Mývatn and their abundance around the lake. From these data I created a model to estimate midge deposition on the land adjacent to the lake that suggests midges provide substantial quantities of nutrients to the shoreline. Second, to examine longer term impacts of midges on I sampled terrestrial arthropod assemblages across a midge input gradient at Mývatn and three other lakes in northeast Iceland. The results show that detritivorous, herbivorous, and predatory arthropods are all positively related to terrestrial midge inputs, across space and time. Third, to understand the influence of midges on short term food web interactions the indirect effect of live midges on terrestrial arthropods through shared predators was examined. Midges are positively associated with predatory wolf spider reproduction, and weakly linked to wolf spider density. However, experiments in the lab and field demonstrated a reduction of spider predation in the presence of live midges. Specifically, when midges are absent wolf spider density is positively related to predation rates, but in the presence of live midges this effect disappears. Reductions in predation by wolf spiders at low midge density suggest that the positive indirect effect of midges persists even at high predator density. As a whole this work has presents a new method of

measuring the movement of aquatic insects to land and insights about possible aquatic insect fertilization of riparian areas, responses of terrestrial arthropods in multiple trophic levels to aquatic inputs, and an apparent mutualism between insects from a lake and those on land.

THESIS INTRODUCTION

The movement of aquatic insects from water to land is a common and ecologically important phenomenon (Baxter et al. 2005), representative of a broader class of cross-ecosystem exchanges (Polis et al. 2004). One of their key roles is as a resource for consumers that feed in riparian zones. Aquatic insects are associated with strengthening top-down control of terrestrial organisms since they can increase terrestrial consumer abundance in their role as alternative prey (Henschel et al. 2001, Nakano et al. 1999). Still, most examinations of indirect effects at the water's edge have not thoroughly examined the influence of predator density or individual foraging response to the presence of aquatic insects.

Evidence is mounting that aquatic insects may also directly affect the base of the trophic pyramid. The ability of aquatic insects to export proportions of aquatic secondary production is well documented (Jackson and Fisher 1986, Petersen et al. 1999). But the ultimate fate of this productivity remains a mystery, as does the possible bottom-up impacts of aquatic insect transfer to land. However, recent advances (Gratton and Vander Zanden 2009, Sabo and Hagen 2012) suggest that predictable patterns in donor system productivity and aquatic insect dispersal could are related to one another.

So it is that we turn to the tiny midges of northeast Iceland to whisper their secrets. These insects make their home in lakes that dot the low-nutrient, low-productivity arctic heathland. One large, productive, midge-filled lake called Mývatn has proved to be place of inspiration and an outstanding case study in the ways that aquatic insects interact with terrestrial ecosystems and food webs.

In chapter one I examine how to answer the seemingly simple question “How many midges are there at Lake Mývatn and where do they all go?" I used a combination of field measurements of midge abundance in and around the lake to determine their rate of emergence from the lake and their distribution over the neighboring landscape. These data were combined into a simple model that estimates midge deposition on land per unit area. This information allows us to place aquatic insect nutrient transport from the lake to the land in context, and points to their important role in promoting rates of primary production that exceeds those that would occur in their absence.

Patterns of terrestrial arthropod abundance in response to midge inputs are the focus of chapter two. Taking advantage of an extensive midge input gradient at four lakes in northeast Iceland I sampled a range of terrestrial detritivorous, herbivorous, and predatory arthropods to look for the influence of midges as a resource to many trophic levels. From these data I aimed to quantify the influence of midge inputs over large temporal and spatial scales, and explain in part abundances of terrestrial insects across the landscape.

Chapter three returns to ideas of aquatic insects as prey for terrestrial consumers. I wanted to know if predator reproduction and density were influenced by midge inputs. Furthermore, I was interested in the possibility of midges reducing consumption rates of individual predators on terrestrial prey and how this may interact with concurrent midge-driven changes in predator abundance. I used field collections of wolf spiders and their egg sacs to explore their response to midges via reproduction and density. Laboratory and field experiments were designed to reveal how midges impact predator consumption rate and predatory density to set rates of predation on terrestrial prey.

Throughout my goal has been to use the midges of Iceland to understand general patterns of cross-ecosystem organism flux and its impact on ecosystems and food webs. The simplicity and strong contrasts inherent in the system have allowed me to uncover processes driven by aquatic insects at the top and bottom of the food chain.

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CHAPTER 1

Transfer of biomass and nutrients to a lake shoreline via aquatic insects

Abstract: Many ecosystems are linked by the movement of material and organisms. These exchanges can alter processes including predator-prey interactions and rates of nutrient-dependent productivity. Aquatic insects are often prey for terrestrial consumers and could also be an important source of nitrogen and phosphorus as detritus on the shoreline. Insects export large quantities of aquatic production to terrestrial ecosystems, but the intensity of their deposition per unit area is not properly understood since their emergence from the water and abundance on land are often measured in differing units and in isolation from one another. This prevents an understanding of their contribution to processes such as nutrient availability. To determine the scale of aquatic insect deposition on the shoreline of Lake Mývatn, Iceland we quantified midge emergence and terrestrial abundance during the summers of 2008-2011. Total midge emergence from the lake ranged from a high of 75 MT dw yr^{-1} (3 g dw m^{-2} yr^{-1}) in 2008 to 3.3 MT dw yr^{-1} in 2011. Midge abundance on land peaked 20-25 meters from the lake with 70% occurring in the first 100 meters, a pattern that was consistent among years. We combined these midge emergence and abundance data to create a landscape midge deposition model. During a high midge year such as 2008 we estimated that midge deposition within 50 meters of the lake edge averaged as high as 100 kg dw ha^{-1} yr^{-1}. Midges may increase terrestrial N deposition by 3-5 times background rates (2-3 kg N ha^{-1} yr^{-1} compared to 10 kg N ha^{-1} yr^{-1}) across hundreds of hectares adjacent to the lake since they are ~10% N by mass. Ours are some of the first per unit area estimates of aquatic insects nutrient deposition to terrestrial habitats, and they emphasize the

potential importance of aquatic insects in shaping patterns of terrestrial productivity. The approach described here may be broadly useful in assessing the importance of aquatic insects to bottom-up processes in terrestrial ecosystems.

1. Introduction

Many ecosystems are strongly influenced by external sources of energy or nutrients such as ocean expanses fertilized by continental dust, anoxic dead zones at the mouth of major rivers fueled by upstream agricultural inputs, and guano-powered “seabird islands.” Aquatic insects may also ferry biomass and nutrients from water to land when they emerge as adults to feed or mate in terrestrial habitats (Hoekman et al. 2011, Sabo and Hagen 2012). Measurement of aquatic insect abundance on land has primarily focused on their role as prey for terrestrial consumers or their ability to disperse among systems(Griffith et al. 1998, J. L. Sabo and Power 2002). With as much as 97% of aquatic insects (~10% N by mass) remaining on land (Jackson and Fisher 1986) they may also be important contributors to terrestrial productivity by transporting nutrients to areas where they are in limited availability. However, to understand aquatic insect deposition from a nutrient perspective requires an estimate of absolute rather than relative rates of input. Recent conceptual approaches have described approaches that could be used to estimate aquatic insect deposition to terrestrial ecosystems(Gratton and Vander Zanden 2009, Sabo and Hagen 2012) but few empirical estimates of this process currently exist.

Insects are difficult to track as individuals, but observing masses of emergent aquatic insects and the geometry of water bodies may provide a simple framework to estimate aquatic insect deposition on land (Gratton and Vander Zanden 2009). Aquatic insect emergence from the water can be measured on a per unit area basis (Davies 1984, Malison et al. 2010). Studies of aquatic insect productivity and emergence suggest that 75-99% of stream secondary productivity may be exported to land as insect biomass (Jackson and Fisher 1986, Gray 1989, Petersen et al. 1999). But biomass export alone cannot be used to estimate aquatic insect deposition to land per unit area since aquatic insect density on land may be concentrated or dispersed widely in space. Measurements of aquatic insects on land show that their density is greatest close to the water's edge (Kuusela and Huusko 1996, Petersen et al. 1999), declining rapidly as distance from the water increases (Francis et al. 2006). Common methods used to measure insect density (malaise, sticky, pan, and cup traps) measure relative abundances only, and may be biased in regards to certain taxa (Lynch et al. 2002) Since deposition is measured in units of area and time, methods that intercept and kill insects are unable to accurately estimate actual deposition. What is required to quantify insect deposition is a passive method or the merging of biomass and abundance data.

One way in which absolute densities of insects on land can be estimated is by assuming that all insects emerging from a body of water must deposit themselves somewhere on land. Using this assumption to combine measurements of aquatic insect emergence from water and abundance on land could provide an accurate estimate of nutrient deposition around bodies of water. Accordingly, Gratton and Vander Zanden (2009) have proposed that aquatic insect deposition to any area on land is a function of emergence from the source water body, the length of the edge of the water body, and distance from the water body. Sabo and Hagen (2012) further suggest that dispersal distance and reticulation of the edge may also create local hotspots of aquatic insect density. The productivity of nutrient poor terrestrial ecosystems adjacent to water could be stimulated by nitrogen and/or phosphorus deposited by aquatic insects (Hodkinson et al. 2001, Hoekman et al. 2011, Menninger et al. 2008). Therefore measuring both aquatic insect emergence from and relative abundance around a single body of water could create a holistic estimate of the importance of their biomass and nutrient deposition to land.

Lake Mývatn in northeast Iceland provides a good opportunity to estimate the extent and magnitude of insect deposition to land from a single water body. This appropriately named lake (Mývatn = "lake of midges" in Icelandic) is famous for the massive numbers of midges (Diptera: Chironomidae) that it produces (Einarsson et al. 2004). Midges are ubiquitous (Merritt and Cummins 1996) and often comprise large proportions of emergent aquatic insect numbers/biomass (Rundio and Lindley 2012, Stagliano et al. 1998). Most midges develop on the bottom of the large naturally productive lake, emerging to form large mating swarms during the summer months at times darkening the sky and vegetation alike. Some midges fall prey to aquatic (Einarsson and Gardarsson 2004) and later terrestrial predators (Gratton et al. 2008), while mated females attempt to return to the lake to lay their eggs. But many more expire on the ground after mating, their carcasses then entering the detrital pool. An experiment close to the shore of a nearby lake with few midges showed that addition of midge carcasses increased numbers of detritivorous and predatory arthropods as well as plant productivity (Hoekman et al. 2011). Further observational studies show that midges have profoundly altered the plant and arthropod communities adjacent to the edge of Lake Mývatn (Dreyer et al. 2012, Raudenbush et al. unpublished data).

In order to understand general patterns of aquatic insect deposition on land, and specific rates of terrestrial midge input at Lake Mývatn shoreline, we developed a method to measure and model their emergence from the lake and distribution over the shoreline. Our study quantified midge biomass exiting Lake Mývatn and their density around it between 2008-2011 using midge emergence traps in the water and "infall" cups on land at various distances from the lake edge. These data were then combined into a spatial landscape model of midge and nutrient deposition to the terrestrial ecosystem. Our simple method allows a spatially explicit estimate of aquatic insect deposition per unit area, for the first time affording a comprehensive understanding of the scale of aquatic insect input to land for a single ecosystem with the ability to assess or predict their impacts on terrestrial productivity.

2. Materials and Methods

2.1 Study System

Lake Mývatn, Iceland (65°36'N,17°0′W) is a large (38 km^2) shallow (4m max depth) lake that is naturally highly productive (Fig. 1). The production of non-biting midges (Chironomidae: Diptera) on the lake bottom is high, averaging 28 g ash free dw m^{-2} yr^{-1} from 1972-74 (Lindegaard and Jónasson 1979). The midge assemblage of Lake Mývatn is mostly (>90%) comprising two species, *Chironomus islandicus* (Kieffer) and *Tanytarsus gracilentus* (Holmgren) (Lindegaard and Jónasson 1979). At maturity (May-August) midge pupae float to the lake surface, emerge as adults, and move to land forming large mating swarms and columns (Einarsson et al. 2004, Gratton et al. 2008; Fig. 2). On land some are consumed by terrestrial predators (Dreyer et al. 2012, Gratton et al. 2008), or enter the detrital pool upon death (Gratton et al. 2008, Hoekman et al. 2012).

2.2 General Approach

Our study aimed to reconcile differences between measured rates of midge emergence from the lake and abundance around the shore by combining information from each into a unified whole. It is important to note here distinctions in terminology (Fig. 2). The mass of midges exiting from the lake, expressed in a per unit area of lake basis is referred to as **emergence**. The mass of midges collected in lethal aerial traps at sampling stations on land, used to develop a decay function, is called **abundance**. Due to the lethality of passive traps this mass is related to but much greater than the actual amount of midge biomass that is deposited naturally. **Deposition** is the mass of midges estimated to remain on land per unit area, using the abundance pattern to spread total emergent biomass around the lake. For four summers we measured both midge emergence and abundance at Lake Mývatn, using these data to estimate terrestrial midge deposition.

2.3 Midge Emergence

We used submerged conical traps to estimate midge (Chironomidae) emergence from Lake Mývatn (Fig. 2). Traps were constructed of 2mm clear polycarbonate plastic (Laird Plastics, Madison, WI) formed into a cone with large-diameter opening of 46 cm (0.17 m^2). The top of the cones were open to a diameter of 10 cm, with a clear jar affixed at the apex. The trap was weighted to approximately neutral buoyancy, since while submerged the jar at the top contained air to allow mature midges to emerge. Traps were attached to a fishing buoy by a ~1m nylon line, the buoy being anchored to the lake bottom using two anchors on lines ~4-6m long set at a 45^{o} angle. Upon sampling traps were raised to the surface and rapidly inverted, preventing midges from escaping. Jars and traps were thoroughly rinsed with lake water to collect all trapped midges and scrubbed before being returned to the lake to prevent overgrowth of epiphytic algae and colonization by midges.

We sampled midge emergence at sites throughout the south basin of Lake Mývatn. During 2008 and 2011 six sites were used, while in 2009 and 2010 an additional four sites were included (Fig. 1) for a total of ten. Site locations selected to represent the basin as a whole and were recorded using GPS. Midge emergence was continuously monitored from two traps at each site during peak midge activity, approximately the last week of May to the first week of August annually (third week of July in 2011; Appendix I). Traps were checked approximately weekly during periods of high emergence (initial and final 2-3 weeks), and bi-weekly when emergence rates were low (July). The density of midges emerging was estimated from emerged adults as well as larvae and pupae that had failed to completely metamorphose. Midges were identified as "large" (>5 mm) or "small" (<5 mm) during counts, the former comprised mostly of *Chironomus islandicus* and the latter *Tanytarsus gracilentus, r*espectively these two species account for ~80% and 9% of total midge numbers in Lake Myvatn (Lindegaard & Jónasson 1979). To determine the mass of midge emergence per unit area (g dw m^{-2} yr^{-1}) at each site the average number of "large" and "small" midges collected from the two traps was multiplied by their average dry mass as determined by a sample of 100 midges of both size classes measured in 2008 and 2010 ("large" ≈ 0.001 g, "small" ≈ 0.0001 g, unpublished data) and divided by the area of the trap for a per unit area estimate of midge emergence.

We estimated total annual emergence from Lake Mývatn by multiplying the area of lake bottom suitable as midge habitat and the rate of midge emergence. The midge producing area of the lake was constrained to the portion capable of supporting significant quantities of midges; e.g. away from rocky shorelines and dominated by epibenthic algae (A. Einarsson pers. comm, Einarsson et al. 2004; Fig. 1). This area was then subdivided so that emergence rates from individual sites were applied to areas in closest proximity using Euclidean distance Voronoi tessellation polygons centered on the site locations. Since we did not measure emergence from the north basin of Lake Mývatn all data we report here are for the south basin and its surroundings only. The two basins are joined by a single narrow channel, and function mostly as independent hydrologic bodies (J. Ólafsson 1979). During each unique collection period midge emergence at each site was multiplied by the area of the corresponding Voronoi polygon. We estimated the mean annual emergence and 95% confidence intervals of total annual emergence from 999 permutations of a randomized selection of one trap per site.

2.4 Midge Abundance on Land

Transects of passive, lethal aerial traps were used to estimate midge abundance on shore during the summers 2008-2011 (Fig. 2). Ten transects were established around the southern basin of Lake Mývatn in 2008, with a single transect on the lake's northern basin (Fig. 1). Each transect was perpendicular to the lake edge, with traps located at approximately 5, 50, 150, and 500 m (where possible) for a total of 31 traps. Sampling locations were recorded using GPS and distances from the lake were calculated with a geographic information system. Traps consisted of a single 1000 mL clear plastic cup (0.0095 m^2 opening) elevated 1m on a stake and filled with 300mL of a 1:1 mixture of water and ethylene glycol and trace amounts of unscented detergent to capture, kill, and preserve insects landing inside (Gratton et al. 2008, Dreyer et al. 2012). Midges and other insects were collected weekly. To determine rates of midge abundance collected (g dw d^{-1}) the number of "large" and "small" midges was multiplied by their average dry mass (see "*Midge Emergence*" above).

2.5 Midge Density Decay Function

We standardized midge abundance measurements to a proportion to allow comparison across sampling periods which experience orders of magnitude differences in total abundance, but still show a similar abundance decay function with distance from lake edge. To estimate total abundance along the transect the trap abundance measurements we integrated the polygon circumscribed by both axes and midge abundance values at the distances they were collected out to 300 meters. From this, the proportion of abundance at all distances at 1 m increments was calculated. If any of station observations were missing or when measured abundance at the most distant sample (~150m or 500m) within a transect was higher than closer samples the entire transect was excluded from analysis for that sampling period. In such cases, calculation of area under the curve for conversion to proportional abundance was not possible. Finally, we excluded data from two transects on the Kálfaströnd peninsula since these transects were short compared to the others (103m vs. >123m for all others) and probably did not adequately capture the abundance decay with distance. Proportion data were arcsine-square root transformed for further analysis.

We developed a local minima decay function model to predict the proportion of midge abundance as a function of distance from the lake edge. An examination of our data indicated a local minima model form, in which abundance increases from zero at the lake edge to a maximum some short distance from the lake and then declines to zero with increasing distance. The model form was:

$$(1)\ \arcsin\sqrt{I_{\hat{p}d}} = ab^{d}\, e^{cd}$$

where Iphatd = proportion of abundance at distance *d* from the lake, and *a*, *b*, and *c* represent parameters describing the shape of the local minima decay curve. Note that the value of *d* at the first derivative of Eq. 1 is the distance at which maximum abundance occurs. We solved for *a*, *b*, and *c* using PROC NLMIXED in SAS v. 9.3 (SAS Institute Inc 2011) using either the "Weekly" or "Annual" proportion standardized data. In our model, we weighted observations by total measured abundance at a sample site. This was necessitated by using proportion data; weighted nonlinear regression reduced the influence on the model of dates having low abundance or abundance rates approaching background levels, the times at which abundance patterns would be expected to be highly variable. We initially tested a mixed effects version of the model in which year of sampling was treated as a random effect, but found no statistically significant differences in parameters *a*, *b* and *c* by year. Therefore the parameters in the results we report apply to all years.

We developed unique local minima decay functions taking into account varying methods of data and midge aggregation. Unique functions were generated for data collected throughout the summer ("weekly" model, station X weeks N=603), and on the cumulative data collected at each station during a year ("annual" model, station X year N=108). Furthermore, "weekly" and "annual" models were generated for the "small", "large", and "all" (summation of "small" and "large") midges for a total of six models (3 midge types X 2 data types). We evaluated the robustness of each model through jack-knifed cross-validation (Appendix II). Specifically, we dropped each year of sampling sequentially, re-developed our predictive model, and tested that model on the dropped year. Model evaluation included analyses of both arcsine square-root transformed data as well as the data backtransformed to total abundance. Differences between model parameters and predictive ability were minor compared to the overall pattern (Appendix II and III), thus all data reported here are derived from the "all annual" model unless otherwise noted.

2.6 Midge Deposition Model

We developed a spatial model to estimate deposition of midges as a function of the total mass of emergent midges and the local minima decay function (Eq. 1). The local minima decay function was further modified so as to take into account the spatial extent of the model as well as the nature of the landscape surrounding Lake Mývatn. First, the decay model was normalized to its maximum distance, defined as the distance beyond which midge proportion approximates to background levels of aerial insect activity (< 0.0001). Next, the decay function was area weighted in 5m bands from 0m from the lake edge to the maximum distance. This weighting adjusts the decay function for the landscape surrounding Lake Mývatn and is important since each 5m band is not equal in size (Appendix IV). To illustrate, if a lake is perfectly round and surrounded by concentric rings of 5 meter width, the amount of area within any ring must be less than the ring that is next farthest away from the lake. Conversely, a highly convoluted shape like the Lake Mývatn shoreline has rings close to its borders that occupy *more* area than the next farthest ring out. Following area weighting the decay function gives the proportion of total emergence in each band, and when divided by the area within the band, provides the proportion of total emergence deposited at that distance per unit area.

Annual midge deposition to the landscape adjacent to Lake Mývatn was estimated by combining annual midge emergence with the abundance decay function. Using raster-based modeling (performed in Python 2.7 and visualized in ArcGIS), we generated a 5 m resolution grid of distance from lake from which the proportion of total deposition was calculated based on the normalized, area-weighted decay function (Appendix V). For annual estimates of midge deposition we multiplied the total annual midge emergence by the landscape raster. Our model assumes that all midges emerging from the lake are deposited on shore, appropriate since error in emergence estimates is likely on the same scale as the fraction of midges that return to the lake.

Estimated midge deposition was compared to observed midge abundance using ordinary least squares regression of observed abundance as a function of predicted deposition. When compared with the predictions of the deposition model, midge abundance (g dw d^{-1}) was divided by the area of the cup opening. All data were natural log transformed to meet assumptions of normality of residuals, and predicted deposition of traps at greater than the maximum distance of the model were dropped. We included “year” and “transect” as factors to determine the importance of time and location around the lake to the predictive ability of our deposition model. These analyses were performed using R 2.13.2 (R Development Core Team 2011).

3. Results

3.1 Midge Emergence

Mean annual midge emergence declined sharply from a high of 75 tons dw in 2008 to less than 4 tons dw in 2011 (Fig. 3). This represents an average per unit area midge emergence of 3.7

and 0.15 g dw m^{-2} yr^{-1} respectively. Emergence was greatest at the beginning and end of the summer, with low levels of emergence during July (Appendix II).

3.2 Midge Abundance

Midge abundance also declined greatly over the four year period (Table 1). The 5m and 50m stations averaged >200g dw yr^{-1} during 2008, but those same locations averaged only 25g dw yr^{-1} in 2011. Midge abundance decreased as distance from the lake increased (Table 1, Fig. 4). In 2008 stations at appoximately 5m from the lake edge averaged >300g dw yr^{-1} while those at around 500m collected ~20g dw yr^{-1}. The pattern of decreasing abundance with distance was consistent across years (Fig. 4).

3.3 Decay Function

The decay function showed a congruent pattern of midge density slightly increasing and then rapidly decreasing with distance from lake edge (Fig. 5). The ability of the decay model to predict observed midge abundance was high (R^2 = 0.89). This high R^2 values coupled with a lack of significance across years demonstrates that the pattern of decreasing midge abundance with increasing distance from shore is consistent over time (Fig. 5).

3.4 Midge Deposition

Model results based on measurements of midge emergence and relative density on shore estimate that midge deposition on the landscape adjacent to Lake Mývatn is large in both magnitude and extent. In the peak midge year 2008 the first 50 meters of shoreline adjacent to the lake has an average estimated midge deposition slightly above 100 kg dw ha^{-1} yr^{-1} midges (Table 3, Fig. 6). In 2009 – 2011 this number is reduced to approximately 50, 30, and 4 kg dw ha yr^{-1} respectively. Since midges are approximately 10% N and 1% P by mass (Fagan et al. 2002, Gratton et al. 2008), this amount of deposition adds 0.4 – 10 kg N ha^{-1} yr^{-1} and 0.04 – 1 kg P ha^{-1} yr^{-1} to the terrestrial ecosystem. The first 50 meters of shoreline into which we estimate that 35% of midge deposition occurs is over 330 ha in extent, while over 590 ha are contained within the first 100 m that experiences >60% of midge deposition. The maximum extent of our model covers an area >2,300 ha, fully 60% of the surface area of the lake (3800 ha).

Midge abundance without a connection to midge emergence greatly inflates midge deposition estimates. There was a strong positive relationship ($F_{1,99}$ = 240.1, P <<0.0001, adj. *psuedo*-R^2 = 0.701) between estimated midge deposition from our model and observed midge abundance. Year ($F_{3,88}$ = 2.92, P = 0.038) and transect ($F_{8,88}$ = 6.51, P <<0.0001) had significant effects as well. Our regression model predicts 50 kg dw ha^{-1} yr^{-1} of midge deposition where our emergence constrained model predicts deposition to be nil. Across all midge deposition predictions aerial abundance traps overestimate midge deposition by 20-30 times (Figure 7). Despite the overestimate of aerial traps the relationship between estimated deposition and observed abundance was strong, so while abundance is a repeatable and relatively precise measure of relative midge abundance, it is a biased method for determining aquatic insect deposition if not constrained by total emerging biomass.

4. Discussion

Using combined measurements of aquatic insect emergence and abundance on land around a large arctic lake we developed a model to estimate aquatic insect deposition in terrestrial ecosystems. Emergence of aquatic midges was estimated to be nearly 80 tons dw yr^{-1} in a high midge year, testament to the large amount of insect secondary production that can be supported in a large lake basin. We distributed this biomass over the landscape adjacent to the lake using a decay fitted to measurements of relative midge density by aerial abundance traps at various locations around the lake and distances from the lake edge. The observed pattern of decreasing midge density with increasing distance from shore that was consistent across years of varying midge productivity. The model estimates that over 100 kg ha^{-1} yr^{-1} of midges, equivalent to ~10 kg N ha^{-1} yr^{-1}, are deposited within the first 50 m of shoreline during a year of high midge emergence. Background rates of N deposition at northern latitudes range from 2-3 kg N ha^{-1} yr^{-1} in arctic systems (Bobbink et al. 2010). Thus midge inputs result in a 2-3 fold increase in annual N additions over hundreds of hectares.

Midges from Lake Mývatn are an important source of nutrients to the adjacent terrestrial ecosystem. In addition to nitrogen, midge biomass also transfers phosphorus (P) to the land; we estimate up to 1 kg ha^{-1} yr^{-1} during high midge years. The addition of these two elements to nutrient limited arctic heathlands has been shown elsewhere to cause significant shifts in vegetative cover and primary productivity (Bobbink et al. 1993, Britton and J. M. Fisher 2007, Shaver et al. 2001). Unlike the shrubs and ericaceous plants that dominate the landscape at distances >500 meters from Lake Mývatn, the areas close to shore are dominated by grasses and forbs more typical of areas with greater N availability (Raudenbush et al., unpublished data). Anecdotes from the farms that border Lake Mývatn tell of the "midge grass" that feed their sheep following periods of high midge density (Á. Einarsson, *pers. comm.*). Nitrogen-absorbing resin bags placed at various aerial trap stations during 2008 show increased nitrate concentration close to shore concurrent with an increase in midge deposition (Fig. 8). These data suggest that where aquatic insects follow similar terrestrial abundance patterns, productive water bodies may increase productivity and/or alter community composition of nutrient limited terrestrial ecosystems (Wedin and Tilman 1996).

The critical step in creating an accurate determination of terrestrial deposition is using emergence traps to constrain aquatic insect deposition estimates. Midge abundance data at Lake Mý　vatn from aerial traps inflated the rate of aquatic insect deposition to land by 20-30 times when simply divided by the area of trapping surface (Fig. 7). While measures of relative abundance on land are important to understanding the terrestrial concentration of aquatic insects (Petersen et al. 1999), these measurements alone are insufficient to inform actual rates of terrestrial deposition. We suspect that this overestimation is the result of the lethality of the aerial traps. Given enough time, in terms of both the trap and insect duration, a single trap could theoretically capture all insects within its vicinity (“black hole”). Therefore, unless constrained by maximum available biomass, lethal methods of insect abundance measurement will overestimate deposition per unit area and greatly increase estimates of insect biomass and nutrient deposition.

Our findings corroborate those of previous studies of insect deposition. Using literature values Gratton and Vander Zanden (2009) derive general decay functions that describe patterns of aquatic insect abundance around water bodies. Lake Myvatn midge deposition values of the Gratton and Vander Zanden model were estimated by applying our local minima decay function using their negative exponential and inverse power decay functions taken from lakes only.

Simple linear models using only the results of the negative exponential and inverse power function deposition estimates are consistent, with R^2 values of 0.365 and 0.645 respectively. While the accuracy of our local minima function is superior (R^2 = 0.701, AIC local minima = 183.4 < AIC inverse power =196.1 < AIC negative exponential = 224.1), it comes at significant labor cost. Given that the increase in accuracy due to a system specific model of aquatic insect abundance on land was marginal, we suggest that if the goal is to estimate terrestrial deposition of aquatic insects then greatest emphasis should be placed on accurate measurement of insect emergence rather than a characterization of the decay with distance from ecosystem boundary.

The concentration of nutrients by insects may be common, especially in riparian areas. This process may be similar to nutrient "hot spots" formed by vertebrates (Anderson and Polis 1999, Helfield and Naiman 2006, Holtgrieve et al. 2009). Many productive water bodies are bordered by low productivity terrestrial ecosystem, such as deserts (Jackson and Fisher 1986). To date there has been little effort to explore the capability of fertilization to occur along streams, rivers, and lakes (but see Francis et al. 2006). Previous observations have shown a consistent pattern of decreasing aquatic insect abundance with greater distance from the water, and models based on those data have predicted nonetheless that significant aquatic insect deposition may occur (Gratton and Vander Zanden 2009, Sabo and Hagen 2012). Our work supports those predictions, and suggests that insect deposition has the potential to deliver large amounts of limiting nutrients to shore and that this process may be quite general. Large numbers of insects that cross ecosystem boundaries should be studied because while they may be individually small, their effects *en masse* may be both important and easily measureable.

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	Mean Midge Abundance at Distance Class (g yr $^{-1}$)											
	5m			**50m**			**150m**			**500m**		
Year	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE
2008	7	304	13.7	7	278	12.5	7	89.0	3.23	4	20.2	1.29
2009	9	212	6.06	9	215	6.82	9	93.6	2.39	4	29.9	2.75
2010	9	199	3.98	9	161	3.32	9	45.2	0.73	4	10.5	0.33
2011	6	25.1	1.43	6	12.5	0.49	6	5.54	0.14	3	2.31	0.12

Table 1. Sample size, mean, and standard error of total midge infall as measured by lethal aerial traps along transects around Lake Mývatn, Iceland from May-August 2008-11. Distance classes are approximate distances (meters) at which traps were set from the lake edge.

Year	Max Deposition (20-25m)	Mean Annual Deposition (kg ha $^{-2}$ yr $^{-1}$) at Distance Class (meters)								
		0-50	50-100	100-150	150-200	200-250	250-300	300-350	350-400	400-450
2008	110	100	75	47	28	17	10.0	5.8	3.4	2.0
2009	59	55	41	25	15	9.1	5.4	3.2	1.8	1.1
2010	35	32	24	15	9.1	5.4	3.2	1.9	1.1	0.63
2011	4.5	3.9	3.1	1.9	1.2	0.69	0.41	0.24	0.14	0.081
	Proportion in Class	0.35	0.25	0.16	0.10	0.06	0.03	0.02	0.01	0.01
	Cumulative Proportion	0.35	0.61	0.77	0.87	0.93	0.96	0.98	0.99	1.00

Table 2. Predicted total annual midge deposition within 50m bands moving outward from the North and South basins of Lake Mývatn, Iceland shoreline.

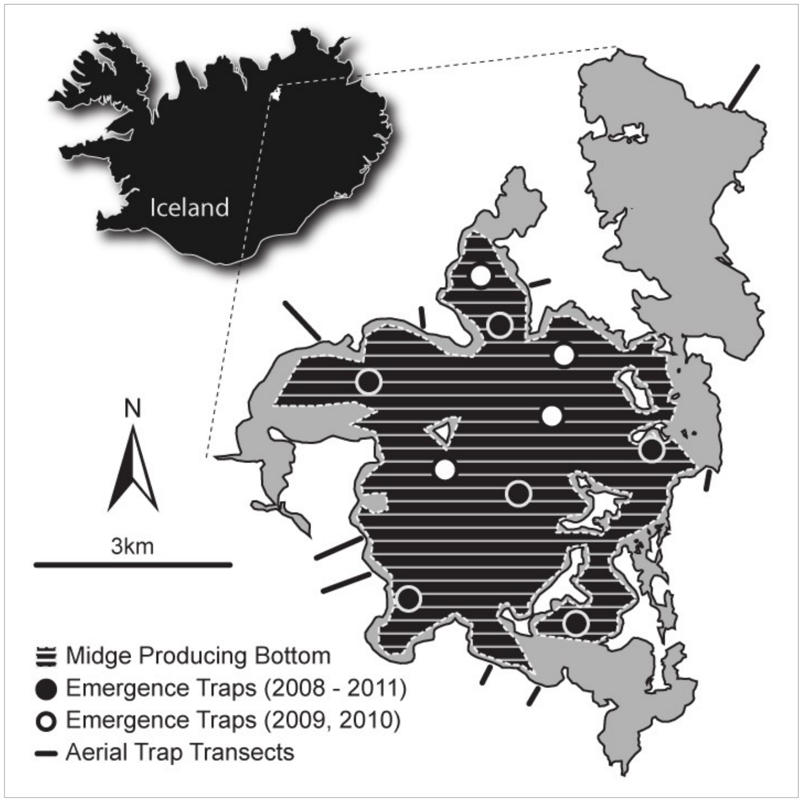


Figure 1. Location of Lake Myvatn, Iceland, and placement of sampling sites in and around the lake.

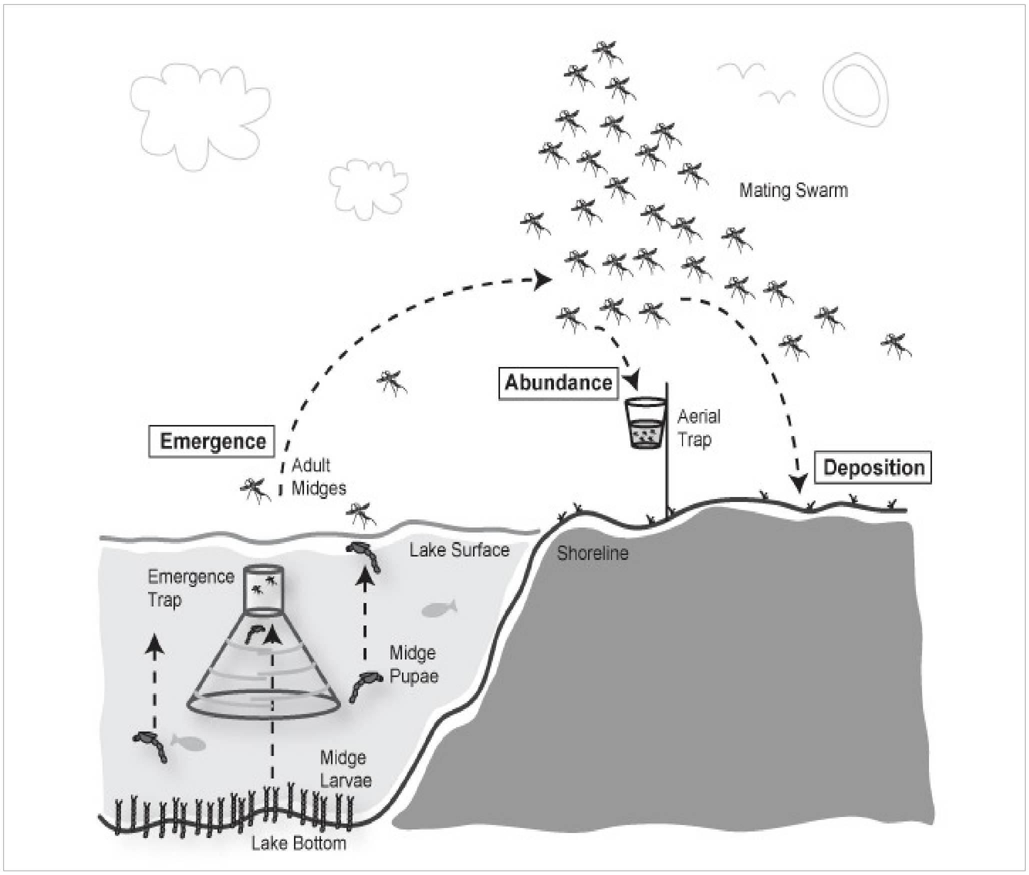


Figure 2. Cartoon illustration of aquatic and terrestrial midge sampling scheme. Midges develop as larvae on the lake bottom. When they rise to the surface to emerge as adults submerged conical traps capture them for a per area estimate of midge emergence. Adults swarm on land in large mating swarms which are most dense close to the lake edge. Lethal aerial traps placed at appoximately 5, 50, 150, and 500m from the lake edge characterize these difference in midge abundance. Together these aquatic and terrestrial data were combined into a model of midge flux from lake to the land.

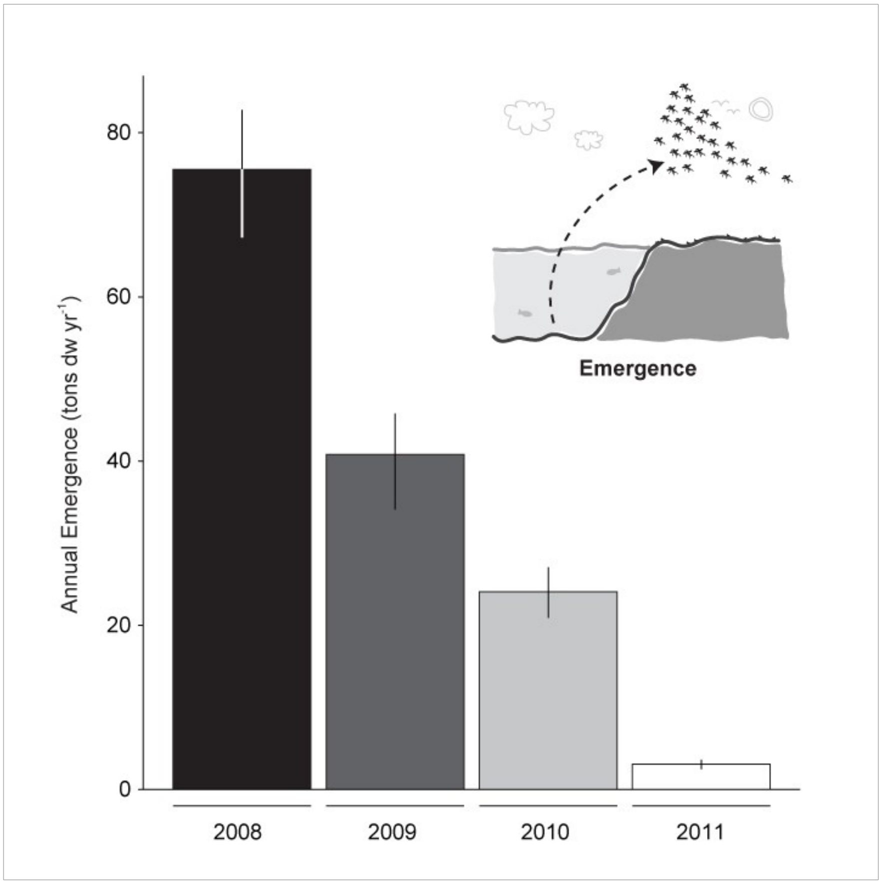


Figure 3. Total midge emergence from Lake Myvatn, Iceland from May-August during 2008-11 (tons dw yr^{-1}). Colors indicate the size of midges captured by submerged emergence traps (“small”≈ 0.0001g, “large”≈ 0.001g). Emergence from both basins have been combined. Error bars are +/- 95% confidence interval.

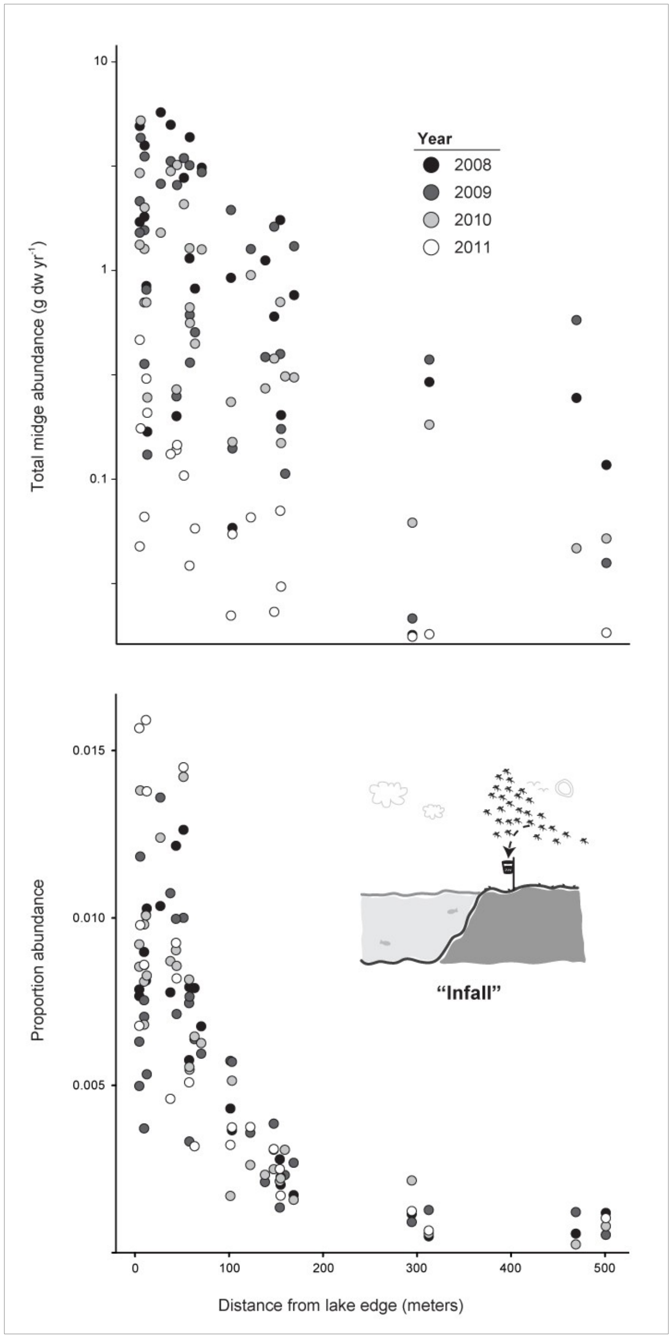


Figure 4. Midge infall absolute (top) and proportion (bottom) as collected by lethal aerial traps sited at various distances from the edge of Lake Mývatn, Iceland from May-August 2008-2011.

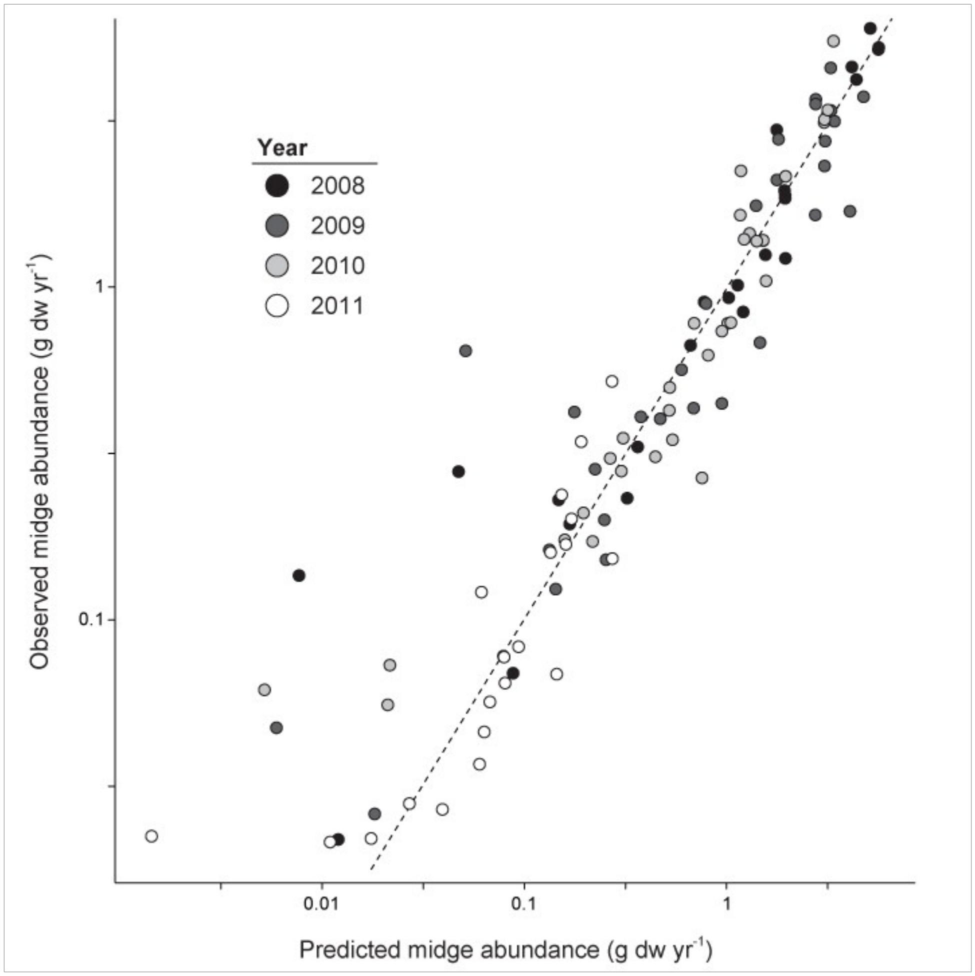


Figure 5. Predicted vs. observed infall from the minima decay model of midge abundance as a function of distance from lake edge. Dashed line is the 1:1 line.

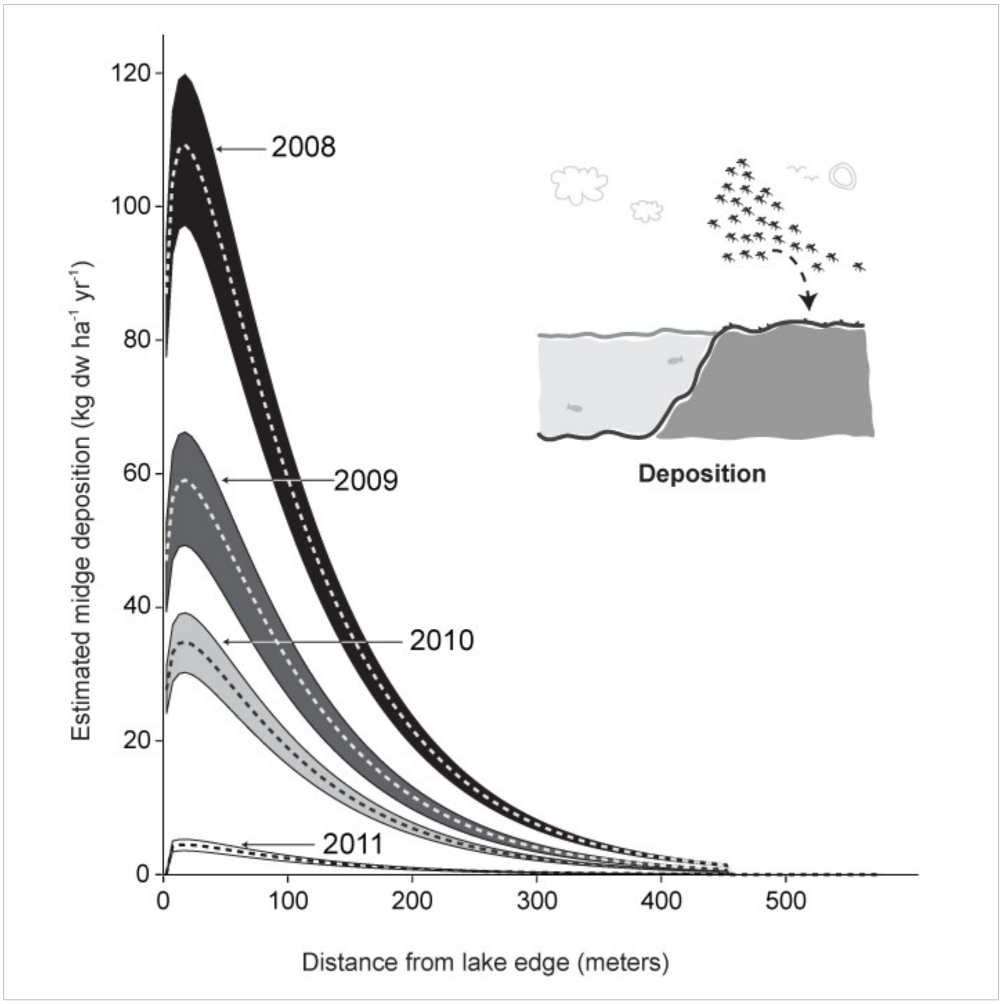


Figure 6. Predicted midge deposition (kg dw ha^{-1} yr^{-1}) around the Lake Mývatn, Iceland as a function of distance (meters) from the shoreline, May-August during 2008-11.

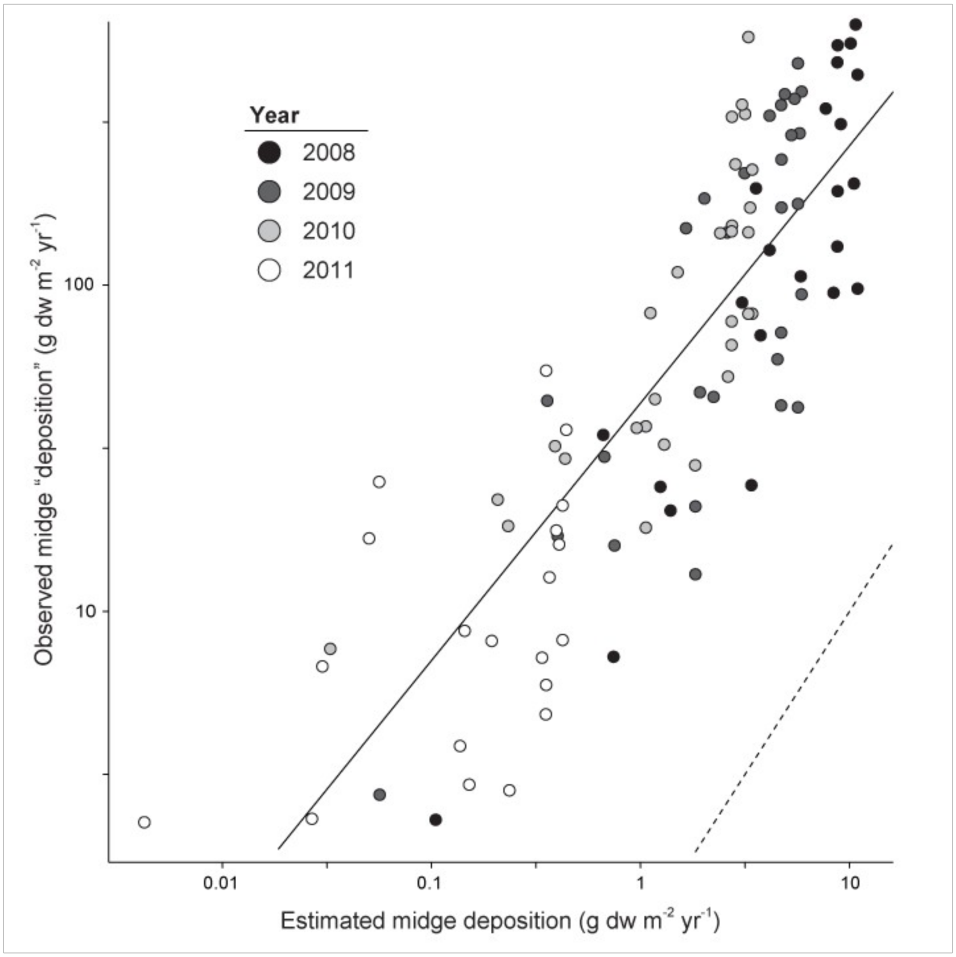


Figure 7. Estimated vs. observed midge deposition around Lake Myvatn, Iceland May-August during 2008-2011. This comparison indicates that lethal aerial traps along transects capture ~20-30X more midges than are likely deposited in the same area. Dashed line is the 1:1 line.

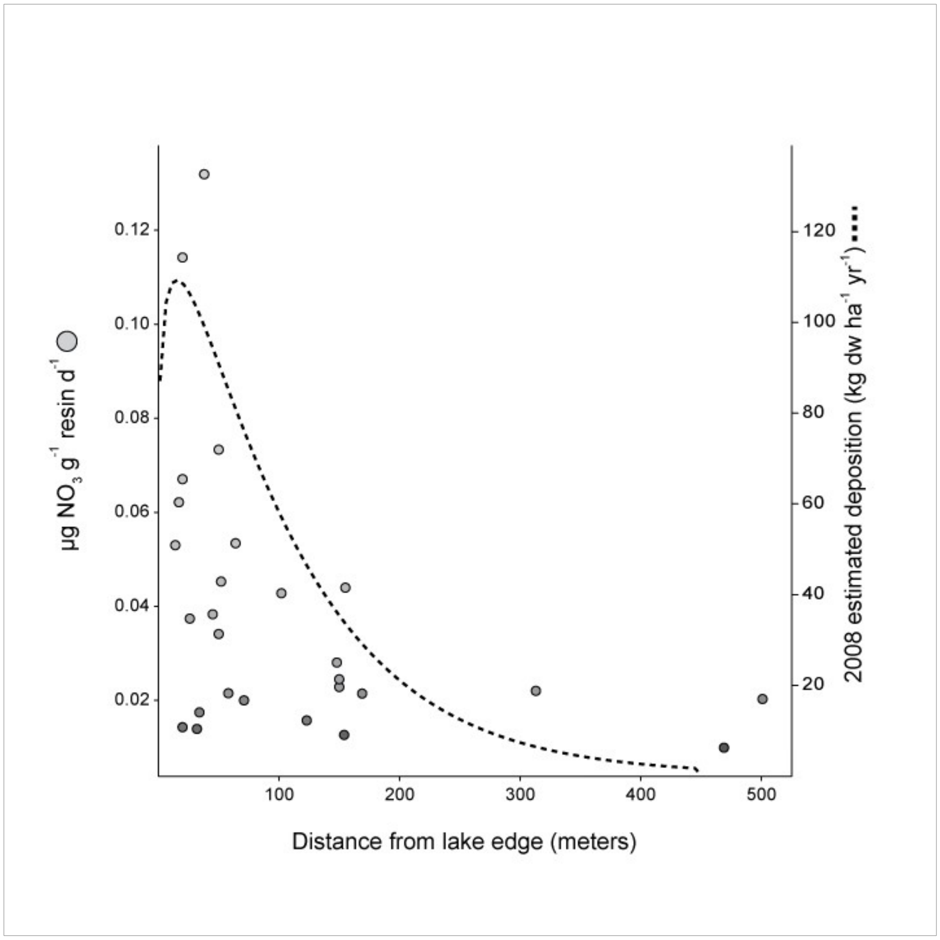


Figure 8. Nitrate captured by resin bags (µg NO_3^- g^{-1} resin d^{-1}) buried along transects around Lake Mývatn, Iceland show a similar pattern as predicted midge deposition (g dw m^{-2} yr^{-1}) with increasing distance from shore during the summer of 2008. This is evidence that midges are adding substantial quantities of additional N to the terrestrial ecosystem that neighbors the lake.

Year	Sampling Period	N	Emergence g m^{-2} d^{-1}	SE
2008	24 May – 1 June	11	0.1779	0.0508
2008	1 June – 10 June	11	0.1569	0.0274
2008	10 June – 14 June	4	0.3268	0.1064
2008	10 June -20 June	6	0.0143	0.0047
2008	14 June – 20 June	5	0.0172	0.0078
2008	20 June – 3 July	12	0.0005	0.0002
2008	3 July – 19 July	12	0.0010	0.0003
2008	19 July – 29 July	12	0.0081	0.0023
2008	29 July – 4 August	12	0.0188	0.0090
2009	22 May – 1 June	8	0.0069	0.0016
2009	23 May – 1 June	4	0.0217	0.0109
2009	1 June – 8 June	20	0.1186	0.0200
2009	8 June – 15 June	20	0.0449	0.0140
2009	15 June – 26 June	20	0.0026	0.0005
2009	26 June – 17 July	19	0.0064	0.0018
2009	17 July -24 July	20	0.0704	0.0131
2010	22 May – 30 May	17	0.0492	0.0106
2010	30 May – 8 June	18	0.0333	0.0073
2010	8 June – 17 June	18	0.0147	0.0069
2010	17 June – 6 July	18	0.0010	0.0002
2010	6 July – 17 July	17	0.0297	0.0074
2010	17 July – 6 August	18	0.0010	0.0004
2011	26 May – 7 June	11	0.0033	0.0011
2011	7 June – 16 June	12	0.0049	0.0016

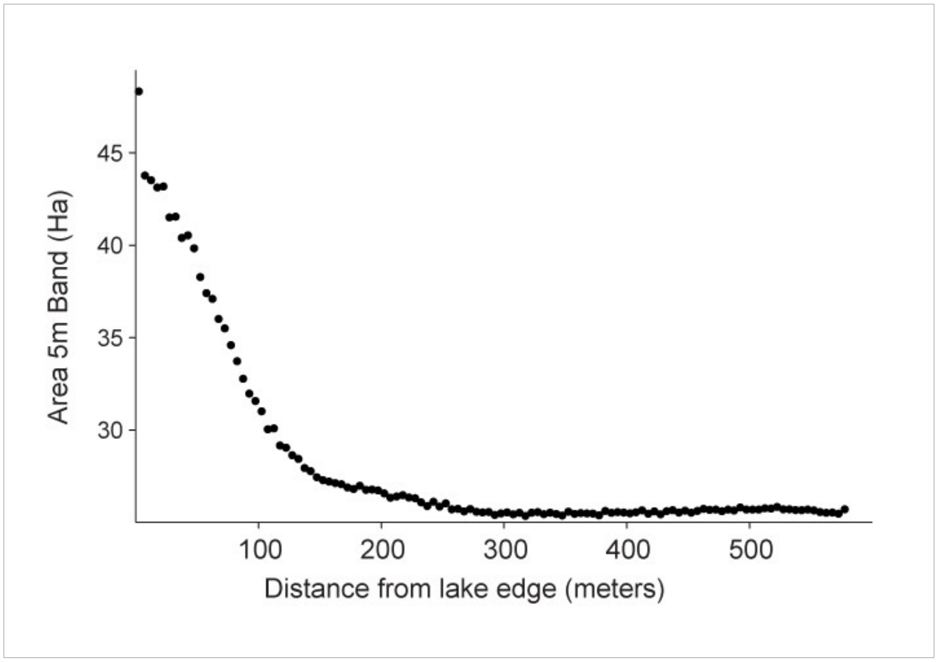
Appendix I. Table of daily rates of total midge emergence from Lake Myvatn, Iceland during May-August 2008-2011.

			Full Model		Model on Year Left Out	
Year Removed	Data	Midge	Pseudo R^2	Pseudo Adj. R^2	Pseudo R^2	Pseudo Adj. R^2
None	Annual	Large	0.8281	0.8255	NA	NA
None	Annual	Small	0.8393	0.8378	NA	NA
None	Annual	All	0.8887	0.8876	NA	NA
None	Weekly	Large	0.8472	0.8465	NA	NA
None	Weekly	Small	0.8290	0.8287	NA	NA
None	Weekly	All	0.9212	0.9211	NA	NA
2008	Annual	Large	0.8039	0.7997	0.6487	0.6311
2008	Annual	Small	0.8008	0.7983	0.9401	0.9378
2008	Annual	All	0.8304	0.8283	0.9474	0.9451
2008	Weekly	Large	0.9239	0.9234	0.7286	0.7217
2008	Weekly	Small	0.7779	0.7775	0.8889	0.8883
2008	Weekly	All	0.8052	0.8047	0.9740	0.9738
2009	Annual	Large	0.8879	0.8860	0.3453	0.2635
2009	Annual	Small	0.9172	0.9162	0.6847	0.6739
2009	Annual	All	0.9416	0.9408	0.7468	0.7381
2009	Weekly	Large	0.8936	0.8929	0.6984	0.6926
2009	Weekly	Small	0.8553	0.8550	0.7538	0.7525
2009	Weekly	All	0.9535	0.9534	0.7936	0.7924
2010	Annual	Large	0.8223	0.8186	0.8624	0.8543
2010	Annual	Small	0.8460	0.8440	0.8743	0.8700
2010	Annual	All	0.9039	0.9027	0.8664	0.8618
2010	Weekly	Large	0.8489	0.8477	0.8311	0.8287
2010	Weekly	Small	0.8464	0.8460	0.7844	0.7835
2010	Weekly	All	0.9366	0.9364	0.8051	0.8041
2011	Annual	Large	0.8046	0.8007	0.3358	0.2967
2011	Annual	Small	0.8199	0.8178	0.5454	0.5201
2011	Annual	All	0.8726	0.8711	0.6587	0.6408

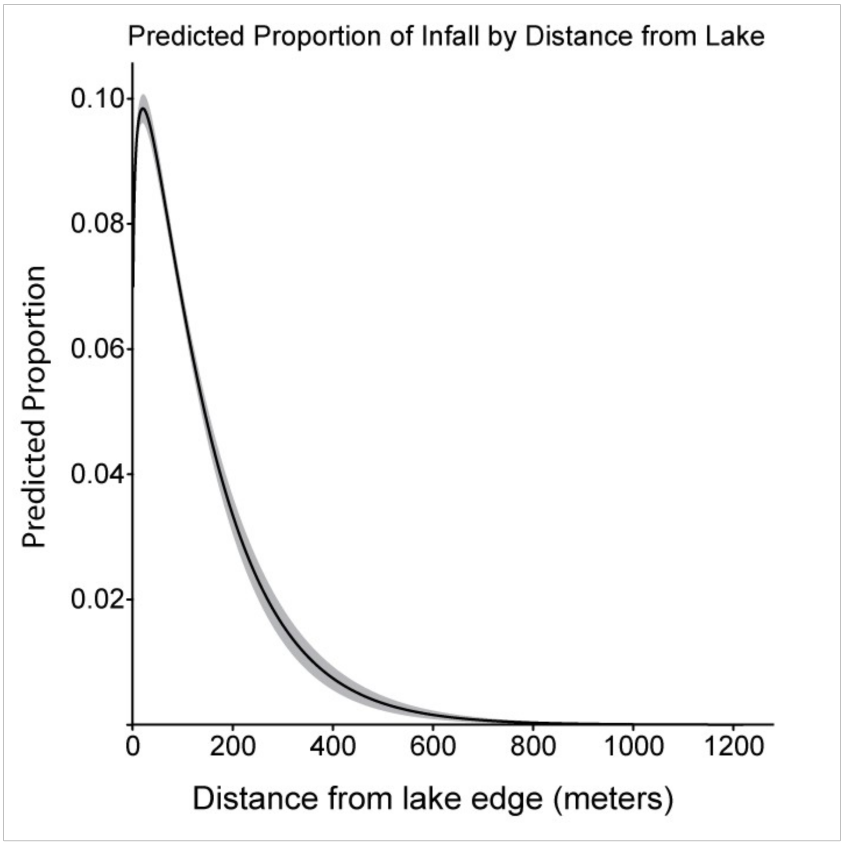
Appendix II. Results of jack-knifed cross validation on prediction models using proportion converted infall data.

Year Removed	Data	Midge	Pseudo R^2
None	Annual	All	0.8887
2008	Annual	All	0.8304
2009	Annual	All	0.9416
2010	Annual	All	0.9039
2011	Annual	All	0.8726
None	Weekly	All	0.9212
2008	Weekly	All	0.8052
2009	Weekly	All	0.9535
2010	Weekly	All	0.9366

Appendix III. Pseudo-R^2 values from a linear regression of the predicted infall values vs. the observed infall values of the six minima decay models.



Appendix IV. There is more area within 100 meters of Lake Myvatn, Iceland than at distances 300-500m from the lake edge. This is due to the convolutions of the shoreline, including islands, that give the lake a perimeter that is 4.34 times the length it would be for a circle of equal surface area (38 km^2).



Appendix V. Model curve of predicted proportion of midge infall as a function of distance from the lake edge.

CHAPTER 2

Lake-derived midges increase abundance of shoreline terrestrial arthropods via multiple trophic pathways

Abstract: Aquatic insects link adjacent ecosystems by transporting nutrients, energy, and material as they move from bodies of water into terrestrial habitats. Insects emerging from streams and rivers are known to benefit arthropod predators such as spiders, but their influence may extend to other arthropod feeding groups as well. We conducted a terrestrial arthropod survey at a series of lakes spanning a strong gradient of midge (Chironomidae, Diptera) emergence. These small, short-lived insects reach high densities in some areas such that their carcasses litter the ground, and serve as a potential resource for non-predatory arthropods. Our study revealed that arthropod assemblages in areas of high midge density were significantly different from those with few midges, the result of an increase of all taxa rather than changes in taxonomic composition. Eight of nine terrestrial arthropod taxa sampled showed a strong positive response to the presence of midges including detritivores and herbivores in addition to predators. Taxa that could consume living or dead midges directly responded especially strongly to midge gradients. Our results strongly suggest that midges enter the terrestrial arthropod food web through multiple pathways, increasing numbers of a wide range of arthropods. Furthermore, they emphasize the importance of lakes as sources of aquatic insects that significantly alter processes in the neighboring terrestrial environment.

1. Introduction

The importance of spatial linkages in regulating ecosystem and food web processes across ecosystem "boundaries" is an important theme of community and food web ecology (Polis et al. 1997). Mobile organisms that regularly traverse ecosystem boundaries have the capacity to deliver nutrients and energy, and affect consumers within a recipient ecosystem (Lundberg and Moberg 2003) including vertebrate (Sabo and Power 2002b) and invertebrate taxa (Henschel et al. 2001b, Yang 2006). Movement of individuals or resources into an ecosystem from the outside may stabilize food webs in recipient systems (Takimoto et al. 2002) or may alternatively destabilize them at very high levels of allochthony (Huxel and McCann 1998). In areas where cross-ecosystem movement of resources is pronounced, such as small islands (Polis and Hurd 1995) or the periphery of water bodies (Gratton and Vander Zanden 2009), these external resources could greatly boost the populations of species that can utilize the resource.

In freshwater systems, aquatic insects can act as a conduit of material from aquatic to terrestrial habitats (Richardson et al. 2009). For example, streams can be highly productive and support a large number of aquatic insects that eventually leave the water as adults (Jackson and Fisher 1986). The flux of these insects can increase the growth of individuals and populations on land (Sabo and Power 2002b), and stable isotopes have revealed consumption of stream insects by riparian predators (Sanzone et al. 2003). Through subsidies to vertebrate (Murakami and Nakano 2002) and invertebrate (Henschel et al. 2001a) predators emergent aquatic insects can also have indirect effects on terrestrial communities.

Although the interconnections between oceans and land (Polis et al. 1995) and streams and their adjacent riparian habitats (Ballinger and Lake 2006) have been the focus of ecotonal studies, the connection of lakes to the surrounding landscape has received less attention (Gratton and Vander Zanden 2009). Because lakes and ponds can also produce large numbers of aquatic insects (Einarsson 2004), it follows that similar effects on consumers may be occurring adjacent to lakes (Jonsson and Wardle 2009, Gratton and Vander Zanden 2009).

Previous studies that have examined aquatic-to-terrestrial linkages have focused upon terrestrial predators, often lizards and spiders, as direct recipients of the aquatic subsidy (reviewed in Ballinger and Lake 2006). While those studies have documented the effects of live aquatic insects, there are alternate pathways by which a resource subsidy can influence the terrestrial ecosystem. For example, aquatic insect subsidies can also increase the numbers of terrestrial detritivores that feed on their carcasses, similar to the effects of masses of terrestrial insects (Yang 2006), should they exist in great enough numbers. Similarly, large amounts of dead aquatic insects may affect groups such as herbivores that benefit indirectly (via plants) from the nutrients they transport (Spiller et al. 2010).

The variation in aquatic insect emergence from lakes in Northeast Iceland provides a landscape-scale gradient of aquatic to terrestrial inputs of insects that offers an opportunity to examine how terrestrial consumers are influenced by aquatic resources (Gratton et al. 2008). Specifically, Lake Mývatn ("lake of the midges" in Icelandic, Fig. 1) is well known for its production of massive emergences of midges (Diptera: Chironomidae) during the summer months (Einarsson 2004). This large (38 km^2), shallow (2-3 m), naturally eutrophic lake exports thousands of kg of midges to the surrounding landscape during peak emergence years (Lindegaard and Jonasson 1979). Emerging midges move over land to mate with perhaps half of the females moving back to the lake to deposit eggs. Analysis of $\delta^{13}C$ isotopes suggest that terrestrial arthropod consumers such as predatory spiders and detritivorous Collembola near

Mývatn consume midges, and the degree of reliance on aquatic insects by terrestrial consumers is related to the relative amount of midge input (Gratton et al. 2008) consistent with findings from stream-based systems (Sabo and Power 2002a, Paetzold et al. 2006). What remains unknown however is whether this allochthonous midge resource results in changes at the population or community level of terrestrial arthropod consumers. We conducted an extensive observational study which included a wide variety of arthropods representing a range of functional feeding strategies. We hypothesized that midges are resources available to distinct groups of of predatory, herbivorous, and detritivorous terrestrial arthropods and that their numbers would be positively related to midge inputs. We furthermore expected that distinct arthropod assemblages would result across the midge gradient at all lakes.

2. Materials and Methods

2.1 Study sites

To examine the influence of lake-derived aquatic insects on terrestrial arthropods, we chose four lakes within a 50 x 60 km area in Northeast Iceland (≈ 65.4º N, 17.0º W) based on preliminary data that suggested variation in midge abundance (Gratton et al. 2008 for details of sampling locations). Mývatn and Miklavatn are considered “midge” lakes, with annual midge deposition within 50 m of shore in excess of 1.5 g dw m^{-2} yr^{-1} (*unpublished data*) over the course of our study. In contrast the “non-midge” lakes Botnsvatn and Helluvaðstjörn produce low levels of midges, with deposition less than 0.5 g dw m^{-2} yr^{-1} (Gratton et al. 2008). The midge community in Mývatn is dominated by two species, *Tanytarsus gracilentus* and *Chironomus islandicus*, which represent 79% and 9% of total abundance respectively (Lindegaard and

Jónasson 1979). The species composition of midges at other lakes is unknown, but likely contains these species along with the nearly 60 other species identified in Mývatn (Lindegaard and Jónasson 1979). Plant communities around all lakes are typical of heathland vegetation of northern latitudes with a mix of grasses (*Poa* spp. and *Deschampsia* spp.), forbs including yellow bedstraw (*Gallium verum*) and yarrow (*Achillea millefolium*), ericaceous shrubs such as heather (*Calluna vulgaris*), bearberry (*Arctostaphylos uva-ursi*) and crowberry (*Empetrum nigrum*), and occasional dwarf tree/shrubs (dwarf birch, *Betula nana*, and dwarf willow *Salix lanata*).

2.2 Midge infall

At each lake we established permanent transects perpendicular to the lakeshore with sampling stations set at distances of 5, 50, and 150 meters from the lake margin. Where possible an additional station was placed at 500 meters from the lake, however due to logistical constraints Mývatn had 500 meter stations at only two transects, both on the west side of the lake, and Miklavatn had no 500 meter stations. At Mývatn, the largest lake sampled, a total of six transects were set up, while at the remaining three lakes we established two transects each. All transects were a minimum of 100m from one another. Each sampling station held a passive aerial insect infall trap consisting of a 1000 ml clear plastic cup (0.0095 m^2 opening) filled with about 250 ml of 50% ethylene glycol and a small amount of unscented detergent to capture and kill insects that landed in the container (Gratton et al. 2008). Infall traps were affixed to metal poles and elevated 1 m above ground level. The traps were emptied and reset approximately weekly at Mývatn and bi-weekly at other lakes beginning in late May and ending in early August in 2008 and 2009, bracketing the period of adult midge activity. For each sampling distance at a particular lake (e.g., Botnsvatn-5m), the total annual midge infall into collection cups was calculated by summing all midges collected in a trap at a station across all sampling times within each year. These values were averaged across the replicate stations at the same distance and expressed as g dw yr $^{-1}$ by multiplying the number collected by the average dry midge mass (0.11 mg individual^{-1}).

2.3Terrestrial Insect sampling

Vacuums were used to sample terrestrial arthropods. Samples were taken (within a single 3 d period) during the first week of June, July, and August in 2008 and 2009 at each sampling station. Vacuum samples were collected using a handheld leaf-vacuum/shredder (Stihl SH-56 C-E, Stihl Incorporated, Waiblingen, Germany) retrofitted to accept a thin vacuum bag over the suction opening. An open-bottomed plastic box (49.5 cm x 35.5 cm; 0.176 m^2) was quickly placed haphazardly on the ground within 3 m of the sampling station. The vacuum was firmly placed on the surface of the vegetation, and passed over the entire enclosed area twice to ensure full coverage. This procedure was completed twice per station, and the entire vacuum sample was aggregated within the vacuum bag during sampling. Each sample bag was brought to the lab and everted into a hanging cloth collapsible Berlese funnel (Bioquip, Gardena, CA) illuminated with a 40W incandescent bulb. Samples were extracted for 48 hours. All arthropods were collected into 70% EtOH and identified under a dissecting microscope to either order (Collembola; Acari) or family and counted (Triplehorn and Johnson 2005). Chironomidae (midges) were excluded from vacuum sample counts. Similar to the midge infall data the total number of arthropods collected in vacuum samples was calculated by summing all arthropods within a taxon collected at a station across all sampling times within a year. The counts were averaged across the replicate stations at the same distance at a given lake and expressed as number of arthropods collected m^{-2} yr^{-1}.

2.4 Statistical analyses

Variation in midge infall (log *x*+1 transformed) across the four lakes and at increasing distances from each lake margin was modeled using a linear mixed model with distance (log *x* transformed), lake, year, and the interaction of lake by distance and lake by year as fixed effects. Station was included as a random effect.

Relationships between the similarities in terrestrial arthropod assemblages were visualized using non-metric multidimensional scaling (NMDS) from a Bray-Curtis distance matrix calculated on log *x*+1 transformed arthropod abundance using the full suite of taxa collected (21), having eliminated rare or infrequently occurring taxa (occurring < 5% of samples). In addition, arthropod abundance data were presence-absence transformed to examine if the ordination patterns of the assemblages changed when differences in abundance are eliminated from the analysis. For these analyses the two annual samples were averaged to create an ordination of all 15 unique lake/distance combinations. The relationship between differences in arthropod assemblage and midge infall (measured using Euclidean distance matrix) was examined using a rank-based Mantel test (RELATE function in Primer; Clarke & Gorley 2001, Clarke & Warwick 2006) that correlated midge infall and community composition for each station.

The relationship between midge infall and arthropod abundance for specific taxa was examined using linear mixed models. For this analysis we focused on nine distinct arthropod taxonomic groupings (Appendix 1): predators: Lycosidae (wolf spiders), Linyphiidae (sheet-web spiders), Opiliones, (harvestmen), and Staphylinidae (rove beetles); detritivores: Acari (mites) and Collembola (springtails), as well as herbivores: Cicadellidae (leafhoppers) and Coccoidea (scale insects). The ninth group, Non-Major Taxa (Appendix 2), was comprised of the sum of the 13 remaining arthropod taxa that do not fall into the former categories. Of the 22 total taxonomic groups collected only two, Mycetophilidae at Botnsvatn and Gnaphosidae at Miklavatn, where not found at least once at all lakes. Taken together the first eight groups account for 94% of total arthropod numbers, with each comprising large portions of their respective functional groups (Appendix 1) and Acari alone representing 86% of the total numbers. For each of the nine taxonomic groups (log x+1 transformed) we used midge infall (log x+1 transformed) and year as fixed effects. Interactions of the fixed effects were not included due to non-significant interactions and comparable AIC values to simpler models with no interaction terms. Lake and station nested within lake were included as random effects to account for additional variation not explained by the fixed effects.

We evaluated the contribution of the fixed effects by calculating a pseudo R^2 value for models with and without fixed effects and then taking the difference as the contribution of the fixed effects (Edwards et al. 2008). Pseudo R^2 for each model was calculated by squaring Pearson's correlation coefficient for the association between observed and predicted values. Thus all R^2 values reported throughout are partial-pseudo in nature. All mixed models were performed in the “nlme” package of R (Version 2.10.1, © The R Development Core Team 2009).

3. Results

3.1 Midge infall

Midge infall varies as a function of lake ($F_{3, 19}$ = 24.03, P <0.001) and to a lesser extent distance from shore (Log(Distance) $F_{1, 2}$ = 7.72, P = 0.11, Lake X Log(Distance) $F_{3,12}$ = 8.21, P = 0.003; Table 1) resulting in a large gradient of midge input to land across the sampling stations used across this study. Average midge infall varied from >40 g dw yr $^{-1}$ at Mývatn to ~0.015 g dw yr $^{-1}$ at Helluvaðstjörn. At Mývatn infall averaged over 30 g dw yr $^{-1}$ at the 5 and 50 meter stations, tapering off to ~0.2 g dw yr $^{-1}$ at 500 meters. There was an interaction between lake and distance, thus the pattern of decreasing midge infall with increasing distance from lake edge changes from lake to lake (Table 1). Midge flux to land was significantly different between years ($F_{1,12}$ = 6.74, P = <0.02), but there was no significant interaction between lake and year ($F_{3,12}$ = 1.82, P = 0.20).

3.2 Arthropod assemblages

The two dimensional NMDS (stress = 0.09) shows clear separation of terrestrial arthropod communities associated in part with midge infall (Fig. 2B). The stations with high numbers of midges (i.e. Mývatn, Miklavatn; near-shore stations) are found on the right-hand side of the plot while those with low midge numbers are found on the left side (i.e. Botnsvatn, Helluvaðstjörn, and all 500 m stations; Fig. 2B). There was a significant correlation between differences in midge infall among stations and the differences in arthropod assemblages (Rank-based Mantel test, ρ = 0.337, P = 0.001). The pattern of stations organizing along a midge gradient disappeared when the presence-absence distance matrix is used in the NMDS ordination (not shown), and there is also no correlation with a midge infall (Rank-based Mantel test, ρ = -0.161, P = 0.942).

3.3 Arthropod abundance

Eight of the nine taxonomic groups examined, including members of all three functional groups, showed a significant positive relationship with midge density ($P \leq 0.05$). In general, an increase in midge density by one order of magnitude was accompanied by an increase in terrestrial arthropods of approximately the same amount (Fig. 3). Notably Opiliones, Collembola, and Staphylinidae, showed the most positive response to midge infall into the terrestrial environment (Fig. 3D, 3F, 3I; Table 2), with these taxa increasing twice as rapidly as most other taxa and infall accounting for much of the variation in these groups. Cicadellidae (leafhoppers) alone showed no linear relationship with midge infall (Fig. 3H; Table 2). Arthropod density varied between years for all taxa except Acari (mites) (Table 2). However, arthropods always responded positively to the presence of midges regardless of the year in which they were sampled, as indicated by the lack of interactions between midge infall and year.

4. Discussion

The abundance of a wide range of terrestrial arthropods including predators, herbivores, and detritivores in northern Iceland is related to the relative abundance of lake-derived midges present near the lake-land interface. The midge input gradient exhibited across lakes and distances from shore in northern Icelandic lakes (Fig. 2A) corresponds with changes in the assemblages of shoreline arthropods (Fig. 2B) although other factors, such as differences in plant communities, also likely contribute some additional variation in the assemblages (Fig. 2B, NMDS Axis 2). Most of the midge effect on terrestrial assemblages is observed as changes in the relative abundance of taxa rather than changes in the taxonomic composition of the assemblages (Fig. 3). The lack of differences in taxonomic composition may be the result of the limited suite of species present at these northern latitudes, which results in a large overlap in the presence of many taxa at sites across our study area.

Increases in arthropod abundance are seen across a wide range of taxa, reflecting the various pathways that midges enter the terrestrial food web (Fig. 4). The movement of lake-derived resources to land can be broken down into a series of steps, each of which can influence different components of the terrestrial ecosystem. Immediately upon emergence, midges congregate on land to form mating swarms (e.g., Fig. 1). As they alight on the ground, they are consumed by predators such as hunting and web-building spiders as well as harvestmen, all of whose numbers were observed to increase in this study suggesting that consumption of midges leads to increasing abundances of predators in the presence of midges. Gratton et al. (2008) found that the carbon stable isotope ratios of spiders and harvestmen were the most enriched taxonomic groups in near-shore environments in the presence of midges, supporting the idea that these predators are directly consuming ^{13}C-rich living midges. Live midges, however, are only available as prey for a relatively short period of time (~two weeks) and this may account for the relatively shallow sloped response to midge availability observed in wolf spiders. In contrast, the relatively lower-order predators Opiliones and Staphylinidae show the strongest positive responses to midge numbers, perhaps a result of their more omnivorous feeding habits which can take advantage of both living, and dead in the case of Opiliones, midges and those organisms that feed upon dead midges.

Although a fraction of midges return to the lake to oviposit, many die in the terrestrial habitat to eventually become fodder for detritivores, which is reflected in increased abundance of Collembola and mites, in both of which Gratton et al. (2008) observed an aquatic ^{13}C signature. Yang (2006) found that the pulsed addition of insect carcasses (cicadas) to the forest floor resulted in a similar increase in abundance of necrophilous and detritivorous taxa. Here the addition of detrital resources via midge carcasses far outweighs the effects of increased predation by midge-subsidized generalist predators. As midge decomposition progresses their elemental nutrients (such as N and P) are recycled through the soil ecosystem with potential benefits to plant growth and plant quality, with the potential to create a long-term source of detritus. Estimates of midge deposition within 50 meters of the lake edge around Mývatn exceed 40 kg dw ha^{-1} yr^{-1} during high midge years (e.g. 2008, Chapter 1) and as midges are ~10% N and ~1% P nutrient availability to the terrestrial ecosystem is greatly increased in their presence. Thus we expected the strong bottom-up subsidy from dead midges to plants to positively influence not only detritivores but also the insects that feed on them.

Herbivorous insects in heathland and grasslands in northern Iceland are dominated by leafhoppers (Cicadellidae) and stem/root-feeding orthozeiid scales (Coccoidea) that differ in their response to the presence of midges. Whether herbivores can increase in abundance in response to midge inputs may thus depend on the balance of the indirect midge effects on both plant quality and shared generalist predators such as wolf spiders. Unlike every other major group of arthropods in this system the Cicadellidae show the greatest variation in response as a function of midge infall, indicating that they are somehow decoupled from the “midge effect”.

While leafhoppers benefit indirectly from increased plant vigor as a result of midge nutrients, they may suffer high rates of predation from midge-feeding generalist predators such as wolf spiders, especially at times of low midge abundance. In contrast Coccoid scales feeding on the roots of the same plants may avoid predation from surface predators by finding a spatial refuge from the midge-feeding generalist predators.

This study supports the hypothesis that aquatic resource subsidies to land can affect the entire terrestrial food web, rather than a limited number of predatory consumers. Other studies focusing on riparian arthropods have shown increases in spiders and beetles near shore where aquatic insect activity is highest (Paetzold et al. 2005, Marczak and Richardson 2007, Jonsson and Wardle 2009). Our documentation of changes across an entire assemblage of arthropods (including detritivores and herbivores) along lakeshores in this region suggests that increases in arthropod density along lakeshores are the result of multiple subsidy pathways. These include feeding directly on live and dead midges, as well as on plants that benefit from midge-derived nutrients. Such multi-channel effects may be a common feature of terrestrial areas adjacent to productive waters that produce especially great numbers of insects and are subject to large aquatic resource inputs (Gratton and Vander Zanden 2009) resulting in changes similar to those observed in systems receiving marine subsidies (Spiller et al. 2010).

Our study highlights the importance of lakes as donor systems via emergent aquatic insects, such as midges. Lakes and other lentic bodies of water are typically thought of as recipients of gravity- and Aeolian-driven terrestrial C, and the dynamics of ecosystem processes are significantly influenced by these allochthonous inputs (Pace et al. 2004). This study shows that processes originating within lakes (e.g., insect production) can have widespread effects on consumers in the surrounding landscape (Gratton and Vander Zanden 2009, Jonsson and Wardle 2009). Though Mývatn offers an extreme example of insect emergence, the range of midge variation observed across our study areas demonstrates that such subsidies are not unusual. At our study lakes with low to moderate aquatic insect productivity (i.e., excluding Lake Mývatn) the pattern of increases in terrestrial arthropods with increasing midge infall is still apparent statistically, with Opiliones, Collembola, and Non-Major Taxa maintaining a significant relationship with midge infall. The quantity of midge input at these lakes is <1 g dw y^{-1}, a seemingly small amount, but one that nevertheless translates to a measurable difference in arthropod abundance. Based on these observed relationships, we hypothesize that lake-derived aquatic insects have significant effects on terrestrial arthropod assemblages elsewhere, and across systems with a wide range of aquatic productivity.

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Table 1. Linear mixed model of midge infall (log *x*+1) as function of Lake (Mývatn, Miklavatn, Botnsvatn, and Helluvaðstjörn), Distance (log *x*) from shore (5, 50, 150, 500 m), Year (2008, 2009) and the interactions of Lake by Distance (log *x*) and Lake by Year (all fixed effects). Station is included as a random effect.

Factor	**nDF**	**dDF**	**F**	***P***
Log(Distance)	1	2	7.94	0.11
Lake	3	12	50.44	**<0.0001**
Year	1	12	6.74	**0.02**
Lake X Log(Distance)	3	12	8.21	**0.003**
Lake X Year	3	12	1.82	0.20
R^2	0.92			

Table 2. Results of repeated measures linear mixed models for ten terrestrial arthropod taxa as a function of midge infall at four Icelandic lakes. R^2 is partial-pseudo coefficient of determination representing the amount of variation explained by fixed effects alone.

			Infall[a]		**Year**[a]	
Taxa	**Group**	**P-P R^2**	**F**	***P***	**F**	***P***
Lycosidae	Predator	0.33	4.83	**0.047**	6.43	**0.025**
Linyphiidae	Predator	0.66	20.11	**<0.001**	28.22	**<0.001**
Opiliones	Predator	0.54	26.75	**<0.001**	6.51	**0.024**
Staphylinidae	Predator	0.68	17.87	**0.001**	13.55	**0.003**
Acari	Detritivore	0.70	23.69	**<0.001**	4.13	**0.063**
Collembola	Detritivore	0.44	13.18	**0.003**	12.77	**0.003**
Cicadellidae	Herbivore	0.48	3.62	0.080	22.42	<0.001
Coccoidea	Herbivore	0.65	6.58	**0.024**	42.91	**<0.001**
Non-Major	Mixture	0.69	7.26	**0.018**	18.82	**<0.001**

Notes:

[a] 1, 13 numerator, denominator degrees of freedom, respectively.

Fig. 1. Swarms of mating midges create a fog along the southern edge of Lake Mývatn, Iceland on 28 May 2010. Photo: Claudio Gratton.

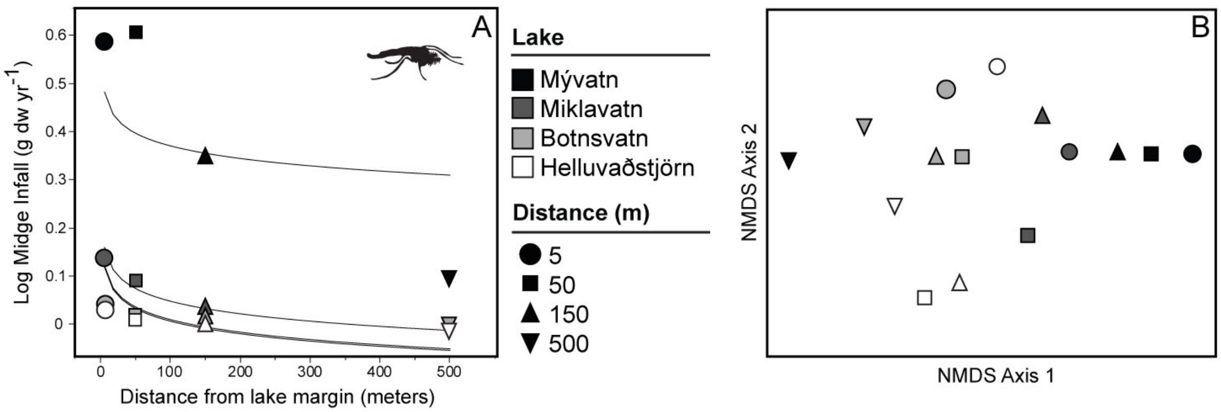

Fig. 2. Relationship of midge infall (log x+1 g dw m^{-2} yr^{-}1) and distance from lake margin (log meters) at four Icelandic lakes (A). Infall is significantly different among lakes. Nonmetric multidimensional scaling ordination of terrestrial arthropod assemblages at four Icelandic lakes, 2-D stress = 0.09 (B). Sites with few midges are on the left (e.g., away from shoreline; Helluvaðstjörn), while sites with high midges are on the right (e.g., near shore, Mývatn). Note the placement of the 500 m station at Mývatn in the left with other low midge sites. The arthropod assemblages are significantly correlated with midge infall (Rank-based Mantel test, ρ = 0.337, P = 0.001).

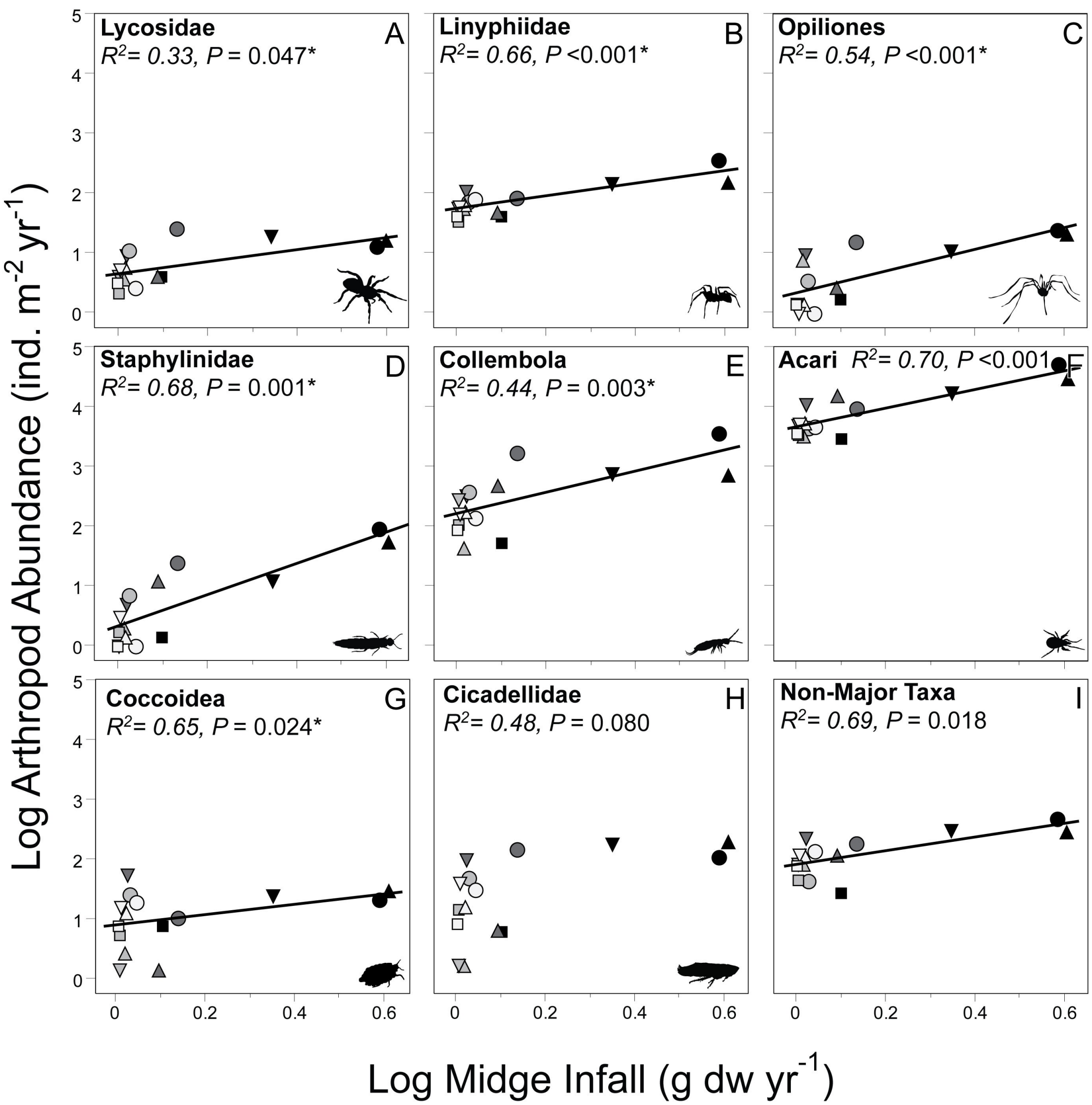

Fig. 3. Relationship of terrestrial arthropod (average no. m^{-2} y^{-1}) taxa collected around four northern Icelandic lakes and midge "infall" (g dw y^{-1}) on land. R^2 is partial-pseudo coefficient of determination representing the amount of variation explained by fixed effects alone. Points and regression line in figure use average values for both sampling seasons while statistical analyses are based on all individual sampling values. See Fig. 2 for symbol/color key.

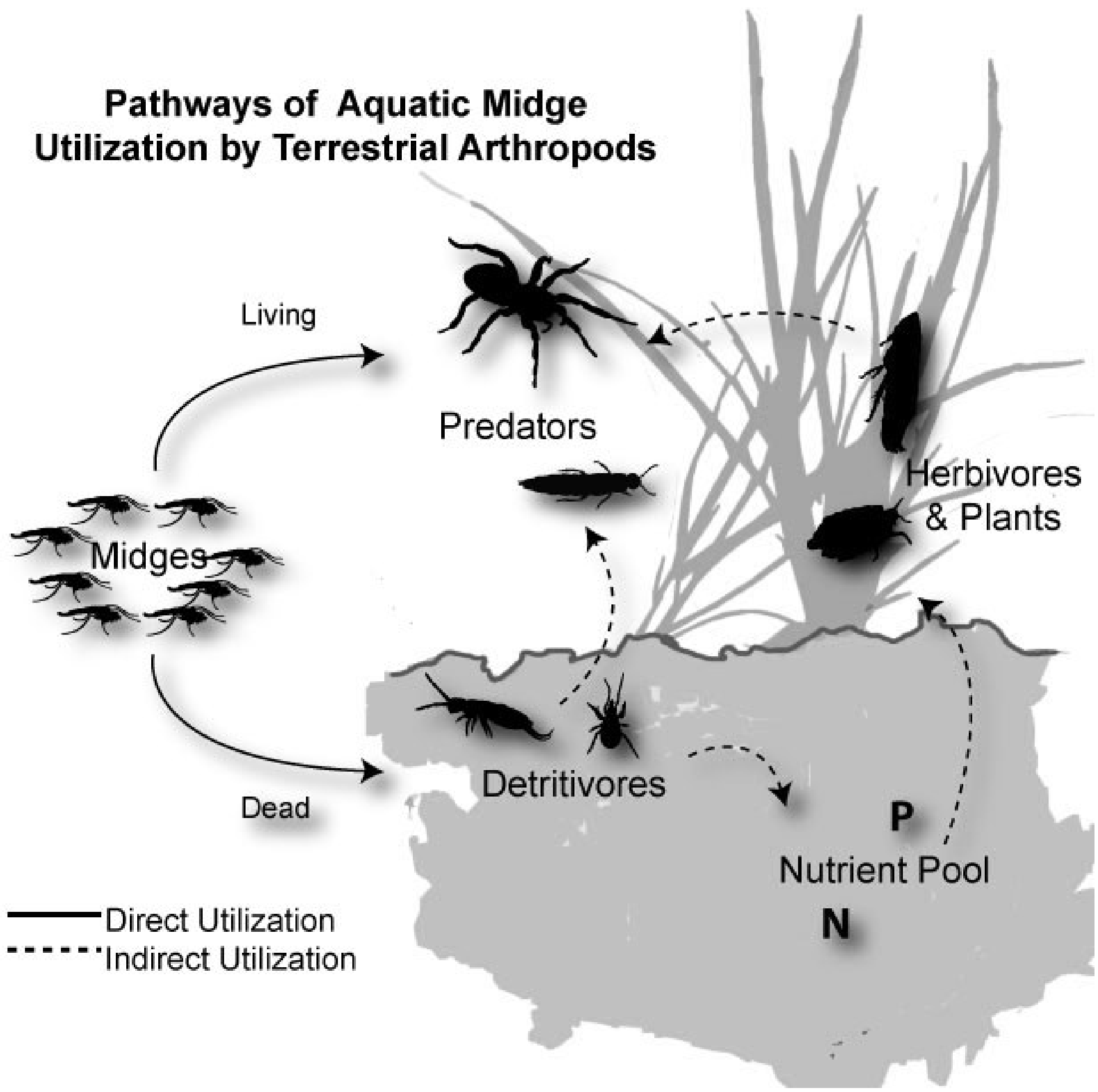

Fig. 4. Hypothesized pathways of aquatic midge utilization by terrestrial arthropods. Direct utilization is shown with solid lines, indirect utilization with dashed lines. Predators consume live midges, while microbes and detritivores feed on dead midges (direct utilization). Predators are indirectly linked to midges through the consumption of detritivores and herbivores, while plants and herbivores benefit from the midge-enriched soil nutrient pool.

Group	Taxa	Common Name	% Total	% Group
Predator	Lycosidae	wolf spiders	0.06	5.8
Predator	Linyphiidae	sheet-web spiders	0.7	75.1
Predator	Opiliones	harvestmen	0.05	5.5
Predator	Staphylinidae	rove beetle	0.1	10.8
Detritivore	Acari	mites	86.8	94.1
Detritivore	Collembola	collembola	5.9	5.4
Herbivore	Cicadellidae	leafhoppers	1.1	41.2
Herbivore	Coccoidea	scales	1.2	46.8
Non-Major*	Mixture	NA	1.4	NA

Notes: *see Appendix 2 for details

Appendix I. Contribution of the top eight taxa to the overall arthropod abundance (% Total) as well as their respective functional groups (% Group). The total number of arthropods collected during this study was 392,329 individuals.

Taxa	Order	Common Name	% Total	% Non-Mite
Gnaphosidae	Aranea	wandering spider	0.01	0.1
Thomisidae	Aranea	crab spider	0.01	0.1
Thysanoptera	Thysanoptera	thrips	0.05	0.4
Sciaridae	Diptera	fungus gnat	0.08	0.6
Mycetophilidae	Diptera	fungus gnat	0.01	0.08
Miridae	Hemiptera	grass bug	0.3	2.5
Tingidae	Hemiptera	lace bug	0.09	0.7
Saldidae	Hemiptera	shore bug	0.5	4.9
Delphacidae	Hemiptera	plant hopper	0.2	2.0
Aphididae	Hemiptera	aphid	0.1	1.1
Hymenoptera	Hymenoptera	wasp	0.01	0.1
Apocrita	Hymenoptera	thin-waisted wasp	0.02	0.2
Ichneumonoidea	Hymenoptera	parasitoid wasp	0.01	0.1

Appendix II. Contribution of the thirteen taxa that comprise the Non-Major Taxa to the overall arthropod abundance (% Total) as well as non-acari arthropods (% Non-Mite).

CHAPTER 3

Positive indirect effect of aquatic insects on terrestrial prey even at elevated predator density

Abstract: Multiple prey species eaten by a shared predator are potentially connected indirectly in food webs. Insects that move from water to land may cause a short term predation release of terrestrial insects by changing the feeding of shared predators. However, over longer time scales aquatic insects could increase predation of terrestrial prey by stimulating an increase in terrestrial predator density. In turn, higher numbers of predators may lead to an increase in predation rates and a reduction in population of one or more prey species. We conducted experiments to examine how individual and population responses by spiders together determine the indirect effect of aquatic midges on terrestrial arthropods. Midges in lab mesocosms caused individual wolf spiders to reduce predation of natural and sentinel prey by ≥50%, suggesting a short term predator release. Surprisingly, field experiments in which we increased spider density to simulate the long term impacts of midges showed that the presence of live midges counteracted the expected influence of increased predator density. At low spider density midges reduced predation of sentinel prey by 10%, but at high spider density predation was reduced by 45%. As expected when midges were absent predation rates were greater at high spider density. A further mesocosm experiment demonstrated that additions of midges from 5-100+ individuals equivalently reduced individual spider predation on sentinel prey, perhaps due to predator distraction rather than satiation. As a whole our results suggest that midges benefit terrestrial arthropods because the predation release by spiders in the presence of midges can counterbalance

the effect of midge-driven increases in spider density.

1. Introduction

When two or more prey species are eaten by a shared predator an indirect food web connection between their populations is possible. Predation on one prey species can increase, decrease, or remain the same depending on the response of the shared predator to the other species. For example, if predator density increases in response to increased numbers of one prey species, predation rates on a second prey species may also increase, reducing the population of both prey species in a negative indirect effect called apparent competition (Holt 1977). Conversely an "apparent mutualism" can result if a shared predator reduces consumption on species one by switching to eat the growing population of species two, which results in both prey species becoming more numerous simultaneously. In some cases multiple prey species may have no impact on another species despite sharing a common predator (Chaneton and Bonsall 2000, non-reciprocal effect), or one species may benefit while the other suffers (Tschanz et al. 2007, asymmetric effect). Furthermore the type of indirect effect a species experiences often changes over time. For example, if a predator switches to eat species one predation on species two is relaxed in the short-term, but over time the consumption of species one stimulates an increase in predator density causing a net increase in predation of species two. Alternatively, a strong predator preference for species one could lessen or eliminate a long-term predation increase on species two even at elevated predator density. Despite ample theoretical support for long-term positive indirect effects stemming from predator preference, relatively few empirical examples have been documented in nature (Abrams 2010).

Both short and long term positive indirect effects on any prey species are a function of the encounter rates between individual predator and alternative prey. Time and energy devoted by a predator to capture and consume one prey reduces mortality of other potential prey (Abrams and Matsuda 1996, Abrams 2010). If predators have no prey species preference, predators will consume all prey species in proportion to their relative abundance. In this case an increase in species one would decrease predation rates on species two if predators are satiated by an overabundance of total prey (Koss and Snyder 2005). Alternatively, generalist predators may prefer alternative prey that are more nutritious or are easier to detect, capture, or handle (van Baalen et al. 2001, Sundararaj et al. 2012). Finke and Denno (2003) found that visually hunting wolf spiders were more likely to capture easily detected mobile prey compared to more cryptic and sedentary prey. If the shared predator prefers to eat species one for reasons independent of prey density, prey species two can still experience positive indirect effects even as predator density grows over the long term (Abrams 2010).

Indirect effects often result from the immigration of a mobile prey species originating from an external source. Mobile prey may arrive from distant (e.g., anadromous fish) or nearby (e.g., habitat spillover) ecosystems. Prey species commonly move from one neighboring ecosystem into another at the water-land ecotone (Nakano and Murakami 2001). The intersection of freshwater and riparian areas commonly has high densities of flying adult aquatic insects. Many of these water-derived insects are consumed by predators that also eat prey on land (Paetzold et al. 2005) such as lizards, birds, and spiders. Terrestrial species may then be indirectly impacted by changing behavior and/or density of shared predators in response to abundant aquatic insects (Abrams 2010). In riparian areas elevated prey abundance may stimulate an increase in generalist predator numbers through aggregation or increased reproduction. Accordingly, unless the predators have a preference for aquatic insects, predation on terrestrial prey is also likely to increase.

Predation of terrestrial prey has been shown to increase when abundant insects originating from aquatic habitats increase generalist terrestrial predator density (Baxter et al. 2005). Patterns of stable isotopes of riparian invertebrate predators such as web-building and hunting spiders indicate that aquatic insects are major (>50%) components of their diet (Sanzone et al. 2003, Paetzold et al. 2005). Observational studies have found that spiders occur at higher densities along streams and lakes where aquatic insect prey are common (Sanzone et al. 2003, Jonsson and Wardle 2009). Experimental reductions of aquatic insects from river banks resulted in reduced abundance and growth of lizard predators suggesting predator movement and development are directly affected by aquatic insect availability (Sabo and Power 2002). Predators reliant on aquatic prey can in turn influence rates of predation near water. Riparian areas thick with spiders show increased rates of predation on resident terrestrial herbivores (Henschel et al. 2001), while stream insect feeding birds depressed leaf-rolling insects along a Japanese stream (Murakami and Nakano 2002). Short term positive indirect effects of aquatic insects on terrestrial prey species may also result, but these could be influenced by changes in predator density and per capita feeding in response to the presence or absence of aquatic prey (Sabo and Power 2002a, b). Therefore, in order to understand the net effect of alternative prey on food webs, their combined effects on predator foraging behavior and density must be jointly considered.

To determine if aquatic insect alternative prey can indirectly affect predation of terrestrial arthropods by shared spider predators we measured predator reproduction and density in response to aquatic insect inputs and performed a set of complementary laboratory and field experiments. First, predators were sampled at three lakes in northeast Iceland that varied in midge abundance. The shoreline of the largest and most productive site, Lake Mývatn, receives significant inputs of aquatic midges that are consumed by predators (Gratton et al. 2008) resulting in increased predator density (Dreyer et al. 2012). Second, we performed laboratory mesocosm experiments in which wolf spider predation of terrestrial prey was examined across a range of live midge densities, examining their ability to cause indirect effects on terrestrial prey. Third, we performed a field experiment where spider density, designed to mimic predator abundance in areas of low and high midge inputs, and midge presence/absence were manipulated and measured their net effect on the predation rate of terrestrial prey. By simultaneously varying both predator density and alternative prey availability, this experiment enabled us to determine if the negative effect of predator density could be offset by the positive effect of alternative prey.

2. Methods

2.1 Study System

To examine the influence of lake-derived aquatic insects on terrestrial arthropods, we chose three lakes within a 50 X 60 km area in Northeast Iceland (≈ 65.4º N, 17.0º W) based on preliminary data that suggested variation in midge abundance (Gratton et al. 2008 for details of sampling locations). Midge abundance at Lake Mývatn within 50 m of shore was in excess of 25 g dw yr^{-1} over the course of our study. In contrast the “low-midge” lakes Botnsvatn and Helluvaðstjörn produced low levels of midges, with deposition less than 0.5 g dw m^{-2} yr^{-1}

(Gratton et al. 2008). After metamorphosing from the pupal state and emergine on the lake surface, the adult midges (0.1 – 1.0 mg dw) form mating swarms along lake edges, where they are eaten by terrestrial consumers including wolf spiders in the genus *Pardosa* that are common at all three lakes (Gratton et al. 2008, Dreyer et al. 2012).

2.2 Aquatic insect abundance

At each lake we established permanent transects perpendicular to the lakeshore with sampling stations set at distances of 5, 50, 150, and 500 meters from the lake margin (see also Chapters 1 & 2). At Mývatn, the largest lake sampled, a total of six transects were set up, while at the remaining three lakes we established two transects each. All transects were a minimum of 100m from one another. Due to logistical constraints Mývatn had 500 meter stations at only two transects, both on the west side of the lake. Each sampling station held a passive aerial insect infall trap consisting of a 1000 ml clear plastic cup (0.0095 m^2 opening) filled with about 250 ml of 50% ethylene glycol and a small amount of unscented detergent to capture and kill insects that landed in the container (Gratton et al. 2008). Aerial abundance traps were affixed to metal poles and elevated 1 m above ground level. The traps were emptied and reset approximately weekly at Mývatn and bi-weekly at other lakes beginning in late May and ending in early August in 2008-2010, bracketing the period of adult midge activity. The total number of "large" (~0.01 g dw individual^{-1}) and "small" (~0.0001 g dw individual^{-1}) midges was counted, and midge biomass was calculated by multiplying the number collected by their average mass.

2.3 Egg sac and wolf spider collection

Pitfall traps at each sampling station were used to capture female wolf spiders with egg sacs. Small (500 mL) plastic cups were sunk into the ground so that their tops were flush with the surface. A weighted plastic cover was suspended ~2 cm over the opening to prevent the entry of rain ,debris, and small mammals. Cups were filled with approximately 100 ml of 50% ethylene glycol and a small amount of unscented detergent to capture and kill walking arthropods that fell in. Pitfall traps were deployed continuously and collected every two weeks at each sampling station. Wolf spider egg sacs were identified under a dissecting scope, counted, and separated into vials.

Wolf spider reproduction was assessed by measuring the mass of unhatched egg cases collected in pitfall traps and counting the number of eggs inside. Egg sacs were opened and the number of eggs inside was counted under a dissecting scope. Afterward eggs were placed into microcentrifuge tubes and dried for ≥72 hours at 50°C. Dried egg sacs were measured (mass of eggs + egg sac casing) to the nearest 0.1 mg (Mettler-Toledo AX105, Mettler-Toledo LLC, Columbus, OH 43240). We found a strong positive correlation between clutch size and the combined mass of eggs/egg sac (Appendix I).

Vacuums were used to sample wolf spider density. Samples were taken (within 3 d) during the first week of June, July, and August 2008-2009, and June and July 2010, at each sampling station. Vacuum samples were collected using a handheld leaf-vacuum/shredder (Stihl SH-56 C-E, Stihl Incorporated, Waiblingen, Germany) retrofitted to accept a thin vacuum bag over the suction opening. An open-bottomed plastic box (49.5 cm x 35.5 cm; 0.176 m^2) was quickly placed haphazardly on the ground within 3 m of the sampling station. The vacuum was placed firmly on the ground and vegetation, and passed over the entire enclosed area twice. This procedure was completed twice per station, and the entire vacuum sample was aggregated within the vacuum bag during sampling. Sample bags were everted into a hanging cloth collapsible Berlese funnel (Bioquip, Gardena, CA) illuminated with a 40W incandescent bulb and were extracted for 48 hours into 70% EtOH. Wolf spiders (*Pardosa sphagnicola* (Dahl) and *P. palustris* (Linn.), Araneae: Lycosidae) were identified and counted under a dissecting microscope. Counts were converted to arthropods m^{-2} for each sample date at a station, after which the three sample dates within a year were averaged together.

2.4 Mesocosm Experiments

To test the hypothesis that the presence of alternative midge prey has a positive indirect effect on local prey, we performed mesocosm experiments where we manipulated midge density and measured rates of predation by a single wolf spider on either natural or sentinel prey. Mesocosms were constructed from thin transparent plastic tubes (15 cm diameter, 50 cm height) with mesh windows on the sides and top, placed in substrate in a 15 cm diameter plastic pot. Mesocosms were kept at approximately 22ºC on laboratory benches, and treatment assignment was randomized.

In the summer of 2009 mesocosms were used to test predation rates of wolf spiders on leafhopper (*Javacella*, Hemiptera: Cicadellidae) natural prey in the presence and absence of midge alternative prey. Small discs of sod were cut from a nearby grassy field and placed into the pots, thinned to 5 culms of grass, and covered by the plastic sleeve. Twenty leafhoppers were introduced into each mesocosm and allowed to settle on plants, after which three treatments were established: (1) no wolf spiders and no midges (“control”, n = 15), (2) one wolf spider only (n =

15), and (3) one wolf spider + midges (n = 15). The experiment ran from 29 July – 3 August, with ~100 live midges being added every 24 hrs to the treatment where midges were added. All spiders were hand collected locally, isolated in individual containers, and starved for 24 hrs prior to their introduction to the mesocosm. Midges were collected live from the field every two days using sweep nets and were stored at 10ºC until added to mesocosms. At the end of the 5-day experiment we counted the number of leafhoppers remaining. There was no wolf spider mortality during the experiment, and some live midges were still present in the mesocosms at the end of the experiment.

During the summer of 2011 mesocosms were used to determine rates of wolf spider predation on “sentinel prey” across a range of alternative midge prey. By varying alternative prey density we could examine whether the effects on predation rates were in proportion to the relative abundance of the alternative prey. If predators had no preference for midges, we expected predation on sentinel “resident” prey to decrease as alternative prey density increases (i.e., a “dilution” effect).

Due to practical limitations of capturing and handling mobile prey such as leafhoppers, we developed a sentinel prey assay using larvae of *Drosophila melanogaster.* Fly larvae were raised on sugar-based media following standard lab rearing protocols. Adults laid eggs onto a rearing-media inside egg laying chambers. Third and fourth instar larvae were placed into a small (3.5 cm diameter) petri dish with a 1-cm diameter spot of medium topped with a drop of yeast-water mixture. This combination encouraged retention of larvae on the surface of the media and minimized the degree to which larvae burrowed, thus evading predators. Larvae could burrow into the medium, but these events were rare (<3%) and uniform across treatments.

We established six treatments: (1) no wolf spider + no midge ("control", $n = 13$), (2-6) one wolf spider + with either 0 ($n = 29$), 5 ($n = 15$), 20 ($n = 15$), 50 ($n = 15$), or 100 live midges ($n = 22$) added. A single dish containing 10 *D. melanogaster* larvae was placed in each mesocosm over fine sand substrate and below four ~10 cm thin bamboo rods placed vertically to provide a perch for live midges and spiders. All spiders were field collected locally, isolated individually, and starved for 24 hrs prior to their introduction to mesocosms. The experiment was run overnight for ~12 hrs, with live midges being added at the beginning of the experiment only. The number of *D. melanogaster* larvae remaining in the dish at the end of the experiment was counted; those that had disappeared were assumed to have been eaten by the spiders. The number of midges in each Petri dish was counted as an index of midge density in a mesocosm.

2.5 Field Experiment

Because aquatic prey (including midges) are known to increase predator abundance in riparian areas, net predation rates in the field may increase despite a reduction in per-capita rates of predation due to the presence of alternative aquatic prey. Therefore we conducted a field experiment where we manipulated predator abundance (low and high spider density) and presence/absence of midges. This experiment was intended to simulate the long term numerical response of spider predators to the presence of midge alternative prey in near shore areas.

During summer 2011, arthropod manipulation plots were constructed at a field site ~3m above lake level on the Kálfaströnd peninsula of Lake Mývatn which consistently has abundant naturally occurring midges (Einarsson et al. 2002, Hoekman, Dreyer, and Gratton. *unpublished data*). We constructed 20 square enclosure arrays, each array comprising four contiguous square plots 1.2 m on a side (1.44 m^2), three of which had plastic walls on four sides preventing arthropod em/immigration. The fourth plot in the array was an open plot with only two walls, allowing ground arthropods to move freely in and out. Walls of the enclosures were constructed of 0.5 cm thick white corrugated plastic pieces 1.2 m long by 0.4 m tall (Laird Plastics, Madison, WI). The plastic was inserted into the sod to a depth of ~10 cm, corners of the plots were joined with duct tape, and all edges sealed to prevent movement of arthropods in and out of the experimental plots. Enclosure arrays were constructed in pairs (10 total), with two complete arrays within 5m of one another forming a pair (Appendix II).

One full array in each pair was randomly selected to have fine mesh netting (30 holes cm^{-2}, Barre Army Navy Store, Barre VT, USA) secured over the top as a midge excluder. Midges were observed to be more numerous in open than excluded plots throughout the summer, and during 27-28 July we measured midge density using two clear 10cm wide sticky traps (Alpha Scents, West Linn, OR) fastened to opposing walls of each plot at ground level (Appendix IIIA).

Predator density manipulations were applied to the three enclosed plots in an array in late May 2011. The three arthropod treatments were 1) “full predator removal”: all arthropod predators including wolf (Lycosidae), wandering (Gnaphosidae), and sheet web (Linyphiidae) spiders, harvestmen (Opiliones), and rove beetles (Staphylinidae) were removed, 2) “partial predator removal”: wolf spiders only removed, 3) “wolf spider addition” treatment: wolf spiders added throughout the summer to maintain densities at or above ambient densities (ambient ~5 individuals m^{-2}). Treatments were established by vacuuming the entirety of each plot (including open plots) using a modified Stihl SH-65 Vacuum-Shredder (Stihl Incorporated, Wablingen, Germany) equipped with a fine mesh bag inside the sucking end. All non-predatory arthropods were returned to all plots, while predatory arthropods were returned to plots depending on the treatment combination (see above). Subsequent sampling of “full” and “partial” predator removals showed the presence of non-wolf spider predators, but there were no significant differences in their densities(data not shown) and are hereafter combined into a single “wolf spider reduction” treatment.

We evaluated wolf spider densities throughout the experiment by conducting one-minute visual counts of all enclosed manipulated plots. On 6 and 18 July we actively hand-searched through the vegetation for wolf spiders. If wolf spiders were found in a “wolf spider reduction” plot, they were killed or removed. The relative abundance of wolf spiders and other cursorial arthropods was quantified at the end of the experiment (28 July) using clear sticky traps placed at ground level for 48 hours (Appendix IIIB, IIIC).

For this field experiment in summer 2011 *D. melanogaster* larvae were used as a sentinel prey to assay predation intensity. *Drosophila* larvae are expected to mimic common ground-dwelling prey such as Collembola (springtails), or Coccoidae (scales) at the field sites. To monitor changes in predation intensity as affected by midges and wolf spiders, we placed dishes containing 10 *D. melanogaster* (see methods: *Mesocosm experiments*) into each plot on 1, 6, 11, 19, and 26 July. On all days during which the assay was performed, the weather was sunny and warm (≥10°C). Dishes were deployed late in the morning (1000-1200 h) and retrieved in the late evening (2000-2300 h) after which the number of larvae remaining in Petri dishes was counted; due to the latitude, plots were sunlit for the duration of deployment. To assess the rate of larval disappearance not due to predation (i.e., larvae wandering off of dishes), an additional set of dishes covered with a fine nylon mesh to prevent predator entry were also placed into the field in the vicinity of the manipulated enclosures. Over the course of this experiment, average non-predator disappearance of larvae was 13 ± 3% (mean ± SEM, n=46).

2.6 Data Analysis

Observational data on egg sac mass and wolf spider density as a function of midge input were analyzed using linear mixed effects model. For regression with egg sac mass we summed the cumulative midge biomass collected at each site from the first sampling period of the year until the date of egg sac collection. In the wolf spider density analysis we averaged midge biomass and spider density during each year at each station. Cumulative and averaged midge biomass, egg sac mass (mg), and wolf spider density + 1 were natural log transformed to meet assumptions of normality of residuals. Egg sac mass and wolf spider density were modeled as a continuous function of midge biomass with an interaction of lake as a fixed effect, year as a non-interacting fixed effect, and transect as a random effect.

The disappearance of leafhoppers and fly larvae in lab mesocosm experiments were modeled as a binomial process of "successes" (leafhoppers or fly larvae remaining) and "failures" (leafhoppers or fly larvae disappeared). Both experiments were analyzed using generalized linear models with a quasibinomial error distribution due to overdispersion. In both experiments prey remaining was the response and individual treatments are the linear predictors.

The effectiveness of midge and spider manipulations in the field experiment were examined by evaluating their densities from sticky cards (both) and visual counts (spiders only) ($\log(x+1)$ transformed) in the midge (presence/absence) and predator (high/low) treatments, respectively, using linear mixed effect models with treatments as crossed fixed effects and array pair as a random effect (Appendix 2).

The disappearance of fruit fly larvae was modeled as a mixed-effects repeated measures model. We used larvae remaining (square root transformed) as the response variable, predator treatment (addition/reduction/open), midge treatment (presence/absence) and their interaction as fixed effects, and a random effect of pair and individual plot with an AR(1) correlation structure to account for repeated measures taken from a unique plot over time.

Analyses were performed with R 2.13.2 (R Development Core Team 2011) using the "nlme" package for analysis of egg sac mass and wolf spider density (function "lme"), 2009 and 2011 mesocosm experiments (function "glm"), and 2011 predator enclosure experiment (function "lme").

3. Results

3.1 Wolf spider reproduction and density

Midge abundance was positively related to wolf spider egg sac mass at the lakes Botsvatn ($F_{9,350} = 2.40$, $P = 0.017$) and Helluvaðstjörn ($F_{9,350} = 5.77$, $P << 0.0001$) with low to moderate amounts of midges, but there was no similar increase in egg sac mass at Lake Mývatn ($F_{9,350} = -0.69$, $P = 0.49$) with the greatest midge numbers (Fig. 1). In contrast, wolf spider density at lakes Botsvatn ($F_{11,87} = 0.57$, $P = 0.59$) and Helluvaðstjörn ($F_{11,87} = 1.55$, $P = 0.12$) was not significantly related to midge abundance, but there was a significant negative relationship between midge and wolf spider density at Lake Mývatn ($F_{11,87} = -2.02$, $P = 0.047$; Fig. 2). On average wolf spider density was greatest at Lake Mývatn, 1.02 compared to 0.86 and 0.68 m^{-2} at Lake Helluvaðstjörn and Lake Botsvatn respectively, though differences between lakes were not significant ($P > 0.05$).

3.2 Mesocosm Experiments

In mesocosms more leafhoppers disappeared when combined with a wolf spider in the presence ($F_{12,42} = -2.72$, $P < 0.009$) and absence of midge alternative prey ($F_{12,42} = -5.07$, $P < 0.0001$; Fig. 3A). After five days approximately 70% of the original 20 leafhoppers in the no spider treatment were missing, but more than 90% disappeared in the presence of a wolf spider alone. However, when midges were present with spiders twice as many leafhoppers survived (~80% eaten) compared to the midge-free spider treatment ($F_{12,42} = 2.86$, $P = 0.007$; Fig. 3A).

In the second mesocosm experiment, the persistence of fruit fly larvae was highest in the absence of wolf spiders (<10% missing after 12 hrs), while predation was greatest in the presence of wolf spiders alone (~60% missing after 12 hrs, $F_{9,103} = -5.10$, $P < 0.0001$; Fig. 3B). When midges were present with spiders in mesocosms fruit fly predation decreased 50% (~40% missing after 12 hrs) relative to larvae exposed to wolf spiders alone. Contrary to expectation, there was no increase in sentinel prey survivorship with increasing midge density ($F_{9,103} \geq 2.49$, $P \leq 0.014$; Fig. 3B).

3.3 Field Experiment

Mesh tops were successful at reducing the numbers of midges by 5 fold over open-topped enclosure arrays ($F_{1,65} = 126.02$, $P < 0.0001$), and this effect did not differ among wolf spider treatments ($F_{2,65} = 2.31$, $P = 0.11$; Appendix 2A). Wolf spider abundance in the spider reduction treatment was depressed by over 50% (visual counts; $F_{12,47} = -3.22$, $P = 0.0023$, sticky traps; $F_{10,}$

$_{65}$ = -3.11, $P < 0.0027$; Appendix 2B and 2C) when compared to the spider addition plots, and there were no differences in wolf spider abundance with respect to the midge treatment (visual counts; $F_{12,47} = 1.70$, $P = 0.20$, sticky traps; $F_{10, 65} = 0.77$, $P = 0.38$; Appendix 2C). Wolf spider abundance as measured by sticky traps at the end of the season was not significantly different between open and spider addition plots ($F_{2,65} = 0.76$, $P = 0.45$, Appendix 2C).

The presence of midges reduced predation of sentinel fly larvae in all treatments ($F_{1,74} = 35.38$, $P < 0.0001$; Fig. 4). Additionally, when midges were present, there was no difference in predation intensity across the spider treatments (50-55%; $F_{19,74} = 1.50, 0.42, 1.01$, $P = 0.14$, 0.67, 0.31, addition-reduction, addition-open, reduction-open respectively; Fig. 2). However, in the absence of midges larval predation was significantly greater in the wolf spider addition treatment (75%) as compared to the open treatment (66%; $F_{19,74} = 2.42$, $P = 0.018$), and marginally lower when compared to the wolf spider reduction treatment (70%; $F_{19,74} = 1.95$, $P = 0.055$; Fig. 4). There was no difference in predation between the reduction and open treatments ($F_{19,74} = 0.85$, $P = 0.40$) when midges were absent.

The presence of midges resulted in a larger decrease in predation in the wolf spider addition treatment compared to the wolf spider reduction and open treatments (i.e. significant Midge x Spider, $F_{2,74} = 3.26$, $P = 0.044$; Fig. 4). Midges reduced predation of larvae by 45% in the wolf spider addition treatment ($F_{19,74} = 5.17$, $P < 0.0001$), by 10% in the wolf spider reduction treatment ($F_{19,74} = 3.11$, $P = 0.003$), and by 25% in the open treatment ($F_{19,74} = 2.32$, $P < 0.023$; Fig. 4). Thus, in the absence of midges higher predator densities increased predation on "resident" sentinel prey, but the presence of midges reduced predation to levels equal to that observed at low predator density.

4. Discussion

Our experiments found that midges correlate with increased wolf spider reproduction, and cause a consistent positive indirect effect on terrestrial arthropod prey by reducing wolf spider predation. Predation on arthropod prey (both leafhoppers and sentinel *Drosophila* larvae prey) was reduced by ≥50% in mesocosm containers with live midges compared to those without (Fig. 3). This effect is independent of midge density, suggesting a rapid prey switching behavior rather than a dilution effect of the alternative prey. When aquatic insects come on land, they often increase predator abundance in the riparian zone; an effect which can increase overall predation on resident prey. Consistent with this prediction, in the field experiment increased predator density increased predation on sentinel prey in the absence of midges. Similar to the laboratory experiment, when live midges were present predation of sentinel prey decreased by 10-45% (Fig. 4). Interestingly, the largest positive effect of midges was at the highest predator density. While aquatic insects can influence predator density, in this study changes in predator behavior apparently offset the effects of increased predator density, resulting in a net positive indirect effect on terrestrial prey. This finding suggests that predator-specific responses to alternative prey are a key factor controlling the direction and magnitude of indirect effects.

Our results suggest that the feeding behavior of wolf spiders changes in the presence of live midges. Surprisingly, sentinel prey survival remained constant as alternative prey density increased from 5 to over 100, suggesting a rapidly saturating predation response of wolf spiders that is unrelated to alternative prey abundance. *Pardosa* wolf spiders are unlikely to reduce predation due to satiation at midge densities of 5-50 since they can consume up to 70 planthoppers (equivalent in size to leafhoppers) in 24 hrs (Döbel and Denno 1994). It is possible, that like for other species of *Pardosa*, live midge movement draws the attention of these visual-hunting wolf spiders, distracting them from consuming other more sedentary terrestrial prey such as leafhoppers (Döbel and Denno 1994, Finke and Denno 2003). Studies in other systems have also shown that predator preference is an important mechanism causing positive indirect effects (Koss and Snyder 2005, Owen-Smith and Mills 2008, Sundararaj et al. 2012). The consequence in our case is that at very low alternative prey (midge) abundance predation is relaxed on resident terrestrial arthropods. This strong predator preference may be a precondition for alternative prey to cause positive indirect effects even in the face of increasing numbers of predators.

Predator density was an important determinant of predation rate in the field, but only when alternative prey were not present, demonstrating that predator preference can override the effect of predator density. In our study we found that midges were positively associated with the reproduction of predators at two of three lakes, but had minor impacts on their density. However along other bodies of water alternative prey- subsidized predators, including web-building spiders (Henschel et al. 2001) and birds (Nakano and Murakami 2001), show increased densities resulting in high levels of predation on terrestrial prey. In most models predators begin to eat alternative prey once the incoming prey outnumbers resident prey, so that "switching" occurs absent preference between prey types (but see van Baalen et al. 2001). However, predators that select prey based on desirable characteristics (e.g. ease of capture, nutritional quality) may accelerate switching and a rapidly saturating functional response, both conditions that Abrams and Matsuda (1996) suggest increase the likelihood of positive indirect effects. While switching to alternative prey appears to cause short-term positive indirect effects, without manipulating predator density it is difficult to tell if the positive effect of alternative prey will persist since alternative prey also typically increase predator density. This study demonstrates that predator selection of alternative prey can reduce net predation on resident prey, weakening the link between increased predator densities and negative indirect effects.

Aquatic insects are important alternative prey to terrestrial predators, increasing their densities while also affecting their behavior. Here we have shown that live midges increase reproduction of predators while also reducing predation on terrestrial prey by changing the foraging behavior of a shared predator. This behavioral change maintains low predation rates on terrestrial prey, independently of the density of the alternative prey, mitigating increases in predator density. Our results stress the importance of predator preference for alternative prey, highlighting its role in determining the strength and direction of indirect effects.

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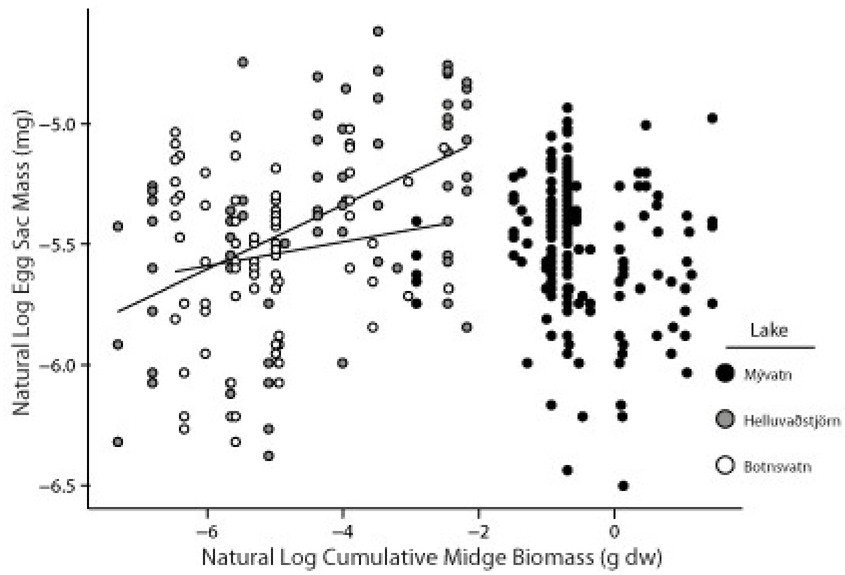


Figure 1. Midge abundance was positively related to wolf spider egg sac mass at the lakes Botsvatn ($F_{9,350}$ = 2.40, P = 0.017) and Helluvaðstjörn ($F_{9,350}$ = 5.77, P << 0.0001) with low to moderate amounts of midges, but there was no similar increase in egg sac mass at Lake Mývatn ($F_{9,350}$ = 0.69, P = 0.49) with the greatest midge numbers.

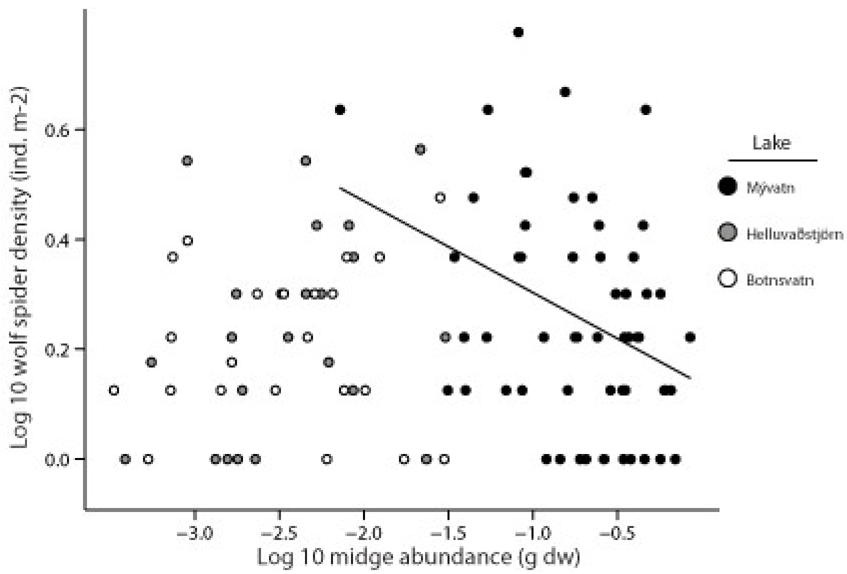


Figure 2. Wolf spider density at lakes Botsvatn ($F_{11,87} = 0.57$, $P = 0.59$) and Helluvaðstjörn ($F_{11,87}$ $= 1.55$, $P = 0.12$) was not significantly related to midge abundance, but there was a significant negative relationship between the two at Lake Mývatn ($F_{11,87} = 2.02$, $P = 0.047$).

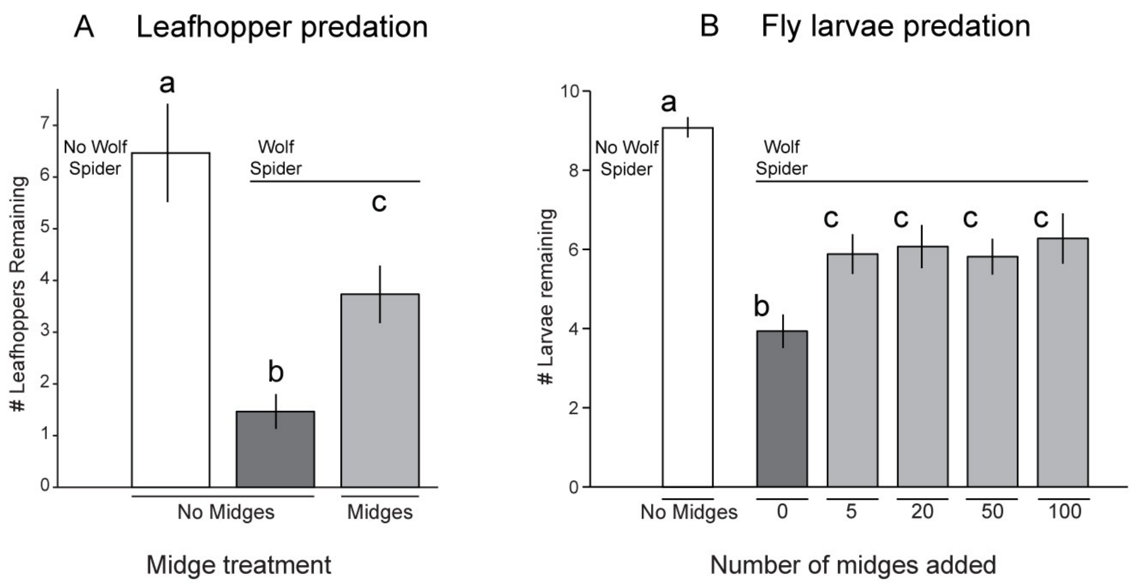


Figure 3. A: Predation of leafhoppers is significantly increased in the presence of a wolf spider (medium and dark grey bars). However, the addition of live midges reduces predation of leafhoppers in the presence of a wolf spider (medium grey bar). B: Predation of *Drosophila melanogaster* larvae sentinel prey is significantly increased in the presence of wolf spiders (medium and dark grey bars). However, the addition of live midges to mesocosms with wolf spiders reduced predation (medium grey bars). This effect is equal across midge densities of 5 to >100 individuals suggesting that the response is caused by behavior rather than satiation. Letters indicate means that are significantly different ($\alpha = 0.05$; mean+/-SEM).

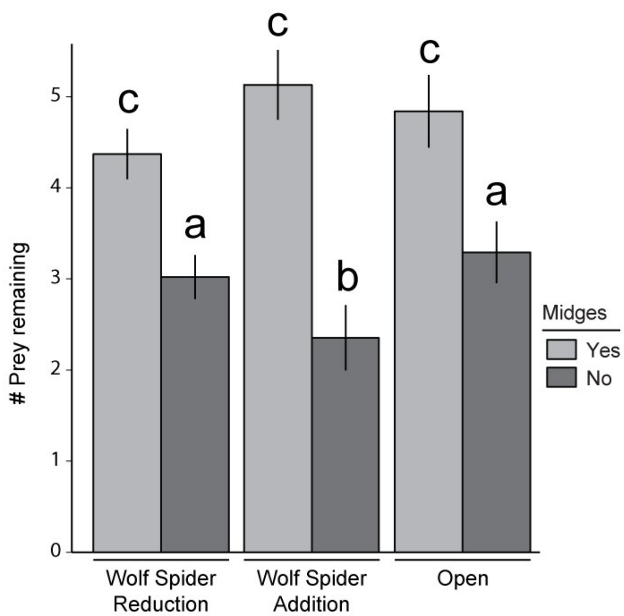
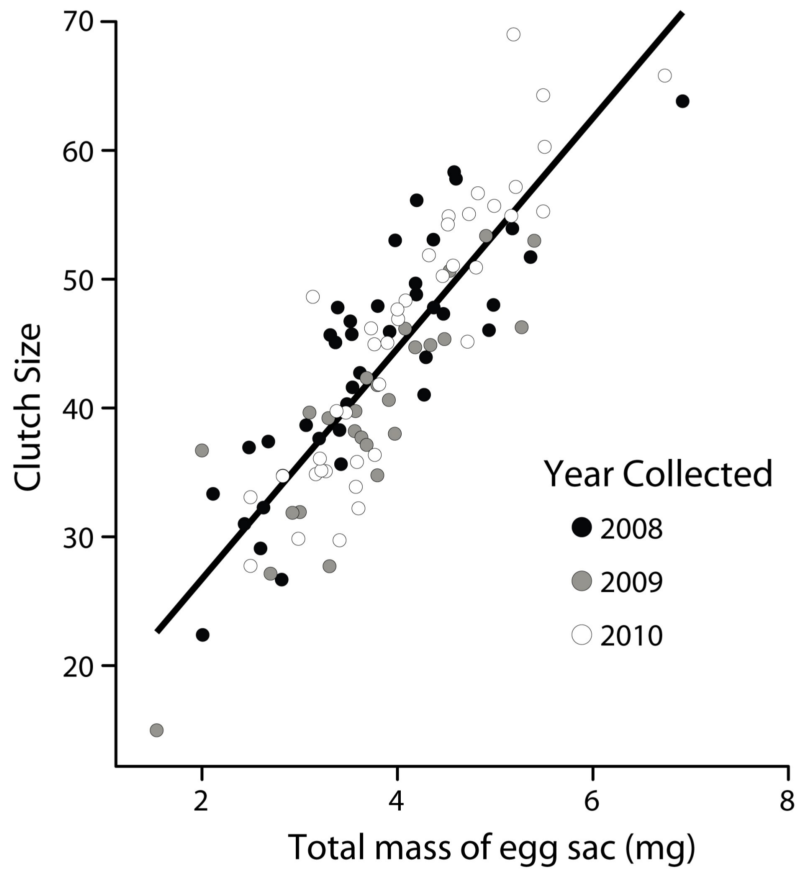
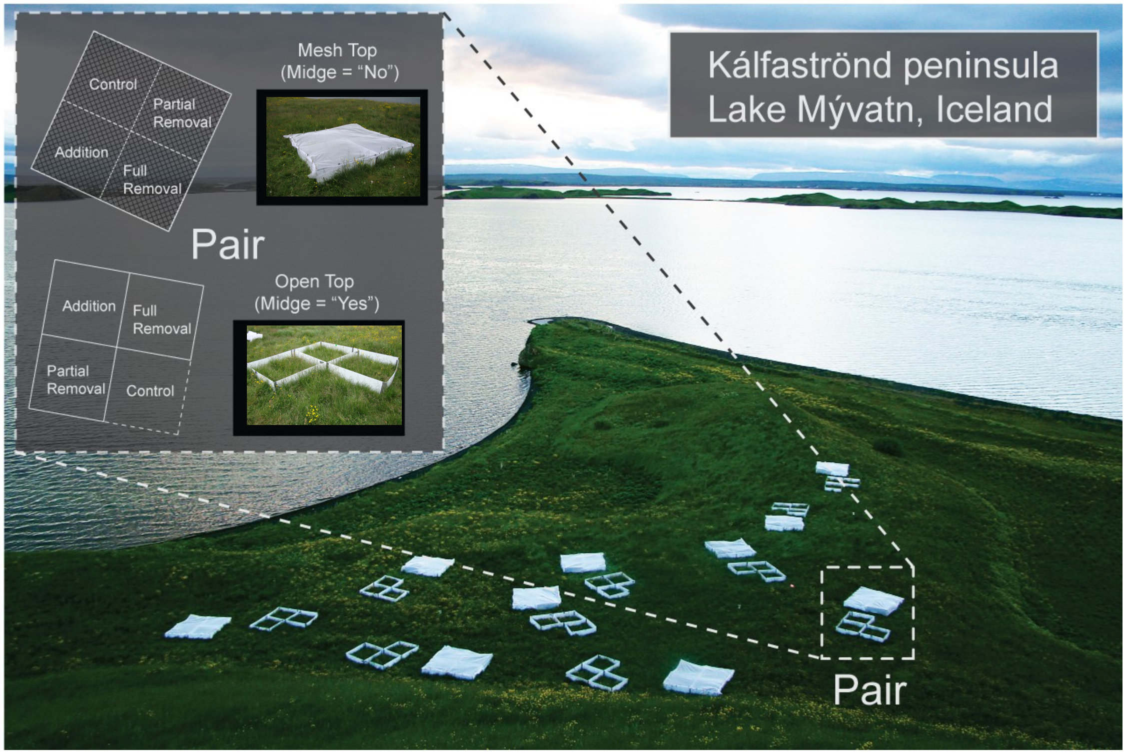


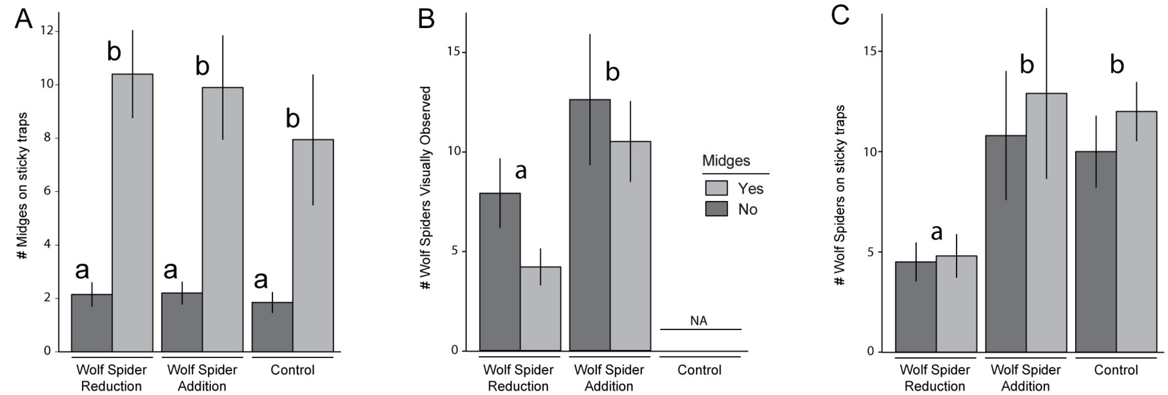
Figure 4. Predation of *Drosophila melanogaster* larvae sentinel prey is decreased where midges are present (light grey bars) compared to when they are absent (dark grey bars). Predation is greatest in the wolf spider addition treatment when midges are absent (middle dark bar). However there are no differences in predation rates between treatments when midges are present (light grey bars). This is due to a significantly greater effect of midges in the wolf spider addition treatment (middle columns) than in either the wolf spider reduction or open treatments (outside columns). Letters indicate means that are significantly different ($\alpha = 0.055$; mean+/-SE).



Appendix I. Egg sac mass and clutch size (number of eggs) are strongly correlated ($F_{1, 99}$ = 324.3, p<<0.0001; adjusted R^2 = 0.7618). Clutch size was used as the response variable and the factorial interaction of egg sac mass (continuous) and year (categorical) was used as the main effects.



Appendix II. Photograph of experimental area located on the Kálfaströnd peninsula in the SE corner of Lake Mývatn (65°36'N,17°0′W) and design/layout of experimental units. Inset shows schematic of an array pair, with one open-topped enclosure array paired with a second mesh-covered array. Control plots were open on two sides. Since there was no difference in wolf spider numbers between "full removal" and "partial removal" enclosed plots these were combined into a single "wolf spider reduction" treatment for analysis and interpretation. Photo 28 July 2011, D. Hoekman.



Appendix III. Mesh tops were successful at reducing the numbers of midges by 5 fold over open-topped enclosure arrays ($F_{1,65}$ = 126.02, P < 0.0001; Panel A), and this effect did not differ among wolf spider treatments ($F_{2,65}$ = 2.31, P = 0.11). Wolf spider abundance in the spider reduction treatment was depressed by 50+% (visual counts Panel B; $F_{12,47}$ = -3.22, P = 0.0023, sticky traps Panel C; $F_{10, 65}$ = -3.11, P < 0.0027) when compared to the spider addition plots, and there were no differences in wolf spider abundance with respect to the midge treatment (visual counts; $F_{12,47}$ = 1.70, P = 0.20, sticky traps; $F_{10, 65}$ = 0.77, P =0.38). Wolf spider abundance as measured during the single sticky trap measurement in open plots was not significantly different from addition plots ($F_{2,65}$ = 0.76, P = 0.45). Letters indicate means that are significantly different (α =0.05; mean+/-SEM).

THESIS CONCLUSIONS

1. Measurements of aquatic insect emergence and terrestrial abundance can be conceptually unified to estimate terrestrial deposition of aquatic insects. Most current methods of insect capture on land may be taxon biased or inaccurate for determining deposition because they are lethal. This has led to a lack of understanding of rates of aquatic insect inputs to land. By measuring aquatic insect emergence and relative abundance on land a simple estimate can be made of actual insect deposition, useful when trying to determine the impact and importance of insect linkages at the water-land boundary.

2. Nutrient deposition to terrestrial ecosystem by aquatic insects can rival other major sources. Since most insects are approximately 10% nitrogen and 1% phosphorus by mass, large numbers of insects entering an ecosystem can increase nutrient availability there. Estimates of midge deposition at Lake Mývatn, Iceland suggest that during years of high abundance midges can double or triple the annual rate that nitrogen is added to terrestrial ecosystems close to the lake. This begs the question of how many other terrestrial habitats, perhaps on a lesser but still significant level, are being fertilized by insects from adjacent water bodies.

3. Arthropods of many trophic levels respond to resources provided by aquatic insect inputs. When alive, midges are fed on by terrestrial predators such as spiders. When dead, they are available to detritivores including mites, and provide nutrients to primary producers that eventually benefit herbivorous insects too. Since midges are entering at the top and bottom of the food web, nearly all terrestrial arthropods respond together by increasing in number.

4. The effects of chronic aquatic insect inputs from lakes can be seen over large areas. Significant midge inputs can occur tens and even hundreds of meters away from shore. Across the landscape of northeast Iceland the signature of aquatic insect input to land can be seen in increased numbers of detritivorous, herbivorous, and predatory arthropods. This is testimony to the important top-down and bottom-up processes on land that are maintained or supported by lakes, a source of aquatic insects that until recently has received scant attention from ecologists.

5. Aquatic midges can increase predator reproduction and decrease individual predator consumption of other species. Midges are an important alternative prey item to terrestrial consumers, especially where terrestrial productivity is low and other arthropods are scare. As midge numbers on land increase to moderate levels, so too does the reproductive rate of spiders. These same actively hunting spiders individually reduce their feeding on typical terrestrial prey when presented with live midges, relaxing predation pressure in a positive indirect effect.

6. While predator numbers can grow in response to aquatic midges, predation may remain low since aquatic insects can also distract predator feeding. At low predator density midge availability reduced rates of predation on sentinel prey. At high predator density the "rescue effect" of midges actually grows so that there is no increase in predation rate as long as live midges are present. This is accounted for by the strong and rapid switching of wolf spider predators to midges when available, an effect observed in the lab when as few as five midges had the same distraction effect as over 100.