A Common Garden Experiment Comparing Antlion Pit Sizes at Douglas Lake and Sturgeon Bay: Genotype by Environment Interactions

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*This was a group experiment done by myself as well as Heather Williams and Natalie Blackwood, but this is my report of the data collection and analysis.

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Abstract

Genotype by environment interactions are important to consider in the total phenotypic variance of an organism as well as genetic variance and environmental variance separately. Phenotypic plasticity is likely to occur when the environment changes due to these genetic and environmental effects. A genotype by environment interaction shows that different genotypes change based on different environment conditions. Our experiment focused on antlions (*Myrmeleon immaculatus*). Antlions are invertebrates that build conical sand pits and wait for their prey at the bottom of the pit. We conducted a common garden experiment comparing two sites in Michigan: Pine Point at Douglas Lake (PP) and South Sturgeon Bay at Lake Michigan (SSB). We wanted to know if intrinsic factors, the environment, or the interaction between the two were more influential on the size of the pit built. We hypothesized that pit size would be different in the same environment because intrinsic factors, such as learning or genotype, play a greater role than environmental factors. Specifically, we postulated that SSB antlions would build bigger pits than PP antlions. From our data, we found that the antlions built different sized pits based on their site of origin. In general, SSB antlions built bigger pits than PP. Our hypothesis was supported because the intrinsic factors influenced pit size more than the environmental factors of current location.

Introduction

Phenotypic plasticity, or the ability of an organism to change its phenotype in response to changes in the environment, takes into account many different aspects of biology including genetics, development, ecology and evolution (DeWitt & Scheiner, 2003). In the genome, alleles interact differently in relation to the environment; favorable alleles remain in the population while the others go extinct (DeWitt & Scheiner, 2003). Variance in genes and the environment should be taken into consideration when comparing the total phenotypic variance, but a more important effect needs to be involved as well: a genotype by environment interaction (DeWitt & Scheiner, 2003). A genotype by environment interaction states that the environment's effect on some genotypes is different than others (DeWitt & Scheiner, 2003). Variance in an organism can never be fully plastic or genetic because both interact to create a phenotype unique to that individual (DeWitt & Scheiner, 2003).

The costs, benefits and limits of phenotypic plasticity play an important role and are essentially very different. The benefit of plasticity is the ability to produce a better phenotype-environment match across more environments than would be possible by producing a single phenotype in all environments (having low or no plasticity) (DeWitt et al., 1998; Levins, 1968). Constraints generally exist because the best trait in every environment pays a cost. The costs are indicated in a specific environment when the plastic organism has a lower fitness while producing the same trait as a fixed organism (DeWitt et al, 1998). The limits of plasticity are different than the costs; a limit is present when the plastic organism cannot produce the optimum trait that the fixed organisms can (DeWitt et al., 1998).

Phenotypic plasticity has been modeled differing on just how the genes and the environment relate (Scheiner, 1993). The first is overdominance of that plasticity as a function of homozygosity where the amount of change in phenotypes across environments in a decreasing function (Scheiner, 1993). The second is pleiotropy of that the same gene having different expressions depending on the environment (Scheiner, 1993). The third is epistasis or that genes interact and change the average expression of a character which is a response to environmental effects (Scheiner, 1993).

In our common garden experiment, we wanted to determine if differences in behaviors existed in relation antlions for pit size. Antlions (*Myrmeleon immaculatus)* are generally sit-and-wait predators that capture arthropod prey using conical sand pits. Pits are constructed to maximize prey capture, while prey capture is important for the growth and reproduction of the antlion (Arnett & Gotelli, 2001). Our hypothesis is that pit size will be different in the same environment because intrinsic factors, such as learning or genotype play a greater role than the environment. The interaction between genotype and environment (GxE interaction) can tell us whether all genotypes show the same response to environmental variation or not (DeWitt & Scheiner, 2003). If the GxE interaction is present, selection for a specific relationship between phenotype and environment is likely to occur (DeWitt & Scheiner, 2003). Thus, all of the antlions should produce certain pit sizes depending on the environment. If we see the same size pits at the same site, then we can infer that the environment plays a greater role than intrinsic factors (learning or genetics). But if the antlions from the different sites build different sized pits at the same site, we could infer that intrinsic factors are playing a greater role than the environment. In addition, we postulated that South Sturgeon Bay antlions would build bigger pits than Pine Point antlions.

The phenotypic effect of different pit sizes could be a due to intrinsic factors or environmental factors. Intrinsic factors such as learning and genotype can be tested if the environmental factors are all controlled. Environmental differences can be tested at the same time by narrowing down specific factors, such as temperature. Differences such as prey density, temperature, weather, substrate size, or crowding could all be studied.

We know that environmental factors play an important role in the size of the pit the antlion builds (Arnett & Gotelli, 2001; Devetak et al., 2012; Scarf et al., 2009). But intrinsic factors have been studied more recently in antlions (Klokocovnik et al., 2012; Lomascolo & Farji-Brener, 2001; Scharf et al., 2010; Tsao & Okuyama, 2012). Our experiment is needed to determine what factors play a greater contribution to the pit diameter. Using the common garden experiment, we should be able to see differences in pit diameter across both sites and should be able to attribute those differences mostly to either the environment or intrinsic factors. If our hypothesis is supported, pit sizes will be different at the current site and we can attribute the similarities to intrinsic factors.

Materials and Methods

Common Garden

For our common garden experiment, we went to two different sites: Sturgeon Bay at Lake Michigan in Wilderness State Park, northern Michigan (SSB) and Pine Point at Douglas Lake at the University of Michigan Biological Station in Pellston, Michigan (PP). The two sites were vastly different. The first site (South Sturgeon Bay) was on the side of a sand dune perpendicular to the lake off the shoreline. The second site (Pine Point) was off a much smaller lake on a plot of sand and dirt that had more coverage by trees. Our experiment lasted a total of two weeks, starting on July 18th and ending on August 1st, 2013. We had a total of five experiment days and four feeding days.

We had four groups and two groups started at their home site while the other two groups started at the opposite site. At each site, we measured the weight and pit diameter for a total of 30 at each site and a grand total of 60. The weight range that we accepted to be in the experiment was between 13 and 40 milligrams to get a normal distribution to weight. First, we went to Douglas Lake and after the pit diameter and pit depth were measured using uncooked spaghetti noodles and calipers, we returned 15 antlions to their home site in separate 11.5 cm x 8 cm cylindrical tubs with a mesh bottom to create a separate uniform habitat for easy data collection. The other 15 antlions were transferred to South Sturgeon Bay. Then we collected 30 antlions from South Sturgeon Bay, left 15 and took 15 back to Douglas Lake. The four groups we made on the first day were SSB at SSB, SSB at PP, PP at PP, and PP at SSB. After four days, we came back to each site, fed the antlions, measured their pit sizes and transferred them to the opposite location. After another three days, we came back to each site and measured the weight and pit diameter. Since the first measurement was taken at four days, we came back and measured the pits at each site the next day as well. The following week, we came back to both sites and measured pits again because of inclement weather with a drop in temperature. This ensured that we were obtaining an accurate reading of pit size. To minimize differences in prey density, we fed all the antlions with a pit at the same time on the fourth day. Each antlion could be fed a maximum four times if they had a pit built each time we sampled.

In the past, substrate density was found not to have a major influence on pit size at these two specific sites (per unpublished info. D. Anderson, 2009), so the sand that we used was sifted from the

University of Michigan Biological Station Beach on Douglas Lake using a one millimeter sieve to create uniform sand; any error due to the substrate was potentially prevented.

We also built a cover made of plastic roofing and a 5' by 6' by 15'' platform to protect the antlions' pits from being destroyed from the rain. After some rain, we made appendages to the protective cover; we added a 5'' mesh cover that was added to the bottom of the plastic rim to protect against any rain splattering. We also dug motes around the large plastic structure, again for less environmental differences from the rain. Human interaction was also limited by protective covers.

To take into account edge effect and slight differences in the immediate environment, we placed the antlions in a uniform five by six array and alternated the antlions according to their home environment (Figure 1).

The microenvironment at each site could be slightly different in temperature and weather, so we tracked temperature using data loggers to see differences in location. We placed five data loggers at each site. They were evenly distributed with one in each corner and one in the center, buried at the same depth that the antlion built its pit (labeled as Center (C), North East (NE), North West (NW), South East (SE), and South West (SW)).

To account for a possible difference in pit size, we also collected five antlions from each site and placed them in the same 11.5 cm x 8 cm cylindrical tubs and in the same one millimeter sifted sand under a uniform environment in the Creaser classroom at the University of Michigan Biological Station to see if the antlions reached a maximum pit size and then stopped building and to also see if they maintained their pit size over a certain period of time. We measured these every day for 15 days, and we fed them during the same time we fed the experimental group (every three to four days for a total of four times if they still had a pit) but without disturbing them after.

From the results, we found that we needed to test to see if antlions at Pine Point and South Sturgeon Bay were behaviorally similar to other antlions found around Douglas Lake and Sturgeon Bay respectively. On the same day, we went to a total of seven different locations where antlions are found. We sampled four sites around Douglas Lake (DL) and three sites around Sturgeon Bay (SB). At each site, (using the same methods for measuring as before) we measured the pit diameter, and took the weight for 20 – 30 antlions at each site, and then returned them to their location.

Data Analysis

To start statistical analysis, we tested for normality for weight and pit diameter for all four site conditions (for a total of 16). Both weights and pit diameters were not normally distributed. We then constructed a boxplot comparing weight with the site of origin, the first site, and the pit number (Figure 2). The SSB antlions starting at SSB were significantly larger than any of the other test groups. To account for these weight differences, we used a small range of overlap in weight depending on the groups that we compared. We first ran the homogeneity of slopes model. Then we ran individual analyses of covariance (ANCOVA) at each site. First, we contrasted site of origin, and controlled for the current site and pit number. Then, we contrasted current site, and controlled for site of origin and pit number. We used a small set of weight ranges for each test (for a total of eight separate tests).

For the ten antlions in the control group, we first tested for normality for the two sites to see if they passed the test of normality. Since the sample size is so small, we didn't expect the normality to pass, but since the test is robust, we can continue. We then did a Repeated Measures ANOVA of pit diameter. We also calculated the approach to maximum pit size.

For the day that we sampled seven different sites, four at DL and three at SB, we first separated the ranges in to two weight classes (20-29 mg and 30-39 mg) for the distribution to be normal. We then ran a nested univariate test with site nested in lake.

Results

First, we tested for normality for the weight and pit diameter for all groups. All groups passed the test except for the PP antlions at SSB for pit number 1 (weight p=0.002, pit diameter, p=0.023 respectively) and for the PP antlions at SSB for pit number 2 (weight p=0.011). Since the violation of the untransformed data is minor, we continued to run the tests. We started by contrasting the site of origin and controlling for the current site and the pit number. First, we found that the homogeneity of slopes assumption passed. Then we ran the ANCOVA and found a significant weight effect for one group (the PP antlions at PP and the SSB antlions at PP for pit 1) (p=0.004). The site of origin effect was not significant for any of the groups (refer to Table 1). By calculating the Least Squares Means for the four individual ANCOVAs, we found a general trend that antlions from SSB all had larger pit diameters than antlions from PP (p=0.0625) (Figure 3). Then we ran the homogeneity of slopes by contrasting current site and controlling for site of origin and pit number. No interaction between groups was shown, so we ran the ANCOVA (four individual times). We found a weight effect for three out of four groups (refer to Table 2). The interaction between current site and pit diameter was not significant for all four groups (Table 2). The Least Squares Means showed that two out of the four groups built bigger pits at Pine Point and the other two built bigger pits at South Sturgeon Bay (Figure 4). We are unable to make any conclusions on whether antlions build bigger pits at Pine Point or South Sturgeon Bay.

A drop in temperature during the second part of our experiment occurred, so we continued measuring the pits well into two weeks after the second transfer. We compared this with the control group to see what the optimum degree days were for each site. We found that SSB was generally warmer than PP. The average difference of time-matched points for SSB to PP was 0.818 (Figure 5).

The control group was important in determining how long it takes to build an optimal-sized pit, and if they were different between sites. First, we ran a test of normality for the control groups. We found that even though the sample size was small, the majority of the groups passed the test. We continued because the test of normality is robust. We ran a Repeated Measures ANOVA for pit diameter and found a significant site effect ($F_{(1,7)} = 5.76$, $P = 0.048$) (Figure 6). We also calculated the percentage of the maximum pit built on each day and found that the percent increase was generally the same (Figure 7).

For sampling the seven different sites, after splitting them into weight groups, we found that they passed the test of normality. After running the nested univariate test with site nested in lake, we found no significance difference between lakes or the site effect nested within the lake (lake p=0.144; site(Lake) p=0.658) (Figure 8). The effect of lake appears to have a stronger effect than that of site (but again, not significant). All the pit diameters were similar, except for SSB (from the common garden experiment). All the data from this test show that SB pits are wider than DL pits, but not significantly so and the effect is due to the SSB site. The distance between the SB groups and the DL groups was 26.97 km (refer to Table 3 and 4 for Latitude and Longitude and the distance between sites).

Discussion

Our data support our hypothesis that intrinsic factors play a greater role in determining the pit diameter than the environment. All of our findings point to intrinsic factors playing a larger role in pit diameter length. The first trend that we found was that SSB antlions built bigger pits than PP antlions. This tells us that origin does matter.

Our later experiment comparing behavioral differences between Douglas Lake antlions and Sturgeon Bay antlions did not support the fact that origin matters at all sites because all of the SB antlions were behaviorally similar to the DL antlions (i.e. built similar sized pits) except for the SSB antlions. Gene flow between the sites must be too great so the genetics of these animals are very similar. So, we do know that the SSB antlions are behaviorally different than the PP antlions from these results.

Since our current site data showed that current site did not determine pit diameter, we know that the environment did not play as large a role as intrinsic factors. Our data from the lab experiment showed that SSB antlions built significantly bigger pits than PP antlions. This again leads to intrinsic factors being the major cause of the differences in pit diameter. We also found from these data that the rate of increase for pit diameter is virtually the same for all antlions, and the optimal sized pit is built within 3-5 days for all antlions.

Intrinsic factors play a major role in our findings. Both genetics and learning play different roles. The variation in individuals can be seen in genetic variability and exposure to environmental interaction. Gene by environment interactions occur on a continuous scale and often either genes or the environment influence the individual more than the other. Heritability can never be 100% since all organisms are influenced by both intrinsic factors and the environment.

Intrinsic factors can be broken down into two major factors: learning or conditioning and genetics. The genotype plays a major role in influencing the behaviors and cognitive abilities of every organism (Gerlai, 1996; Roth et al., 2010). But behavioral traits are fairly complex, often variable, and are influenced by a large number of genes as well as environmental factors (Gerlai, 1996). To understand complex behavior in the genotype, including learning and memory, it's important to understand the web of interactions among mechanisms and to control as many variables in the genotype as possible (Gerlai, 1996). Background genes can have confounding effects as well as the original genes influencing the behavior so it's hard to determine which genes are influencing the behavior (Gerlai, 1996). Although genetics play this important role, learning can also play an important role in behavioral flexibility over time.

Behavioral flexibility and learning occur in many situations in an antlion's life. Learning when to relocate their pit, when to jerk sand out of their pit, and determining quality of prey for example. Behavioral flexibility can occur during relocation of the pit (Scharf et al., 2010). After a sudden complete cessation of prey arrival, individuals often relocate their trap, while a gradual reduction does not necessarily trigger this behavior (Scharf et al., 2010). Pit relocation is not a fixed response but rather a learned response to environmental changes (Scharf et al., 2010). A recent study done by Tsao & Okuyama (2012) found potential negative effects when antlions aggregate together (e.g., heightened competition and predation risk). They found a unique ESS where antlions learned from their past foraging experiences because the spatial distribution of prey was not completely random (Tsao & Okuyama, 2012). The results suggest that pit aggregations are formed because antlions reduce their relocation tendency when neighbors exist thus expending less energy (Tsao & Okuyama, 2012).

During pit construction, antlions jerk sand out of their pit to build it. A study found that jerk frequency was negatively correlated with sand particle size and also changed during pit construction (Klokocovnik et al., 2012). Their results demonstrate that variation in pit size under differing environmental conditions stems directly from behavioral plasticity in this species (*Euroleon nostras*) (Klokocovnik et al., 2012).

Antlions are capable of quickly adapting to different types and availability of prey (Lomascolo & Farji-Brener, 2001). This behavior could have been selected as a strategy to survive in poor environments with unpredictable prey availability (Lomascolo & Farji-Brener, 2001). Previous studies have suggested that the ability to inhabit harsh environments may be linked to advanced learning traits (Roth et al., 2010).

Conditioning when the antlions are younger has a greater effect on how they build their pit when they are older. Variations in nutrition and temperature have variable effects on weight, the interval to cessation of growth and growth rates, thus influencing final adult size (Chown & Gaston, 2009). This response to selection is important in determining fitness (Chown & Gaston, 2009).

Both body size and pit size are likely to be under both local and more general proximate control (Chown & Gaston, 2009). At any age, growth depends on food and nutrition density (Chown & Gaston, 2009). Food availability during juvenile stages may be especially important for future growth and reproductive success (Chown & Gaston, 2009). Stressful conditions also condition an antlions behavior (Chown & Gaston, 2009). Changes in size, particularly later reductions, might also have been mediated by changing mortality risks that must have been encountered by juvenile stages (Chown & Gaston, 2009).

While intrinsic factors play a very important role in determining pit size, the environment also plays a role, just not as much as in previous years. The antlions from our experiment could have adapted their pit size to differences in the climate, specifically temperature and rainfall, but no significant result showed that weather was the major cause since differences in pit size between sites were significant.

Climate is a major factor in the environment and has been found to affect insect life span and body size (Scarf et al., 2009). Differences in fecundity and survival are affected directly and indirectly through body size (Scharf et al., 2009).

Since rain destroys pits, antlions must choose a time when to rebuild with enough energy to catch more prey for survival. The plastic cover structures that we used were specifically used to prevent the rain from destroying pits and negatively influencing the pit sizes.

It has been found that temperature (in relation to elevation) influences the tradeoffs between allocation to growth and physiological adaptation in response to cold temperature. Low-elevation provenances allocate more resources to growth and competitive ability whereas high-elevation provenances have evolved in a colder climate under which selection has favored allocation for greater general robustness, including cold tolerance (Loehle, 1998; Körner, 2012). Overall, the pattern of slower growth rate in populations originating from colder climates has been supported (Vitasse, 2012).

Overall, our experiment supported our hypothesis that intrinsic factors play a greater role in determining pit size than environmental factors. But what the differing environments showed was that a gene by environment interaction was occurring. Although we are unable to determine whether genes or learning influence behavior more, previous studies have shown that while genetics are important, learning can also influence behavioral decisions in invertebrates. Future work could be done on learning and just how antlions are conditioned in their juvenile stages.

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Tables

Table 1. Contrast the site of origin while controlling for the current site and pit number.

Origin	Current Site	Pit Number	Min.	Max.	Overlap	Pass the Homogeneity of Slopes? (P values)	ANCOVA weight effect (P values)	ANCOVA category effect (P values)
PP	PP	1	17	34	17-34	0.95	0.004	0.58
SSB	PP	1	13	39				
PP	SSB	1	13	40	14-39	0.05	0.14	0.28
SSB	SSB	1	14	39				
PP	PP	2	17	62	17-36	0.34	0.014	0.09
SSB	PP	2	13	36				
PP	SSB	2	14	42	16-42	0.98	0.000007	0.58
SSB	SSB	2	16	58				

Table 2. Contrast the current site while controlling for the site of origin and pit number.

Origin	Current Site	Pit Number	Min.	Max.	Overlap	Pass the Homogeneity of Slopes? (P values)	ANCOVA weight effect (P values)	ANCOVA category effect (P values)
PP	PP	1	17	34	17-34	0.42	0.002	0.87
PP	SSB	1	13	40				
SSB	PP	1	13	39	14-39	0.098	0.17	0.22
SSB	SSB	1	14	39				
PP	SSB	2	14	42	17-42	0.81	0.000111	0.43
PP	PP	2	17	62				
SSB	SSB	2	16	58	16-36	0.41	0.000249	0.429
SSB	PP	2	13	36				

Table 3. Latitude and Longitude for the seven sites sampled across lakes.

Sites across lakes	Latitude and Longitude
DL 1	N45.56140 W84.667948
DL 2 (PP)	N45.56607 W84.66029
DL 3	N45.57241 W84.66008
DL 4	N45.58540 W84.65416
SB 1 (SSB)	N45.68117 W84.97897
SB 2	N45.68465 W84.97179
SB 3	N45.70500 W84.95224

Table 4. Distance between sites.

	DL1	DL2	DL3	DL4	SB1	SB2	SB3
DL1		0.79 km					
DL2			0.71 km				
DL3				1.52 km			
DL4							
SB1						0.68 km	
SB2							2.73 km
SB3							

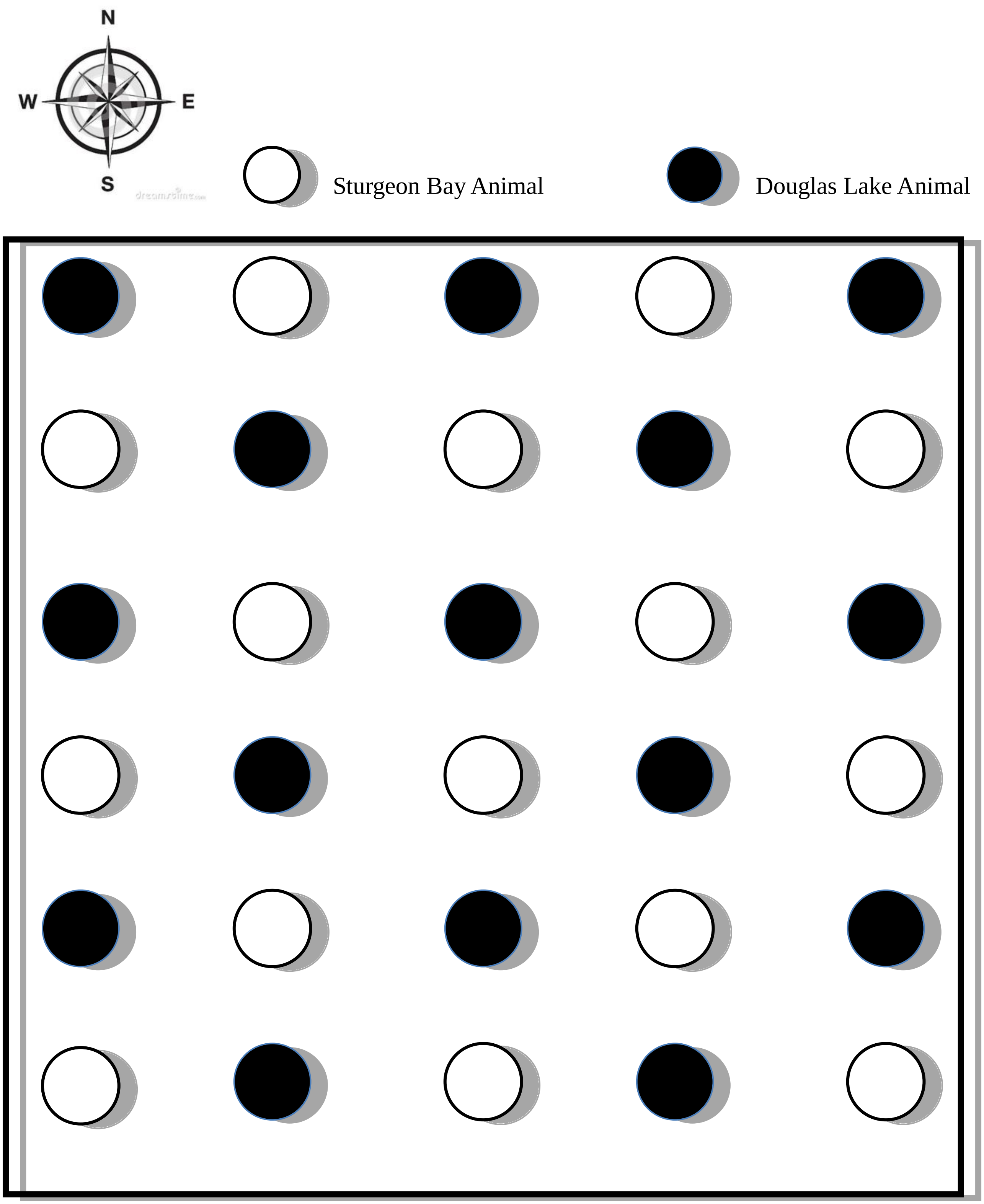

Figure 1. The common garden 5 x 6 array that was the same for both sites.

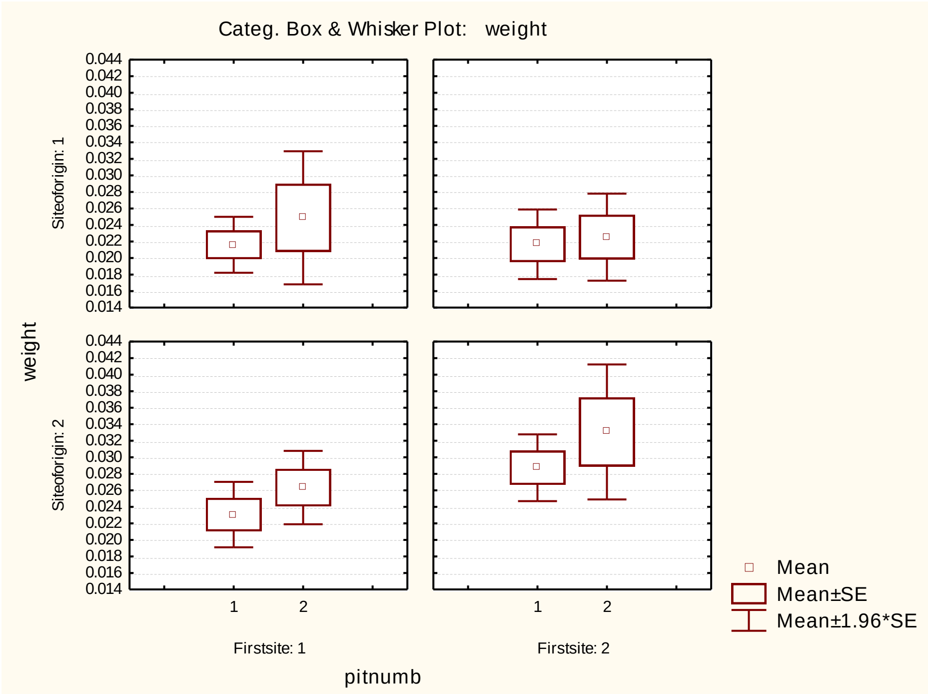

Figure 2. Boxplot for weight comparing the site of origin, first site location, and pit number.

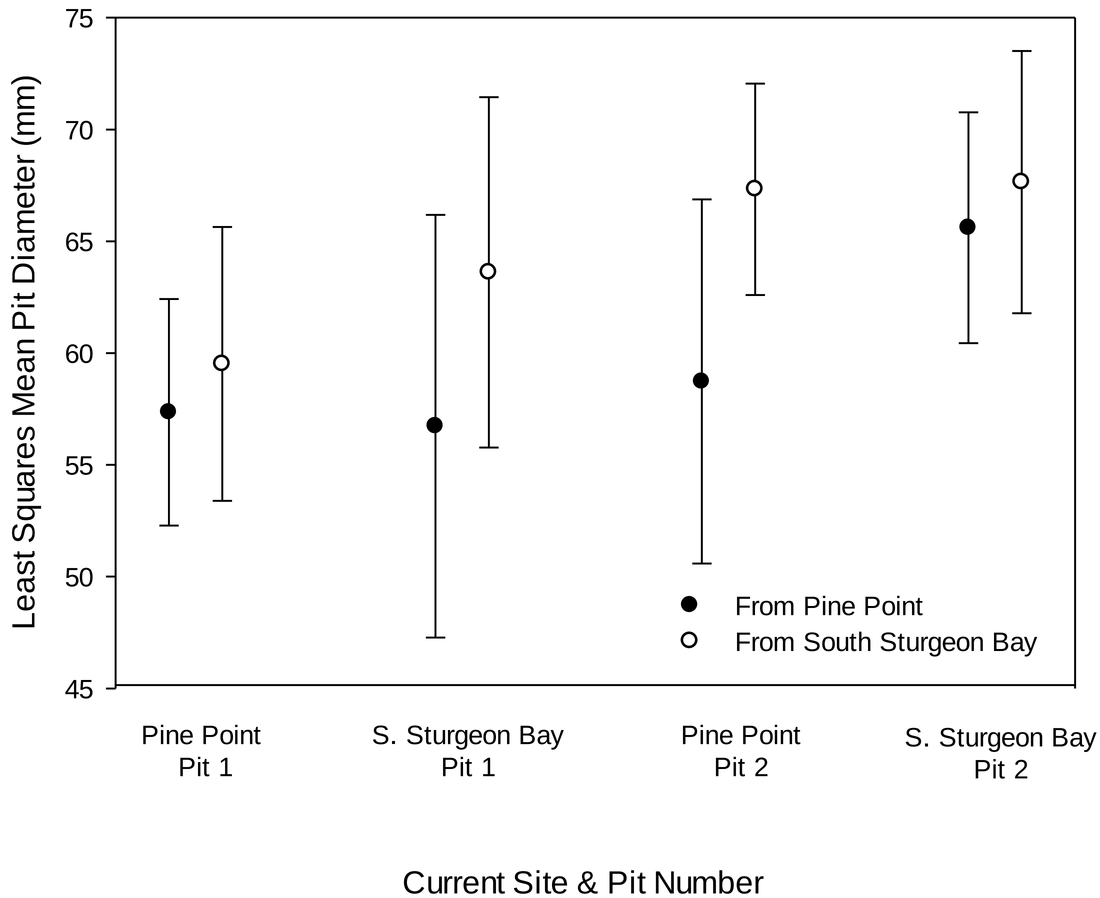

Figure 3. The Least Squares Means of Pit Diameter for differences in origin (from PP or from SSB), controlling current site and pit number.

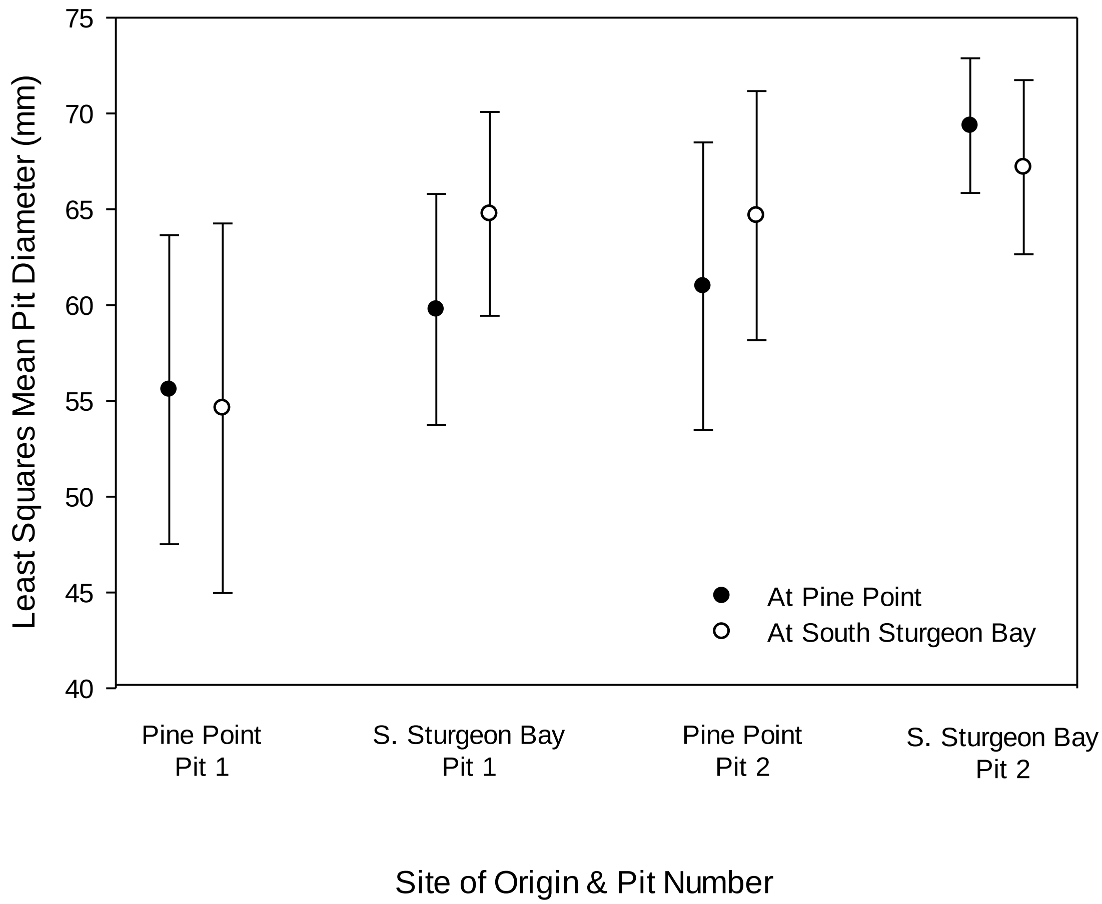

Figure 4. The Least Squares Means of Pit Diameter for differences in current site (at PP or at SSB), controlling origin and pit number.

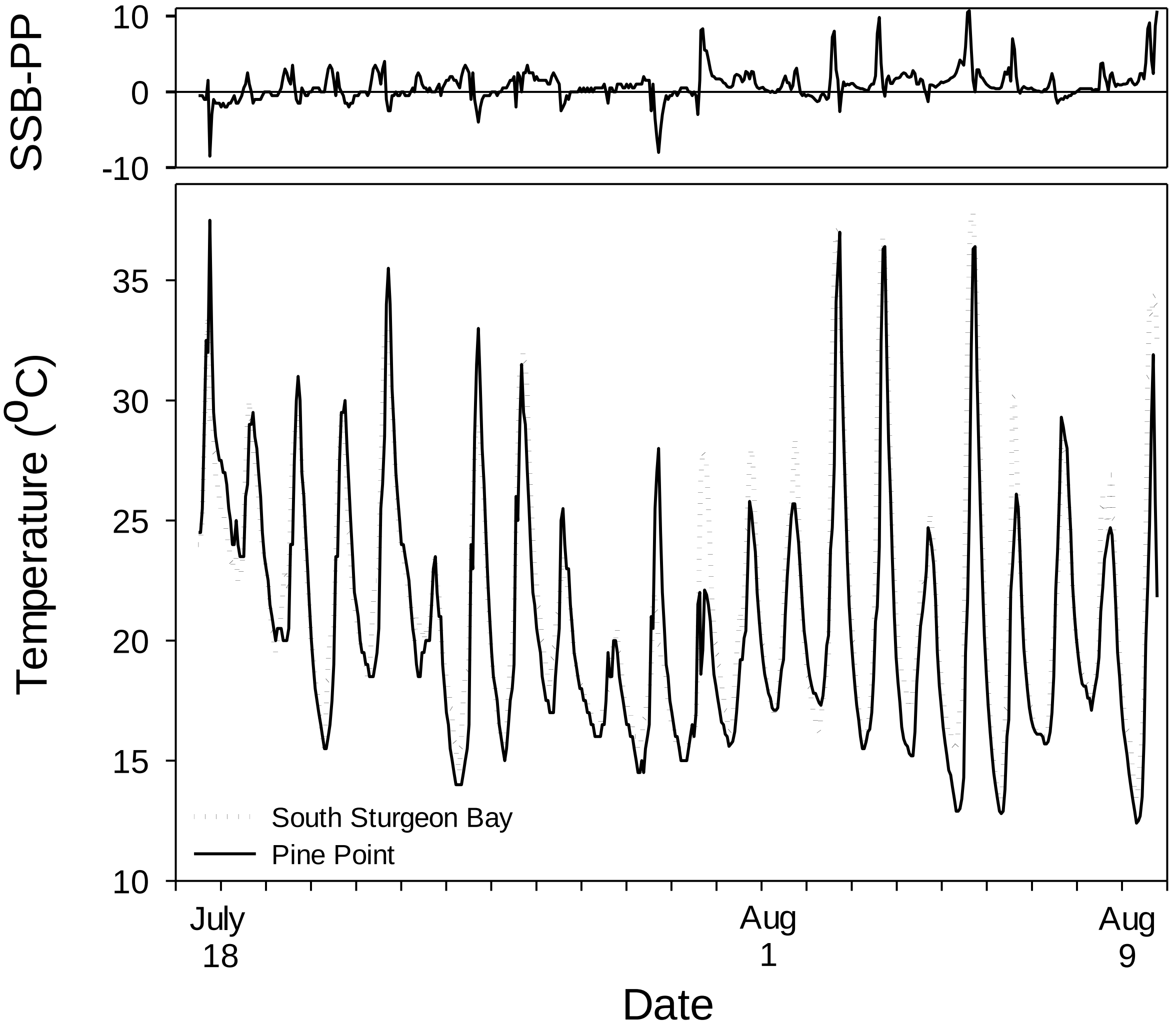

Figure 5. Temperature data from July 18th to August 9th. The average difference of time-matched points (SSB-DL) is 0.818, 95% CI = 0.176.

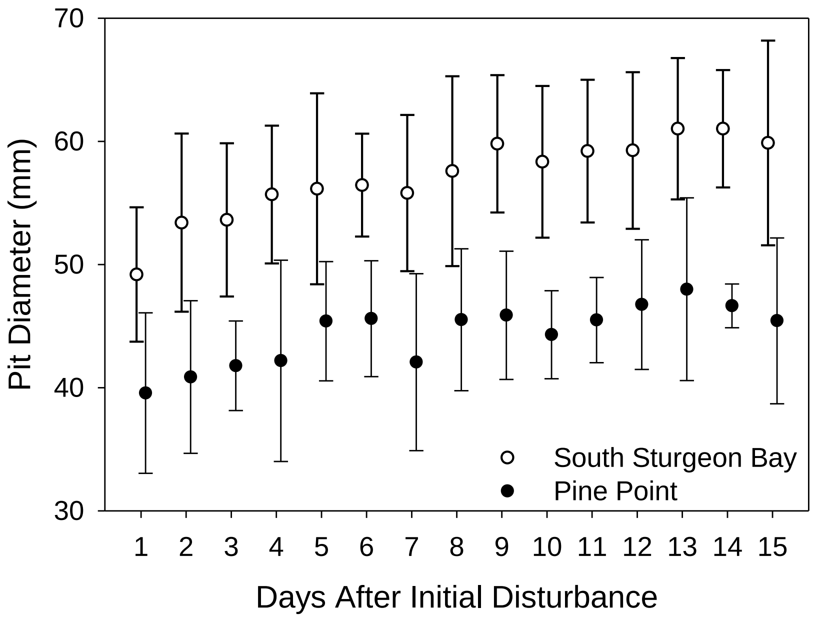

Figure. 6. Repeated Measures ANOVA of Pit Diameter
Site effect: $F_{(1,7)} = 5.76$, $P = 0.048$.

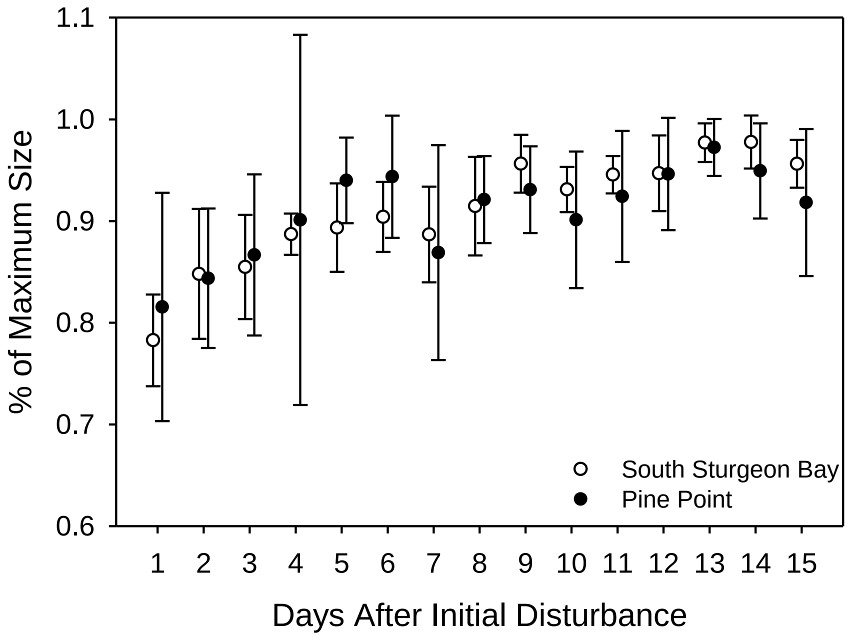

Figure 7. Lab experiment comparing the percent of maximum size pit by days after the initial disturbance for Pine Point and South Sturgeon Bay antlions.

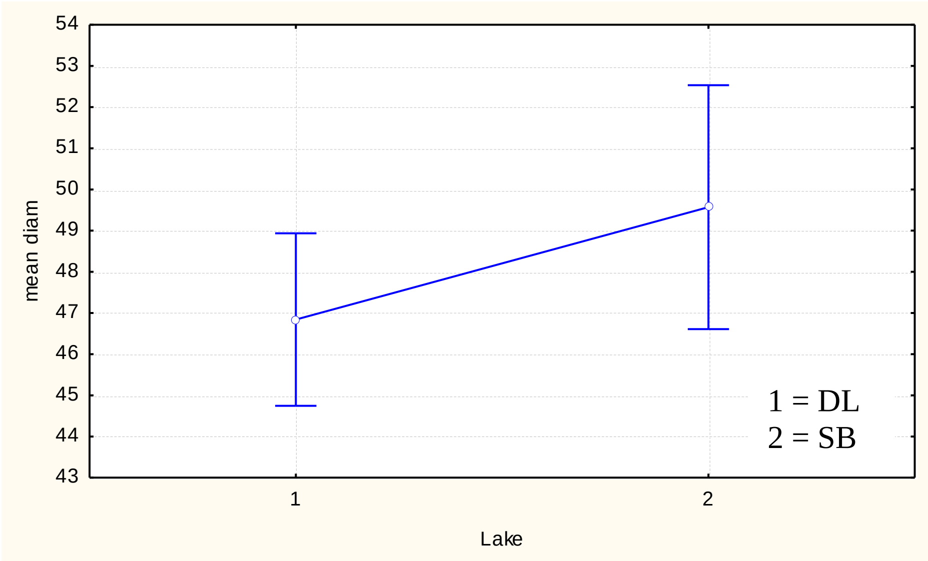

Figure 8. The Least Squared Means for the current effect of lake ($F_{(1,107)}$ = 2.16; P =0.144).