Intrinsic and Environmental Influences on Antlion (*Myrmeleon immaculatus*) Pit Diameters at Coastal Sites in Northern Michigan

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*I am writing this report independently; however, this experiment was a collaborative effort with Natalie Blackwood and Taylor Glick and the assistance of Dave Anderson and Emily Tompkins.

Abstract

Gene-by-environment interactions have the potential to create populations of the same species that display differential phenotypes due to variation in microenvironments. This variation will create a discrepancy in energy-conserving success between individuals that behave differently, and those that are successful in one environment may not be selected for in another. We experimented with the pit-building behaviors of larval antlions (Myrmeleon immaculatus) by evaluating the sizes of pits created by Pine Point antlions on Douglas Lake and South Sturgeon Bay antlions on Lake Michigan. Past data has shown that S. Sturgeon Bay antlions dig larger pits, and we tested the persistence of this behavior when both groups of antlions were transported from their sites of origin. We also ran a lab experiment to determine the time required to reach a maximum pit size in antlions from both sites. After the completion of these experiments, we decided to augment our data with a separate study of the pit sizes of antlions at other sites around Douglas Lake and Sturgeon Bay. In all cases, we controlled for the positive correlation between body weight and pit size by limiting our data points to those within overlapping ranges of weight for each statistical test. Our data suggest an intrinsic difference in behavior that causes S. Sturgeon Bay antlions to dig larger pits than individuals at Pine Point and at other sites around Sturgeon Bay. Further experimentation is required to identify the specific causes of this difference; however, the phenotype of S. Sturgeon Bay antlions is likely due to the interaction between genotype and some variance in conditions of that microenvironment.

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Signed, Heather Williams

Introduction

Phenotypic plasticity between populations of individuals of the same species is produced by differential expression of genotypes due to differences in environmental conditions (Scheiner, 1993). The evolution of behavior favors optimal foraging for a given quantity of energy expended. Individuals should select the most advantageous environment available (Klokocovnik et al., 2012). Conversely, individuals not well suited for their current environment due to a failure to maximize net energy intake by behavioral strategies should be less successful than their competitors and become less common (Scharf et al., 2011). Due to physical and environmental constraints, the actual habitat selections of most organisms are rarely ideal (Scharf and Ovadia, 2006). Antlion (*Myrmeleon immaculatus*) larvae are constrained by their lack of mobility when selecting a habitat in which to dig their pits (Klokocovnik et al., 2012). These sit-and-wait predators dig conical pits in preferably fine and dry sand or soil to trap their prey (Burgess, 2009; Day and Zalucki, 2000). This method of trapping predation requires substantial time and energy during the construction process, but is low in long-term energy cost, because antlions do not need to actively hunt for food (Klokocovnik et al., 2012).

Due to their inhibited motility and limited quality habitat space, antlions must alter their behavior to maximize efficiency in their environment. Individual weight is positively correlated with pit size, so organisms that are larger dig larger pits (Guillette et al., 2009). Food availability also influences the pit-digging behaviors of *Myrmeleon immaculatus*. In a low-food scenario, antlions engage in more pit maintenance than when prey is abundant (Arnett and Gotelli, 2001). As long as the need for food is not urgent, antlions are not willing to pay the high energy cost of maintaining their pits.

Myrmeleontidae use past experience to make decisions about pit-building (Tsao and Okuyama, 2013). The information they apply includes former success in prey capture as well as the communication they receive from other individuals in the same population. Antlions use social cues to gain information about their environment, as is predicted by an Evolutionarily Stable Strategy (Tsao and Okuyama, 2013). Social information is passed when another organism is merely present (Tsao and Okuyama, 2013). If many other Myrmeleontidae are around, the current environment must be a suitable one. One antlion knows that another is near by the presence of sand tossing or vibrations in the substrate (Tsao and Okuyama, 2013). The use of information like this in foraging strategies and behavior suggests a high capacity for learning (Tsao and Okuyama, 2013).

Learning and informed decision-making have the potential to produce differential behaviors from one antlion to the next under comparable environmental conditions. Experiments with antlions and associative learning have shown that they have a capacity to associate a stimulus with feeding (Guillette et al., 2009; Hollis et al., 2011). If two organisms have had different life experiences and have retained them through learning, they should use this knowledge to respond differently to environmental stimuli. The possibility also exists that some of the differences in behavior from one antlion to the next are due to genes (Arnett and Gotelli, 2001). If some genetic component to pit maintenance exists, different forms of that allele could dominate at two different sites. Both learned behavior and genetic predispositions to behavioral tendencies can cause individuals to respond to environmental conditions differently.

This differential response to environmental conditions is due to the mechanism by which the environment influences behaviors that are selected for in a population. In one type of environment, displayed behaviors may influence fitness in a different way than they do in another (Scheiner, 1993). The conditions of the environment also interfere with the development of an individual and consequently influence phenotype (Scheiner, 1993). The combination of the ability to apply information from early life experiences to current behavior and the influence of the environment on the evolution of an optimal phenotype creates a scenario in which separate populations of organisms like antlions may display different behaviors.

Antlion populations at South Sturgeon Bay in Wilderness State Park (N45° 68' 1.17", W84° 97' 8.97") have been consistently digging larger pits than those at Pine Point (N45° 57' 2.41", W84° 66' 0.08") on Douglas Lake only 26.97 miles away (D. Anderson, pers. comm, 2013). This discrepancy may

be due to intrinsic differences between the populations like genetic differences, variance in early learning, or an interaction of genes with different environmental conditions.

Lake of Origin Hypothesis

Based on data collected in the past from antlion populations at Pine Point and South Sturgeon Bay, we hypothesize that Pine Point specimens will dig smaller pits than those from S. Sturgeon Bay even when placed in a new environment, because they possess some intrinsic difference from the organisms at S. Sturgeon Bay. A persistent difference in pit size when these organisms are moved from their site of origin will suggest an intrinsic difference in pit-building behaviors between the populations.

Change in Pit Size Hypothesis

Because antlions must expend time and energy to dig an initial pit, we hypothesize that they will not reach their final pit size until three days have been allowed for undisturbed maintenance. After that time period, we hypothesize that pit diameters will remain stagnant for each animal.

Within Site Variation Hypothesis

We hypothesize that populations of antlions at different sites around Douglas Lake and Sturgeon Bay will display differences in pit building behavior to the same or greater magnitude expressed between lakes. Under the assumption that there is gene flow between populations at each lake, differences between each site will suggest the power of varying micro-environments over genes as an influence on behavior between sites.

Materials and Methods

Lake of Origin Experiment

In the summer of 2013, I and two other researchers from Dave Anderson's Behavioral Ecology class designed an experiment to test the origin of the difference in pit sizes for South Sturgeon Bay (SSB) on Lake Michigan and Pine Point (PP) on Douglas Lake antlions. We collected 35 specimens from each site each weighing between 13 and 40 milligrams to avoid differences in pit sizes due to significantly different body masses. We constructed containers for each site by cutting the bottoms out of round plastic tubs measuring 115 millimeters in diameter and 80 millimeters in height. We replaced the bottoms with mesh to allow drainage of water without the potential for escape of the specimen and its sand. Each organism was designated a number by site that matched the label on its tub.

On July 21, at both Pine Point and S. Sturgeon Bay, we located an area with a high concentration of antlion pits and designated an experimental area of 1.524 square meters. This zone was covered with a shade structure that we constructed out of wooden boards and a translucent plastic cover that allowed some sunlight to pass through. The structure sat approximately 30.48 centimeters off the ground. This was to prevent damage or alteration of the pits by rain during the experiment. Antlions were collected by scooping the sand beneath a pit into a sieve. We took weight measurements in the field and placed each in a labeled vial to be transported to its starting experimental location that same day.

Within the zone, we created a five tub by six tub array, alternating between Sturgeon Bay and Pine Point specimens every 15.24 centimeters (See Figure 1). The array controlled for skewed data that could be produced if certain edges received more wind and rain interference or greater prey capture than the center of the setup. The impact of these factors would be controlled for by the alternation of Pine Point and S. Sturgeon Bay animals. The mesh bottom tubs were labeled by original location, designated number, and first experimental location. We started the experiment with fifteen S. Sturgeon Bay and Pine Point antlions at each location to test for an effect due to order of locations. We buried the tubs so the rim

was level with the sand and filled each with uniform one millimeter sifted sand from the shore of Douglas Lake before placing the appropriate specimen inside. Within each array, we placed five temperature-collecting data tools. One was in the center, and four were just inside the corner regions. We placed the two arrays of thirty antlions at each location underneath the shade structure and waited four days.

Returning to the Pine Point site on July 25, we measured each antlion pit and recorded the largest and smallest diameter as well as the height in millimeters. Measurements were taken by breaking an uncooked spaghetti noodle to slightly over the estimated diameter of the pit and laying it over the top. We used calipers to measure the distance from one end of the pit where the noodle touched the sand to the other. This was repeated with the perpendicular diameter, and height was measured by inserting a noodle vertically into the pit until it lightly touched the vertex and marking the spot where it intersected with the noodle across the top of the pit. The same measurer was kept consistent throughout the duration of the experiment to control for error due to individual interpretation. We then fed each of the antlions one nonformic acid containing ant collected from the same colony. We allowed a few hours for prey consumption before transporting the antlions.

The antlions were transported to S. Sturgeon Bay by placing the plastic tubs in wooden boxes, maintaining the pattern of the array. At Sturgeon Bay, we measured the 30 pits in the same fashion, then fed those specimens and removed the tubs after a few hours of digestion time and replaced them with those that had been at Pine Point. We transported the Sturgeon Bay antlions to Pine Point within the wooden boxes and placed them in the ground. The specimens were all inserted in the same location within the array that they had occupied in the first run. We returned to both sites three days later to take final pit measurements, but found that many pits at both sites had not been dug. We took pit measurements but left all specimens in place and returned two days later.

July 27 showed little change in the number of animals with pits built. Our shelter had not completely prevented rain from altering the pits on some of the edges at both sites, so we attached a mesh enclosure around the edges of the structures and dug a trench around the arrays, took another set of measurements and returned on the 29th. With only a few new pits constructed, we decided again to wait a few more days to remove the specimens. On August 1, we took final measurements at both sites, collected the antlions in labeled vials, and brought them back to the lab for weight measurements. We also collected the temperature loggers from each site and extracted the data for analysis. On all days of attempted data collection, the specimens at both sites were fed one ant from the same colony as in the data collection before the location switch. We measured and recorded the final weight of each specimen in the lab on August 1 before releasing the animals back into their original populations.

Change in Pit Size Experiment

To determine if the time in the field during the portion of the experiment before the location switch was long enough for the antlions to reach their final pit size, we set up a side experiment to measure pit sizes of specimens from each site over the course of fifteen days. We collected five antlions within our restricted weight range from each site and transported them back to the research lab to be placed in the same plastic tubs with the same sifted one millimeter Douglas Lake sand. Their undisturbed pits were measured in the same manner as the others at the same time every day for fifteen days to evaluate the possibility of increasing pit size beyond the three days allowed for the other experimental antlions. Each of these specimens was fed a non-formic acid containing ant on the same day that the experimental antlions were transported and fed.

All measurements of weight and pit size were recorded by individual specimen in Excel spreadsheets. Day of measurement was recorded, and data from antlions of the same population that started at each site were kept separate. Diagrams were drawn of the arrays to confirm the same edge effects at each site for all trials. We took note of pits that appeared to have been disturbed by water or other environmental conditions and did not measure pits that appeared to have been abandoned or partially filled in.

Within Site Variation Study

After executing an experiment to evaluate the differences in pit building behavior at two individual sites, each on the beaches of different lakes, we considered the possibility that these sites might be micro-environments not consistent with other sites around the same lake. To test whether our results would represent Douglas Lake antlions and Sturgeon Bay antlions overall or just the two populations sampled, we collected pit diameter data from our two sites as well as five additional sites on the same day. Three additional sites were found around Douglas Lake and two at Sturgeon Bay (See Table 1).

We traveled to each site and measured the largest and smallest diameter of 15-30 pits, the exact number per site depending on time availability an animals present, and only collected data for antlions between 13 and 40 milligrams. Specimens were returned to their environment after weights were taken.

Statistical Analysis

All tests of normality were run in SPSS, while the other statistical tests were executed using Statistica. Figures were created using Sigma Plot. P values of < 0.05 were considered significant.

Site of Origin

We ran Shapiro-Wilks tests of normality on the body masses, pit diameters, and pit heights for each experimental group. Groups were identified as Pine Point specimens on their first pit at Pine Point (PPP_{P1}), S. Sturgeon Bay specimens on their first pit at Pine Point (SSB_{PP1}), Pine Point specimens on their first pit at S. Sturgeon Bay (PP_{SSB1}), S. Sturgeon Bay specimens on their first pit at S. Sturgeon Bay (SSB_{SSB1}), Pine Point specimens on their second pit at Pine Point (PP_{PP2}), S. Sturgeon Bay specimens on their second pit at Pine Point (SSB_{PP2}), Pine Point specimens on their second pit at S. Sturgeon Bay (PP_{SSB2}), and S. Sturgeon Bay specimens on their second pit at S. Sturgeon Bay (SSB_{SSB2}). Non-normal distributions of mass were accounted for by the robustness of the tests we intended to run.

We had intended to test the Homogeneity of Slopes Assumption and run an ANCOVA (Analysis of Covariance) testing the effects and interactions between site of origin, first site, and pit number (whether the specimen was on its first or second pit in the experiment) on the grounds that it was satisfied. We were halted in this statistical analysis when we evaluated the overlapping ranges of specimen weights from each site.

Despite having selected for a narrow weight range (13 to 40 milligrams), we found after creating box plots that the overlap of weight ranges for each site was minimal (See Figure 2).

Under these small sample sizes, we determined an omnibus statistical test to be an inaccurate interpretation of the data and ran eight separate Homogeneity of Slopes tests and eight ANCOVA's, testing the effect of site of origin and controlling for current site and pit number in the first four and testing the effect of current site while controlling for site of origin and pit number in the second four. We calculated overlapping mass ranges within each of the test groups and only used data points within those ranges. We also generated Least Squared Means for each group in each test. One plot was constructed for the effect of site of origin and one for the effect of current site.

Change in Pit Size

Due to small sample sizes ($n_{PP} = 4$; $n_{SSB} = 5$) for each day, tests of normality were not used. Least Squared Means for average pit diameter for each group on each of the fifteen days were calculated. A repeated Measures ANOVA (Analysis of Variance) was run due to its robustness. We constructed plots of percent maximum pit size by day for each site and overall pit diameter for each site on each day.

Within Site Variation

After having determined that the effect of weight on pit diameter is negligible within ranges of 20-29 milligrams and 30-39 milligrams, we restricted our data to two separate weight classes within these ranges. The result was to eliminate the effect of weight on pit sizes and any differences in weight distributions across the seven sites.

We next ran a Nested ANOVA with independent variables site, lake, and weight class to determine how pits at different sites around the same lake differed in comparison to pit sizes at different lakes. We plotted the Least Squares Means for pit diameters at each lake overall.

Results

Site of Origin

Weight effects within each test group were controlled for by restricting data points used to those within overlapping ranges of weight (weight: PP_{PP1} and $SSB_{PP1} = 17-34$ milligrams; weight: PP_{SSB1} and $SSB_{SSB1} = 14-39$ milligrams; weight: PP_{PP2} and $SSB_{PP2} = 17-36$ milligrams; weight: PP_{SSB2} and $SSB_{SSB2} = 16-42$ milligrams). Pit heights did not display normal distributions, most likely due to difficulty in obtaining an accurate measurement, so the average of largest diameter and smallest diameter for each pit were used to quantify pit size in all of the following tests.

All tests of Homogeneity of Slopes for both the test of site of origin effect and current site effect passed with p values of greater than 0.05, so interaction terms were not significant, and we could proceed with and ANCOVA for each case (See Table 2). All ANCOVA's failed to show significance for a difference in pit diameter by site of origin and for difference in pit diameter by current site (See Table 2).

Least Squared Means for pit diameters for groups of organisms originating from South Sturgeon Bay (SSB_{PP1} , SSB_{SSB1} , SSB_{PP2} , and SSB_{SSB2}) were all larger than those for groups of specimens originating from Pine Point (PP_{PP1} , PP_{SSB1} , PP_{PP2} , and PP_{SSB2}) (See Figure 3).

All ANCOVA's testing the effect of current site, controlling for site of origin and pit number also show insignificant results (See Table 3). These Least Squared Means did not show a consistent pattern between sites (See Figure 4).

Change in Pit Size

A plot of Least Squared Means for South Sturgeon Bay specimens and for Pine Point specimens on each day after transfer into the lab revealed the completion of 90% of the maximum pit diameter for both groups of organisms reached after approximately three days. Maximum pit size was generally accomplished at about five days of maintenance for both groups. The average percent of maximum pit size attained for Pine Point animals and S. Sturgeon Bay animals on each day were included in the other's 95% confidence intervals (See Figure 5).

The ANCOVA revealed a marginally significant site of origin effect on pit diameter ($F_{1,7}$ = 5.76; P = 0.048; Figure 6).

Within Site Variation

The Nested ANOVA produced an insignificant effect of lake, site within lake, and weight on pit diameter ($P_{lake} = 0.144$; $P_{site} = 0.658$; $P_{weight} = 0.117$). The pit diameter Least Squared Mean for Sturgeon Bay sites is larger than that of Pine Point sites; however, in both cases, the 95% confidence interval includes the mean of the other plot (See Figure 7). The South Sturgeon Bay site was the only site with a mean that appeared significantly different from those of the other sites and was the most likely reason for an overall larger trend in Sturgeon Bay pits.

Temperature

Temperature data revealed consistently higher temperatures at South Sturgeon Bay than Pine Point (See Figure 8).

Discussion

Although the ANCOVA's for the Site of Origin Experiment within our overlapping mass ranges do not display a significant difference between antlion pit diameters at S. Sturgeon Bay and Pine Point, our knowledge of past data and the consistent trend in Least Squared Means from one site to another suggest a difference that might be significant if larger data sets were available. The results of the ANCOVA run on our data from the Change in Pit Size Experiment support this suggestion as well. Combined with the results of the ANCOVA's testing the effect of current site in each test group, these results indicate an effect of site of origin on pit building behaviors that is not merely due to where the specimens were when we first measured their pits. Antlions do not appear to simply conform to the environment in which they currently reside but retain their behavior from where they originated.

The difference in behavior that is suggested even when mass is controlled for suggests that antlions at S. Sturgeon Bay are not merely larger than those at Pine Point. Because specimens from both locations appear to be nearly finished with their pits after three days as well as finished to the same degree throughout the fifteen day span in the Change in Pit Size Experiment, we can feel confident that the difference is not due to a higher quantity of pit building and maintenance in Sturgeon Bay specimens than Pine Point specimens during our experiment.

Our results from the Within Site Variation Study lead us to believe that genetic differences do not exist between the sites of each lake or between lakes, because significant differences in pit diameters between these groups did not exist. Organisms that disperse, specifically for mating purposes, tend not to have populations that are genetically distinct from one another (Moussy et al., 2013). While larval antlions are sedentary, mating occurs in the adult life stage when antlions are no longer sedentary and are capable of flying, potentially mixing with other populations. Consequently, genetically isolated populations would be unlikely, and our data are consistent with this understanding.

South Sturgeon Bay was the only site at Sturgeon Bay that appeared significantly different from those at Pine Point. This data point is the primary cause of the higher mean diameter for Sturgeon Bay individuals over those at Pine Point. These data suggest that some factor at South Sturgeon Bay that does not exist at any of the other sites is influencing the behavior of the antlions there. This factor may be one or many environmental variables that cause individuals to display a variable phenotype despite a lack of significant differences in genotype between sites.

The phenotypes (pit-building behaviors) that exist in non-genetically distinct populations of the same species of organism due to environmental differences are known as the "norm of reaction", while the degree to which there is a difference due to the environment is deemed phenotypic plasticity (Via and Lande, 1985). This plasticity is structured by the differential reproductive success between individuals behaving a certain way in a particular environment, so natural selection should establish an ideal variant of behavior for each set of environmental conditions (Via and Lande, 1985). Differences in the mean behavior displayed from one population to the next are a possible result of directional selection favoring gene-by-environment interactions that maximize fitness in an area (Vitasse et al., 2013).

Our results suggest that Myrmeleontidae digging larger pits are selected for at South Sturgeon Bay due to some environmental factors that make them more successful when they do this. During our experiment, temperature was generally higher at S. Sturgeon Bay than it was at Pine Point. This may contribute to the building of larger pits, as antlions prefer warmer weather conditions (Klein, 1982). Our data is inconclusive in the area of temperature, however, because we do not know if the temperate at S. Sturgeon Bay was also higher at other sites around Sturgeon Bay.

Selection for larger pit diameters may be due to prey availability and type of prey in an area. If the ants at S. Sturgeon Bay are larger in general at other Sturgeon Bay sites and around Douglas Lake, it may be worth the extra energy expenditure to dig a pit that is large enough to actually catch food. In the

case that most of the ants in an area are smaller or worse at escaping pits, it would not be time and energy efficient to dig a large pit for prey capture, because a small pit would work just as well.

The possibility exists that larger pits are more resistant to environmental variables like wind and water. If factors like these exist to greater degrees at S. Sturgeon Bay than any other sites, the antlions there could save in net energy expenditure by digging a pit that required less maintenance as time passed.

While further experimentation is required to actually isolate the factors of the microenvironment at South Sturgeon Bay that impacts the pit-digging behavior of its *Myrmeleon immaculatus*, our data indicate that these environmental differences and their behavioral constituents do exist. The correlation between differential environment and differential behavior may be due to early learning in antlions that influences later behavior even when they are introduced into a new environment, or it may be the result of phenotypic plasticity in which the way a consistent genotype is expressed varies according to environmental stimuli. The possibility also exists for an interaction between the two scenarios, strengthening the difference between population behaviors at different locations like Pine Point and S. Sturgeon Bay.

Implications for the existence of phenotypic plasticity in organisms from one population to the next include the potential problems with moving individuals of a species from one area to another. Natural selection occurs as a function of the interaction between an environment and the genotypes of its inhabitants. When those individuals are moved to a new environment, the genotypes that had been most successful may become less advantageous, so those that formerly contributed most to the gene pool become less prevalent.

Moreover, the concept that organisms within an environment can learn to behave in a way that maximizes their success at conserving energy establishes a new set of behavioral characteristics that can be acted upon by natural selection. If variation in ability to learn occurs within a population in the same way that other characteristics vary, those individuals that best learn to maximize their net energy gain should have higher fitness. Consequently, observing the ability of an individual to learn in an environment may be a necessary component of estimating its fitness.

If individual success is dependent not just on genes but on the way those genes interact with their environment and if ability to learn is a trait that makes some individuals better competitors than others, the evaluation of how successful an individual may be must be determined in the context of its specific environment and its cognitive capacity.

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Tables

Site	Coordinates
Douglas Lake 1	N45.56140 W84.667948
Douglas Lake 2	N45.56607 W84.66029
Douglas Lake 3 (PP)	N45.57241 W84.66008
Douglas Lake 4	N45.58540 W84.65416
Sturgeon Bay 1 (SSB)	N45.68117 W84.97897
Sturgeon Bay 2	N45.68465 W84.97179
Sturgeon Bay 3	N45.70500 W84.95224

Table 1. GPS coordinates for each site evaluated on Douglas Lake and at Sturgeon Bay on Lake Michigan.

Site of	Current Site	Pit Number	Sample	Homogeneity	Weight	Site of	Least
Origin			Size	of Slopes	Effect	Origin	Squared
						Effect	Mean
PP	PP	1	10	P = 0.95	P = 0.004	P = 0.58	57.35137
SSB	PP	1	7	P = 0.95	P = 0.004	P = 0.58	59.51376
PP	SSB	1	10	P = 0.05	P = 0.140	P = 0.28	56.73158
SSB	SSB	1	14	P = 0.05	P = 0.140	P = 0.28	63.60994
PP	PP	2	4	P = 0.34	P = 0.014	P = 0.09	58.72978
SSB	PP	2	10	P = 0.34	P = 0.014	P = 0.09	67.32909
PP	SSB	2	9	P = 0.98	P < 0.001	P = 0.58	65.61000
SSB	SSB	2	7	P = 0.98	P < 0.001	P = 0.58	67.65000

Table 2. Separate tests of Homogeneity of Slopes, ANCOVA's for site of origin effect, and Least Squared Means for each test group.

Site of	Current Site	Pit Number	Sample	Homogeneity	Weight	Current Site	Least
Origin			Size	of Slopes	Effect	Effect	Squared
							Mean
PP	PP	1	10	P = 0.42	P = 0.002	P = 0.870	55.58350
PP	SSB	1	7	P = 0.42	P = 0.002	P = 0.870	54.61572
SSB	PP	1	11	P = 0.098	P = 0.170	P = 0.220	59.77897
SSB	SSB	1	14	P = 0.098	P = 0.170	P = 0.220	64.76331
PP	SSB	2	8	P = 0.81	P < 0.001	P = 0.430	64.67908
PP	PP	2	6	P = 0.81	P < 0.001	P = 0.430	60.98457
SSB	SSB	2	6	P = 0.41	P < 0.001	P = 0.429	67.19596
SSB	PP	2	10	P = 0.41	P < 0.001	P = 0.429	69.36942

Table 3. Separate tests of Homogeneity of Slopes, ANCOVA's for current site effect, and Least Squared Means for each test group.

Figures

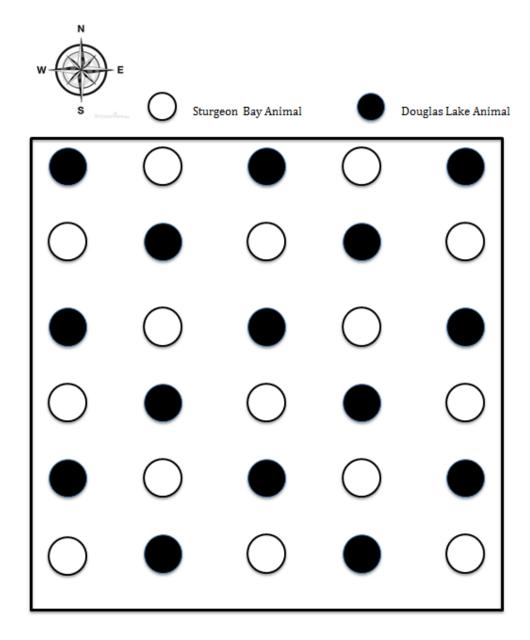


Fig. 1. Array of antlion tubs at Pine Point and South Sturgeon Bay.

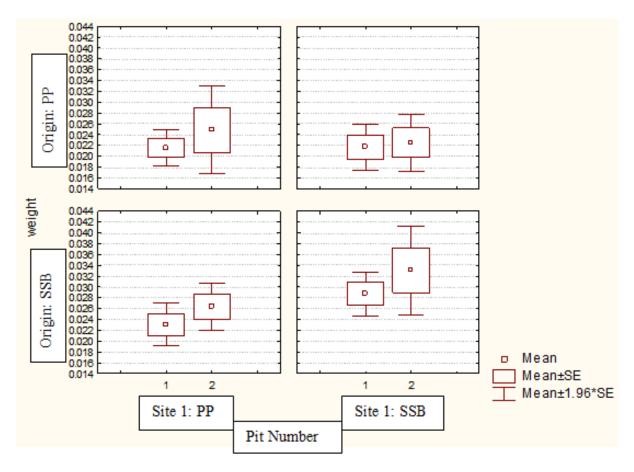
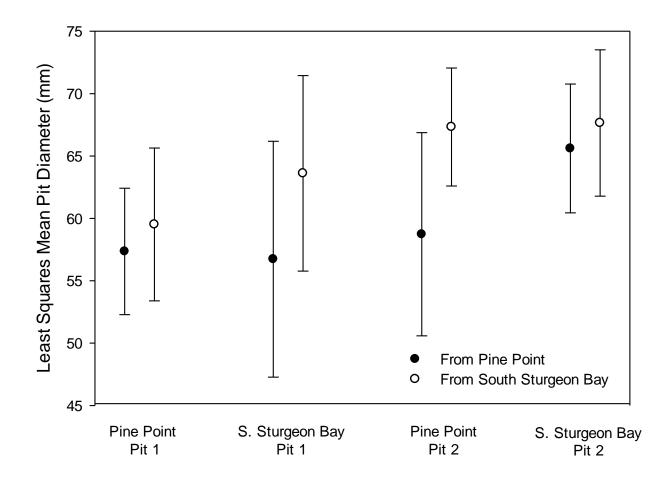


Fig. 2. Distributions of masses for each test group divided by site of origin, initial site, and pit number. Points represent means, and lines display ranges of values.



Current Site & Pit Number

Fig. 3. Least squared means of pit diameters for Pine Point and S. Sturgeon Bay antlions controlling for current site and pit number. Points represent averages, and lines display 95% confidence intervals.

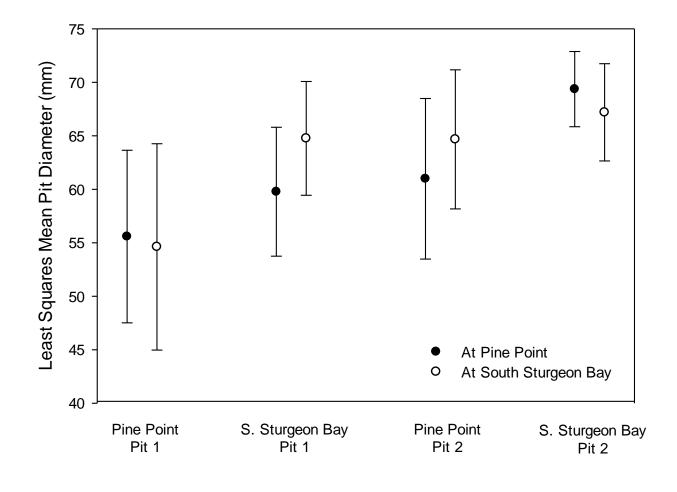


Fig. 4. Least squared means of pit diameters for specimens at Pine Point and S. Sturgeon Bay controlling for site of origin and pit number. Points represent means, and lines display 95%

confidence intervals.

Site of Origin & Pit Number

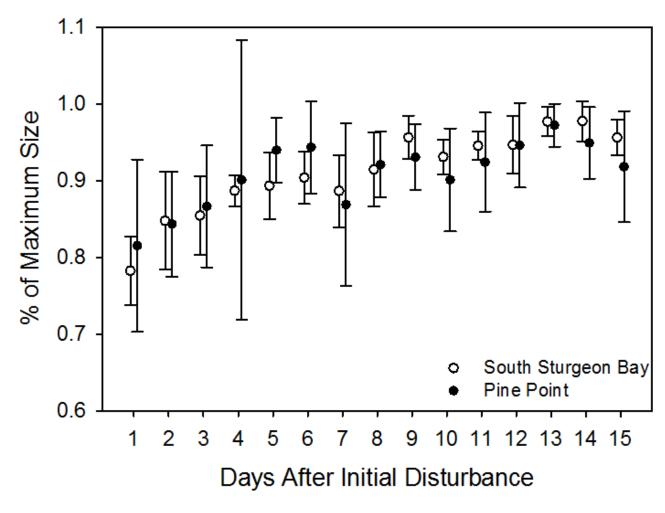


Fig. 5. Average percent of maximum pit size reached for Pine Point and S. Sturgeon Bay antlions at each day measured. Points represent the mean for each test group, and lines display 95% confidence intervals.

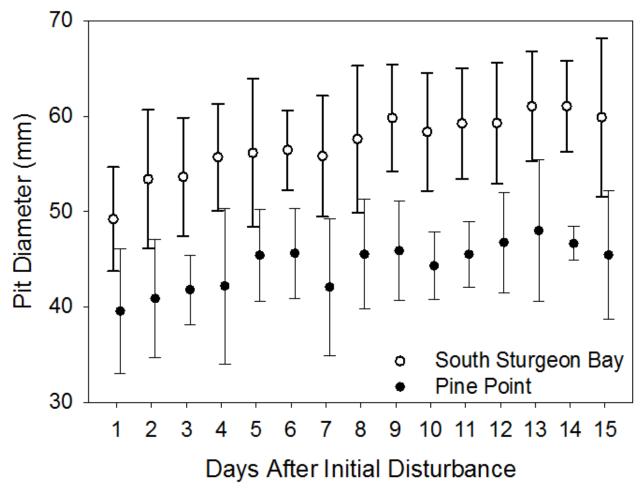


Fig. 6. Average pit diameter constructed for Pine Point and S. Sturgeon Bay antlions in the lab after each day measured. Points represent the mean for each test group, and lines display 95% confidence intervals.

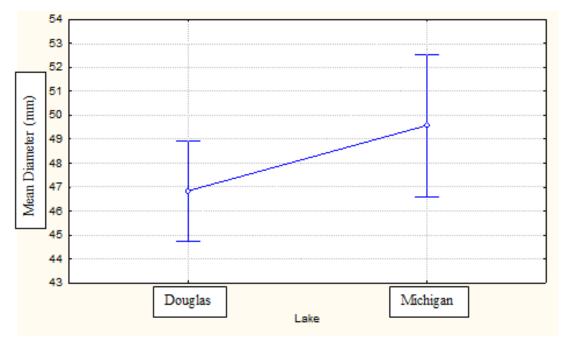


Fig. 7. Least squared means for Douglas Lake antlion pit diameters and Sturgeon Bay (Lake Michigan) antlion pit diameters. Points represent means; lines represent 95% confidence intervals.

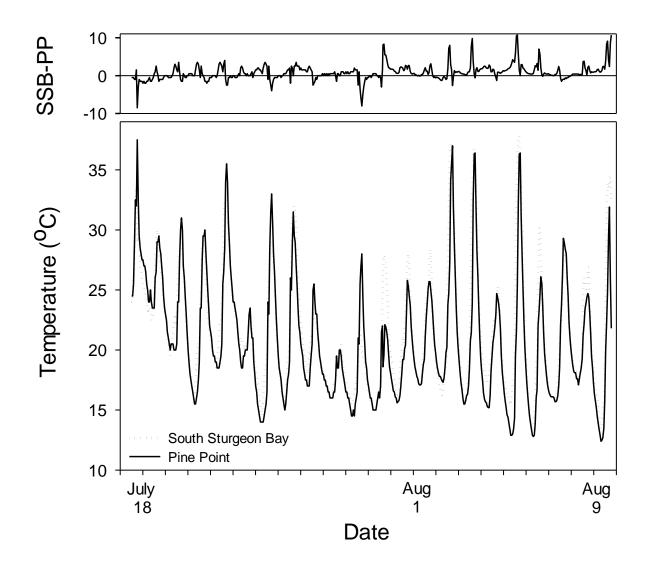


Fig. 8. Temperature data collected during experiment. SSB-PP represents the trend in temperature differences between the sites.