

Can Antlions Discriminate? : Testing the Limits of Associative Learning in  
Antlion *Myrmeleon immaculatus*

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<sup>\*</sup>The conception, implementation, and analyses described herein were conducted in a group setting with three other students: Ashley Rose, Zoë Allen-Wickler, and Ryan Eskuri. All writing is my own.

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## Abstract

Despite the abundance of literature on associative learning in insects, the ability of insects to learn to discriminate between different stimuli through associative learning remains largely unstudied. Antlion *Myrmeleon immaculatus* larvae construct steep conical pitfall traps in the sand that they use to capture prey. Previous studies have **show** that *M. immaculatus* larvae can learn to associate vibrational stimuli with food through conditioning. In this study, we attempt to **replicate** these results and determine whether *M. immaculatus* larvae can learn to discriminate between different vibrational stimuli. We failed to demonstrate any associative learning capacity in our larvae, hypothesizing that this failure is due to our experimental design. I discuss recommendations for future studies on discriminatory learning in antlions.

## Introduction

The insect family Myrmeleontidae (Neuroptera) contains about 2,000 species (Scharf & Ovadia, 2006) collectively referred to as antlions. Antlions spend most of their lives as larvae, constructing steep conical traps in sand to capture nearby arthropods for food (Lucas, 1989; Arnett & Gotelli, 1999; Scharf & Ovadia, 2006). Antlions tend to build these traps at the angle of repose of their substrate, making it harder for their prey to escape (Botz et al., 2003). Because building and maintaining these pits is energetically costly (Lucas, 1985), antlions have developed strategies to minimize energy expenditure and maximize capture success. For example, when a prey item enters an antlion pit the antlion will respond by flinging sand up from the bottom of the pit, causing sand on the sides of the pit to slide down and making it harder for the prey to escape.

A number of factors influence antlion foraging strategy. Arnett & Gotelli (2001) found that food availability, temperature, and population source all influenced antlion pit-building decisions. Pit relocation is influenced by the placement of nearby antlions (Linton et al., 1991; Tsao & Okuyama, 2013), food availability, disturbance (Griffiths, 1986), and exposure to sun (Scharf et al., 2008). Antlions can detect the presence and direction of prey using substrate vibrations (Fertin & Casas, 2007; Mencinger-Vračko & Devetak, 2008) and can learn to associate vibrational cues with food (Guillette et al., 2009; Hollis et al., 2011).

As Hollis et al. (2011) note, the fact that sedentary antlions are capable of associative learning is somewhat surprising, as most insects capable of learning do so to actively search for food or to avoid undesirable situations. Bumblebees, for example, can learn to rob nectar by observing other bees, including those of another species (Goulson et al., 2013). Parasitoid wasps can learn a number of cues, some of which help them locate suitable hosts (Hodjes et al., 2011). Several insects are capable of olfactory learning, such as cricket *Gryllus bimaculatus* (Matsumoto & Mizunami, 2000), *Camponotus* ants (Dupuy et al., 2006), moth *Maduca sexta* (Daly & Smith, 2000), *Drosophila* flies (Fiala, 2007), locust *Schistocerca gregaria* (Simões et al., 2011; Simões et al., 2012), and coccinellid beetles (Glinwood et al., 2011). Some insects are also capable of visual learning, including locust *Locusta migratoria* (Raubenheimer & Tucker, 1997), grasshopper *Melanoplus sanguinipes* (Bernays & Wrubel, 1985), and butterfly *Agraulis vanillae* (Weiss, 1995). Vibrational learning in insects other than antlions is much less studied, though results from Buehlmann et al. (2012) show that desert *Cataglyphis* ants can learn and navigate by vibrational cues. Learning has also been associated with increased fitness in certain insects (Dukas & Bernays, 2000; Dukas & Duan, 2000), including antlions (Guillette et al., 2009; Hollis et al., 2011), and can affect mating behavior (Villagra et al., 2005; Kujtan & Durkas, 2009).

Although Guillette et al. (2009) and Hollis et al. (2011) demonstrated that antlions are capable of vibrational associative learning, the extent of this capability remains unclear. For example, some insects can learn to discriminate between different stimuli. Female *Leptopilina heterotoma* wasps can learn to discriminate between different odors (Vet et al., 1998), as can honeybee *Apis mellifera* (Vergoz et al., 2007). *A. mellifera* can also discriminate between

different visual stimuli (Giurfa, 2004; Avarguès-Weber et al., 2010). However, of the few studies on vibrational learning in insects, none to date have studied whether insects can discriminate between different vibrational stimuli.

In the present study, we seek to determine whether *Myrmeleon immaculatus*, an antlion common throughout southern and eastern United States (Arnett & Gotelli, 1999), is capable of associative learning with vibrational stimuli and, if so, whether it can differentiate between two different vibrational stimuli. To do this, we will set up three treatment groups: A, B, and Control. Each group will receive food (one non-formic acid-bearing ant) every day in either the night or morning, assigned randomly each day. Group A will receive Stimulus 1 – vibrations from a single large metal nut falling – immediately before being fed, providing an opportunity to associate an irrelevant stimulus with a reward. Group B will receive both Stimulus 1 and Stimulus 2 – vibrations from three smaller metal nuts falling in succession – with half of Group B being fed only after Stimulus 1 and the other half being fed only after Stimulus 2. The Control Group will receive Stimulus 1 but be fed independently of it. The Control Group should be unable to associate the stimulus with the reward, and should therefore not display associative learning.

After conditioning, we will perform assays on the antlions by presenting them with stimuli and seeing if they respond in anticipation of food by flinging sand. Our first comparison will be between Group A and Control antlions. We hypothesize that, consistent with past studies, Group A antlions will have learned to associate the vibrational cues from Stimulus 1 with food and therefore fling sand in anticipation of food more than Control antlions. We also hypothesize that Group A antlions, having never been exposed to Stimulus 2, will be unable to discriminate between the two stimuli and will therefore fling sand in response to Stimulus 2 as frequently as they did to Stimulus 1. Finally, we will test whether antlions in Group B can discriminate between Stimulus 1 and Stimulus 2 by comparing the number of responses to the stimulus that preceded food to the number of responses to the stimulus that did not precede food, with our null hypothesis being that they will be incapable of discriminating between the two. Hollis et al. (2011) note that the sand-tossing by antlions conditioned to associate vibrational stimuli with food benefit the antlion by dislodging prey or triggering an avalanche that does so, making it easier for the antlion to capture its prey. Presumably, the benefits of this behavior outweigh its significant energetic costs (Hollis et al., 2011) only when prey is present, justifying our use of sand-tossing as a behavior indicative of successful learning. If antlions have not learned to associate a stimulus with a reward, they should be expected to conserve their energy and not toss sand.

## Materials and Methods

We collected 72 *M. immaculatus* larvae with masses between 8mg and 61mg from Douglas Lake, Pellston, Michigan (45°34'21"N, 84°39'32"W) and grouped larvae with like masses in triplets (Group A, Group B, Control Group) to control for any effects of mass. We constructed our setup by taking 36 open-topped wooden boxes measuring 34.0cm long by 22.4cm wide by 15.0cm deep and attached a sheet of aluminum flashing measuring 38.5cm long by 25cm wide to the top of each box using construction adhesive and washers to prevent any dampening effect from the flashing directly touching the box. We punctured the middle of each piece of flashing and passed a string through the hole, securing it to the underside of the flashing using duct tape and leaving exactly 1ft of string exposed on the topside of the flashing. We then placed all 36 boxes on a table in three rows of 12, one row for each treatment group. We placed one plastic cylindrical deli tub with approximately 700g of sifted Douglas Lake sand of grain size between 1mm and 0.5mm on each end of the flashing so that the outermost edge of the bottom of the tub was tangent to the middle of the short edge of the flashing. We then placed one antlion in

each tub, meaning that each box had a pair of tubs on it, each with one antlion. These antlions “pairs” were of the same treatment group and similar in mass. We waited three days after placing the antlions in their tubs before beginning the treatments so that the antlions had sufficient time to dig their pits. We did not feed any antlions in the week between when they were collected and the beginning of the treatments.

Before beginning the treatments, we divided Group B into two subgroups: B<sub>1</sub> and B<sub>2</sub>. B<sub>1</sub> and B<sub>2</sub> received both stimuli, but B<sub>1</sub> was fed after Stimulus 1 whereas B<sub>2</sub> was fed after Stimulus 2. We administered treatments at two times each day: 10 AM (morning) and 9 PM (night). Groups and subgroups were randomly assigned to either morning or night each day. Since treatments could only be administered to two antlions (one pair) at a time, we also randomly assigned, by box, the order in which the pairs received their treatments to control for order effects. For Stimulus 1, we dropped an 18.9g metal nut down the string to the middle of the flashing from a height such that the top of the nut was level with the top of string when raised perpendicular to the flashing. For Stimulus 2, we dropped three smaller metal nuts weighing an average of 4.7g each in succession with one second between consecutive drops. These nuts were not strung because their small size made it impractical. We dropped the nuts from such a height that the top of the top nut was level with the top of the string when raised perpendicular to the flashing over the center of the flashing.

For Group A, at one time of day we administered Stimulus 1 to a pair of antlions, waited 5s, then dropped one ant into each pit. We repeated this procedure for the rest of the pairs in Group A and did nothing with Group A at the other time of day. For subgroup B<sub>1</sub>, at one time of day we administered Stimulus 1 to a pair of antlions, waited 5s, then dropped one ant into each pit. We repeated this procedure for the rest of subgroup B<sub>1</sub> shortly after feeding the previous pair. At the other time of day, we administered Stimulus 2 to B<sub>1</sub> pairs but did not follow the stimulus with any food. For subgroup B<sub>2</sub>, at one time of day we administered Stimulus 2 to a pair of antlions, waited 5s after dropping the third nut, then dropped one ant into each pit. We repeated this procedure for the rest of subgroup B<sub>2</sub>. At the other time of day, we administered Stimulus 1 to B<sub>2</sub> pairs but did not follow the stimulus with any food. Finally, for the Control Group, at one time of day we administered Stimulus 1 to all Control Group pairs and fed all Control Group pairs at the other time of day. For an example of a daily schedule, see Figure 1.

We put the legs of the table on which the boxes sat on insulating foam to minimize the amount of vibration transferred from the ground to the boxes. To further minimize the amount of incidental vibration to which the antlions were exposed, we removed the dropped stimulus nut(s) from the flashing as gently as possible. If antlions were fed after a stimulus, we waited at least 10s after feeding the antlion before removing the nut(s). Finally, we accounted for interference past students using our research space have encountered by covering the legs of the table with **tanglefoot** and aluminum foil to prevent insects and rodents from interfering.

We continued our conditioning for 17 days and took one day to perform assays. During the first assay, we administered Stimulus 1 to all antlions and recorded their response. For the second assay, we administered Stimulus 2 to all antlions in groups A and B and recorded their response. For our first statistical analysis, we used a sign test to compare the number of times Group A antlions responded to Stimulus 1 compared to Control antlions. We also used a sign test to compare the number of times Group A antlions responded to Stimulus 1 as compared to Stimulus 2, to which they had never been exposed. Finally, we used a sign test to compare the number of times Group B antlions responded to the stimulus after which they were rewarded compared to the stimulus they received but were never rewarded for.

## Results

No antlions responded to any stimulus during assays.

## Discussion

Our results fail to support the hypothesis that antlions are capable of any associative learning, simple or discriminatory. While no research on discriminatory associative learning in antlions exists, our results on simple associative learning conflict with those from Guillette et al. (2009) and Hollis et al. (2011). Several plausible explanations for this exist, particularly the length of our conditioning period. In general, the length of conditioning periods in studies of insect associative learning varies greatly. Some insects, such as *Gryllus bimaculatus* crickets (Matsumoto & Mizunami, 2000) and *Shistocerca gregaria* locusts (Simões et al., 2011), can form limited associations from a single training session while others, such as the *Camponotus* ants studied by Dupuy et al. (2006), display learning after a number of training sessions. Guillette et al. (2009) trained their antlions over 25 days and Hollis et al. (2011) trained theirs for up to 70 days, though by 46 days half of the antlions in the experimental group had pupated. Our 17-day conditioning period was much shorter than either of these, which suggests that antlions take longer than 17 days to display associative learning. However, Guillette et al. (2009) only exposed antlions to 20 training sessions, as every fifth day during the conditioning period was designated as a rest day during which neither food nor stimuli were administered. These antlions were therefore exposed to only three more conditioning sessions than ours, suggesting that factors other than the number of conditioning sessions to which the antlions were exposed explain our differing results. Regardless, further studies should seek to determine the number of conditioning sessions necessary for antlions to display associative learning.

Another likely factor in our failure to replicate past results is our choice of stimuli. Both Guillette et al. (2009) and Hollis et al. (2011) used stimuli that likely resembled stimuli that would typically accompany prey in a natural setting. Both studies administered their stimuli by dropping sand onto a drumhead-like plastic membrane at the bottom of a small piece of tubing resting on top of the sand away from the antlion pit. A potential prey item walking on the surface of the sand would likely produce vibrations reasonably similar to the experimental vibrational stimuli in these studies, explaining why antlion larvae demonstrated the ability to learn to associate them with food. Such stimuli were also unlikely to disturb the antlion or its pit significantly. Contrastingly, the vibrations from our stimuli were so intense that anything similarly intense in nature (such as the vibrations an antlion might experience from a large nearby mammal) would likely represent a disturbance rather than potential food. Indeed, our stimuli often resulted in significant amounts of sand falling into the antlion pits. The intensity of our stimuli might have therefore elicited an aversive instinctive reaction in the antlions that prevented associative learning. For example, in some cases antlions that were visible at the bottom of their pits before the stimuli were administered disappeared thereafter, either as a result of taxis or being buried by falling sand. Although antlions would often reappear once presented with food, sometimes they did not. If these buried antlions failed to detect their food, we would not expect them to be able to associate the stimulus with the reward, thus preventing learning. Another possibility is that antlions had already learned to associate intense vibrations with a disturbance and our experiment was simply unable to overcome this prior learning. Yet another possibility is that no amount of training would be able to override an instinctive reaction to intense stimuli such as ours.

The direction of our vibrational stimuli is also a potential problem. The stimuli Guillette et al. (2009) and Hollis et al. (2011) used were administered on and likely propagated along the surface of the sand, whereas in our study vibrations most likely reached the antlion from underneath. In nature, vibrations from nearby potential prey would almost certainly come from

the surface of the sand, making surface vibrations a reasonable cue for antlions to be able to learn to associate with food. Vibrations from underneath an antlion would almost certainly not be associated with food and would much more likely represent a disturbance. The ability of antlions to demonstrate associative learning with surface vibrations but not with vibrations from below therefore makes sense. Future studies on antlions should further examine how different intensities and origins of vibrational stimuli affect antlions. Additionally, future studies examining discriminatory associative learning in antlions should use stimuli similar to those used by Guillette et al. (2009) and Hollis et al. (2011).

Contamination was a significant problem throughout our experiment, particularly for Group B. On one occasion Group B antlions received the incorrect stimulus at the time of day at which they were not fed such that B<sub>1</sub> antlions received Stimulus 1 but was not fed thereafter and B<sub>2</sub> antlions received Stimulus 2 but not fed thereafter. We realized our mistake and corrected for it immediately after by administering the correct stimuli to both groups. More common however was contamination from the nuts used to administer Stimulus 2. Unlike the nut used to administer Stimulus 1, these nuts were not threaded with the string attached to the flashing, resulting in the nuts occasionally rolling on the flashing and in some cases even onto the flashing of a neighboring box, causing it to vibrate. In these cases, the stray nut acted as an unintentional stimulus and therefore a source of potential contamination. Although we tried to minimize vibration transfer from the flashing of the target box to other boxes by separating the flashing and the target box with washers and adhesive, given the close proximity of the boxes to each other, vibration transfer is another possible source of contamination. Future studies should account for these problems by using an experimental design that prevents vibration transfer to unintended subjects. For example, Hollis et al. (2011) prevented between-box vibrational transfer by nesting boxes in foam blocks.

Interestingly, changes in temperature might have also affected our results. Fertin & Casas (2007) noted that sand has very irregular wave propagation properties, some of which change drastically with small changes temperature. In similar granular media, changes of as little as 1° C can decrease sound transmission by as much as 50% (Fertin & Casas, 2007). The building in which our antlions were housed lacked heating and cooling and was therefore responsive to the dramatic changes in outdoor temperature during the course of our experiment (Fig. 2). If the sand temperature varied significantly, its wave propagation properties could have changed in such a way that the same stimulus administered at different times propagated differently. If this is the case, antlions might have perceived the same stimulus differently at different times, potentially preventing learning. However, antlions are able to accurately determine the location of their prey through vibrational cues with amazing precision despite the irregularity of sand (Fertin & Casas, 2007), suggesting that antlions have the ability to account for substrate variation. Capacities like this make the prospect of antlion discriminatory associative learning seem feasible.

Overall, our study suggests that antlion learning could be limited by a number of factors, including learning period time, stimulus intensity, stimulus direction, and temperature variation. Future studies examining the separate roles of each of these factors in antlion learning are warranted. Understanding what factors influence antlion learning capacity will help us determine the role, extent, and evolutionary advantages of antlion associative learning and insect associative learning in general. If, for example, substrate changes resulting from temperature variation do not affect antlion learning capacity, it would suggest that antlions are capable of accounting for changes in their substrate when perceiving vibrations. This would indicate that antlion mental capacities exceed our current estimation thereof. The question of whether antlions are capable of discriminatory associative learning remains unanswered. Future studies on this subject should avoid the complications we faced by using an experimental design that administers stimuli similar to those used in prior studies on associative learning in antlions, minimizing contamination, and controlling for the effects of temperature.

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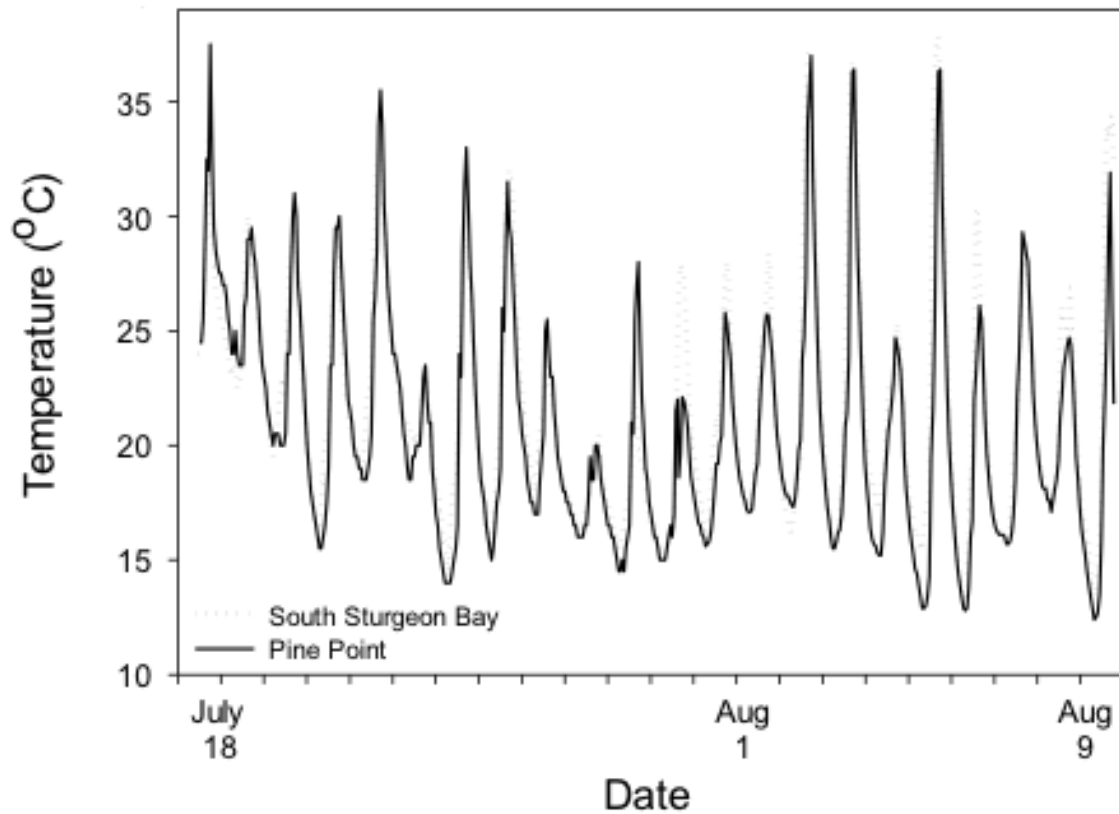
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**Figure 1**

Group	Morning (10 AM)	Night (9 PM)
A	Stimulus 1 Food	No stimulus No food
B <sub>1</sub>	Stimulus 2 No food	Stimulus 1 Food
B <sub>2</sub>	Stimulus 2 Food	Stimulus 1 No food
Control	No stimulus Food	Stimulus 1 No Food

A sample daily schedule. In practice, the order (AM vs. PM) of stimulus-feeding combinations for each group was randomly assigned each day.

Figure 2



Graph of temperature over time in the Pellston, MI area. The dark line represents the temperature at Pine Point – an area about 2km from where our antlions were housed. Our experiment ran from July 22-August

8. These data come from temperature loggers buried in the ground and are therefore not completely representative of the temperature inside the building in which our antlions were housed. However, given the proximity of the sites and the fact that the building in which our antlions were housed had neither air conditioning nor heating, this graph is useful in understanding the wide variation in temperature our antlions experienced.