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Changes in wormlion (Vermilionidae) pit construction in response to energy inputs and disturbances

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ABSTRACT

Wormlions are insects that, like antlions, are sit and wait predators in their larval stages, for whom optimizing energy expenditures is crucial because of potentially long periods of starvation. Initial pit depth and pit growth rates of antlions have been shown to decrease in response to limited food resources. Due to the similar foraging technique of worm and antlions, wormlions were hypothesized to show similar responses. Thirty-two wormlions were randomly divided into four treatments: fed-disturbed (FD), fed-undisturbed (FU), unfed-disturbed (UD) or unfed-undisturbed (UU). An aphid was dropped into wormlion pits of the FU and FD treatments, and pits in “disturbed” treatments were overturned daily. Pit volume was calculated daily from pit measurements, plotted against time and analyzed with regression equations. No statistical difference in pit growth rates ($t_{14} = 0.939$, $p = .364$) or elevation ($t_{15} = .0487$, $p = 0.962$) was reported between fed and unfed treatments. By extrapolating pit volumes of the FU and UU treatments, the optimum pit volume was estimated to be 5.92 cm^3 . Although not significant, a decrease in initial pit volume appeared to exist for unfed wormlions ($t_{17} = 1.848$, $p = 0.082$). The data suggest that wormlions have more efficient pit construction adaptations in response to shorter larval development and limited predation opportunities.

RESUMEN

Los gusanos león son insectos que, como las hormigas león, son depredadores “sit and wait” en sus etapas larvales, para las cuales es crucial optimizar gastos energéticos debido a potenciales largos periodos del hambre. La profundidad del hoyo y las tasas de crecimiento iniciales del hoyo de las hormigas león se ha demostrado presentan una disminución en respuesta a limitados recursos alimenticios. Debido a la técnica similar del forraje del gusano y de las hormigas león, se presume que los gusanos león presentan respuestas similares. Treinta y dos gusanos león fueron divididos aleatoriamente en cuatro tratamientos: alimentado-disturbado (FD), alimentado-imperturbado (FU), hambriento-disturbado (UD) o hambriento-imperturbado (UU). Un áfido fue colocado en los hoyos de los gusanos león de los tratamientos de FU y del FD, y los hoyos en tratamientos “disturbados” fueron volcados diariamente. El volumen del hoyo era calculado diariamente, trazado contra tiempo y analizado con ecuaciones de regresión. No se encontró ninguna diferencia estadística en tasas de crecimiento del hoyo ($t_{14} = 0.939$, $p = 0.364$) o la elevación ($t_{15} = 0.0487$, $p = 0.962$) entre los tratamientos alimentados y hambrientos. Extrapolando los volúmenes del hoyo de los tratamientos de FU y del UU, el volumen óptimo del hoyo estimado es de 5.92 cm^3 . Aunque no sea significativo, una disminución del volumen inicial del hoyo parece existir para los gusanos león hambrientos ($t_{17} = 1.848$, $p = 0.082$). Los datos sugieren que los gusanos león tienen adaptaciones más eficientes para la construcción del hoyo en respuesta a un desarrollo larval más corto y a oportunidades limitadas de la depredación.

INTRODUCTION

Relatively uncommon and unstudied, the only known populations of wormlions (F: Vermilionidae) are found in the United States and Costa Rica (Petersen and Baker 2006; Zumbado 2006). Both wormlions (*Vermilio* spp.) and antlions (*Myrmelion* spp.) exhibit sit and wait predation in their larval stages (McClure 1983; Zumbado 2006). These invertebrates build conical pit traps in dry, fine soil beneath overhang objects in order to trap terrestrial invertebrates. Due to this apparent convergent evolution of predation strategy, the very well-studied ecology of antlions was used to construct my hypotheses.

Optimizing energy expenditures is crucial for organisms without steady inputs of energy. Sit and wait predators can be subject to long periods of starvation, and therefore, must optimize foraging techniques to conserve energy. Previous studies have identified an inverse correlation between food availability and pit depth in antlions (Griffiths 1986). When pit traps of unfed antlions were disturbed daily, initial trap depths decreased over time suggesting that energy costs and gains determine trap depth (Griffiths 1986). Furthermore, Hauber (1999) reported similar data; however, it was concluded that the decrease in initial trap depth was not solely a consequence of food limitation but also a result of the energy expenditures necessary for building a trap *de novo*. Trap measurements also revealed a decrease in pit growth rate in response to starvation (Griffiths 1986). The data further support the idea that energy inputs and expenditures determine pit size.

Therefore, due to similarities in predation strategies, food limitations and energy expenditures were hypothesized to have similar effects on initial pit volume and pit growth rate of wormlions. Here I provide a baseline study of wormlion pit characteristics and theories for changes in wormlion pit construction in response to limited energy inputs.

METHODS

To test this hypothesis, 32 wormlion larvae from the Monteverde cloud forest were gathered and placed in individual containers, 13 cm in diameter and filled with four centimeters of fine grain soil as described by McCarthy (2007). The soil was gathered from the sites where the wormlions were collected. Wormlions were randomly placed into one of four treatments: fed-disturbed (FD), fed-undisturbed (FU), unfed-disturbed (UD) or unfed-undisturbed (UU) with eight wormlions per treatment. Each morning, one aphid (family Aphididae) was dropped into each pit of the FD and FU treatments. "Disturbed" wormlion pits were destroyed daily using a spoon fifteen minutes after the insects were fed. Prior to feeding, the depth and width of each pit was measured with a caliper. Assuming a conical shape, pit volume was calculated from pit depth and width measurements.

Pit depth was plotted against pit width and correlation analysis was performed. Daily pit volume averages for all treatments were graphed against time. FU, UU and UD data were analyzed with a logarithmic regression analysis and the FD with a linear regression. To prevent bias in pit growth rates, day one pit volume of the FU treatment was removed to equilibrate initial average pit volumes between FU and UU treatments. FU data collected on the second day was considered day one data with respect to the UU

treatment. In addition, due an accidental disturbance of a wormlion pit, the final value of the FU treatment was omitted. Inadequate sample size as a result of wormlion deaths limited analysis of the UD treatment to seven days.

Modified t-tests were used to compare corrected pit growth rate and elevation of the FU and UU treatments (Zar 1984). The same tests were also performed on the raw data. To extrapolate the maximum pit volume, mean daily pit volumes of FU and UU treatments were compiled, plotted on a double reciprocal plot and analyzed with a linear regression equation. To compare average daily initial pit volumes of the FD and UD treatments, a student t-test was performed between the FD and UD treatments.

RESULTS

The pit width increased when the pit depth increased ($r = 0.879$, $n = 283$, $p < 0.05$; Fig. 1). The pit volume increased logarithmically with time for the FU ($F_{1, 6} = 128.7$, $p < 0.0001$) and UU treatments ($F_{1, 8} = 106.9$, $p < 0.0001$; Fig 2A). There was no difference found between pit growth rates ($t_{14} = 0.939$, $p = 0.364$) or elevation ($t_{15} = .0487$, $p = 0.962$) of FU and UU treatments. Even when comparing raw data, no significant differences exist between pit growth rate ($t_{16} = 1.293$, $p = 0.215$) and elevation ($t_{17} = 1.848$, $p = 0.082$) (Fig. 2B). Using a linear regression equation ($F_{1, 16} = 2264.542$, $p < 0.001$), maximum pit volume was estimated to be 5.92 cm^3 (Fig. 3).

Initial pit volume in the FD treatment increased over time ($F_{1, 8} = 9.033$, $p = 0.017$), whereas there was a trend for a decrease in initial pit volume of the UD treatment ($F_{1, 5} = 4.166$, $p = 0.097$) (Fig. 4). (Note that after eight days, three wormlions in the UD treatment failed to rebuild a trap, so the final sample size is five.) Average daily initial pit volume of the FD treatment (1.23 cm^3) was significantly higher than for the UD treatment (0.85 cm^3) ($t_6 = 2.691$, $p = 0.036$).

DISCUSSION

Energy conservation is critical for survival of sit and wait predators such as wormlions. The data presented here provide a baseline ecological study and cost-benefit analysis of wormlion pit dynamics.

Wormlion pit biology is apparently very similar to that of antlions. For both insects, a strong correlation exists between pit width and depth. Logarithmic pit growth is also a shared characteristic (Griffiths 1986). Wormlion pit volume approaches a maximum of 5.92 cm^3 . According to the optimum pit size theory proposed by Griffiths (1986), this pit size maximizes net energy return.

The data presented here suggest that wormlions respond differently to restricted energy inputs than do antlions. Increased food consumption increases development rate of antlions (Arnett and Gotelli 1999). Wormlions have a shorter larval development (11 months) than antlions (one to two years) and therefore, should require more constant energy inputs making them more susceptible to starvation (Zumbado 2006; Gotelli 1997). If this were the case, a greater decrease in pit growth rate should be observed, but this was not the case.

Instead, an increased efficiency in trap building may explain the observed trend. If minimal energy is required for pit construction, pit growth will not be affected by starvation. Development of energy efficient adaptations would be strongly selected for in response to shorter larval development and limited predation opportunities. The confinement of wormlions to sheltered microhabitats may be another adaptation to avoid unnecessary energy expenditures. In the protected microhabitats, pit maintenance is kept to a minimum.

Although there was no significant decrease in initial pit volume in the UD treatment, a negative trend was found. The failure of three wormlions to rebuild a pit after starvation further supports this trend. These data would most likely be more conclusive with a larger sample size and longer study period. Additionally, there was a decrease in daily mean initial pit volume for the UD treatment. The decrease may be attributed to a combination of starvation and unnatural pit disturbances.

The slight increase in initial pit volume of the FD treatment is most likely due to an increase in worm lion size. Increased food consumption in antlions increases insect growth (Arnett and Gotelli 1999). Constantly fed wormlions are likely to increase in size as well. As a result, pit size would increase because pit size is proportional to body size (McCarthy 2007). Pre- and post-experimental measurements of wormlion length and initial pit size are needed to support this claim.

Although the foraging techniques of wormlions and antlions are similar, the data presented here suggest wormlions respond differently to restricted energy inputs. Adaptations to prolonged malnourishment may have arisen due to wormlions' longer development. The same experiment with a longer study time and increased sample size should be conducted. Also, comparing initial pit sizes of unfed-disturbed wormlions and ones prevented from pit construction as done by Hauber (1999) will give a greater insight into energy costs of pit construction. This study provides a strong base of preliminary data on wormlions and possibilities for future studies.

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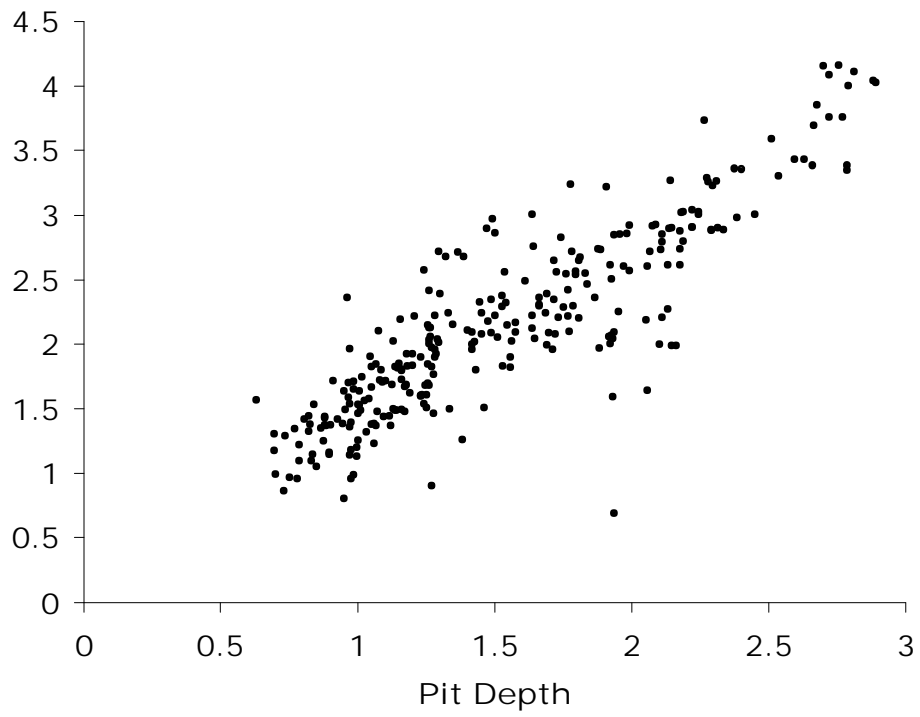


Figure 1. Correlation between pit width and pit depth of wormlions ($r = 0.879$, $n = 283$, $p < 0.05$).

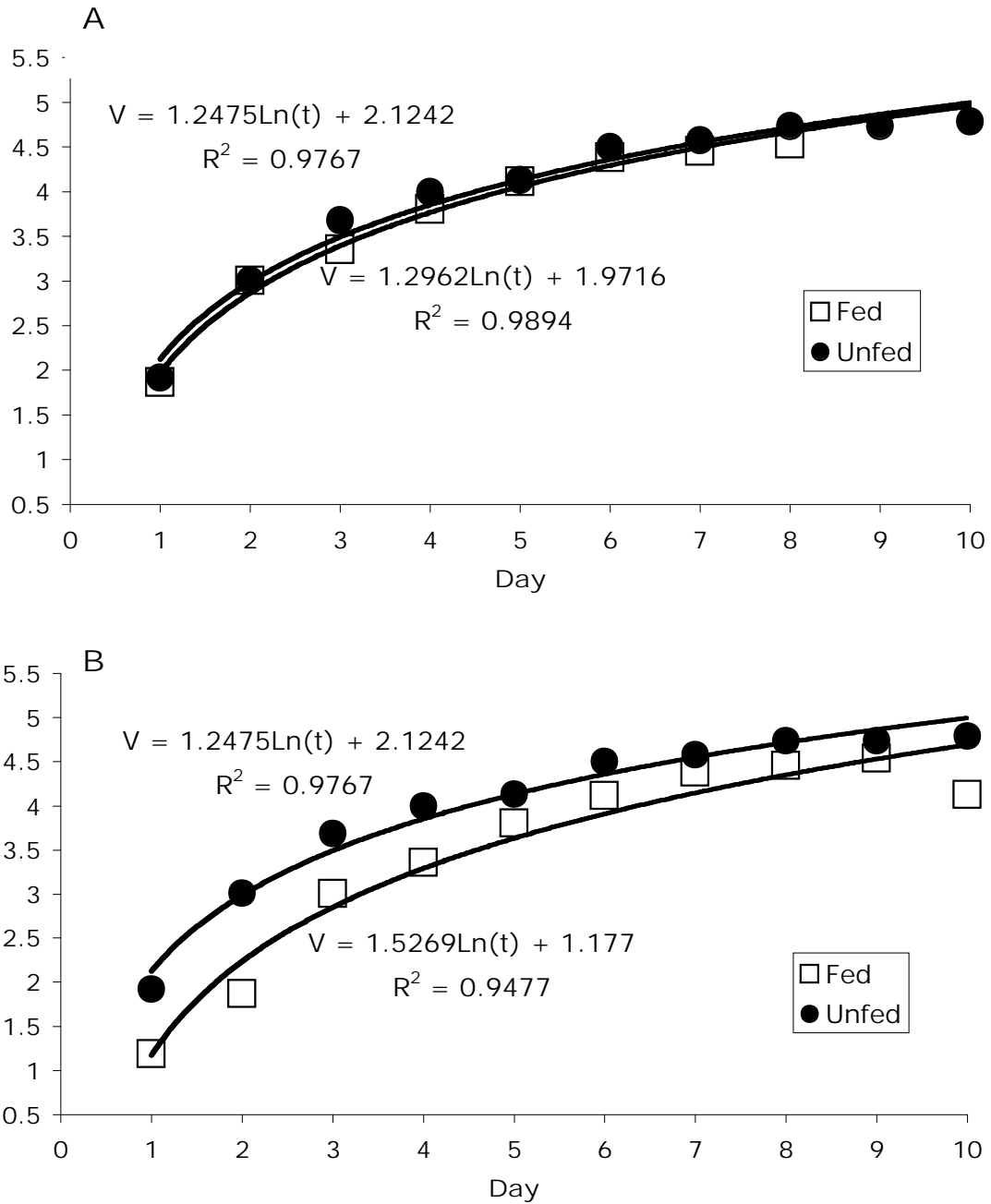


Figure 2. Mean pit volume growth of fed and unfed wormlions over a 10-day period: (A) Corrected data (fed, $F_{1,6} = 128.7$, $p < 0.0001$; unfed, $F_{1,8} = 106.9$, $p < 0.0001$), (B) Raw data.

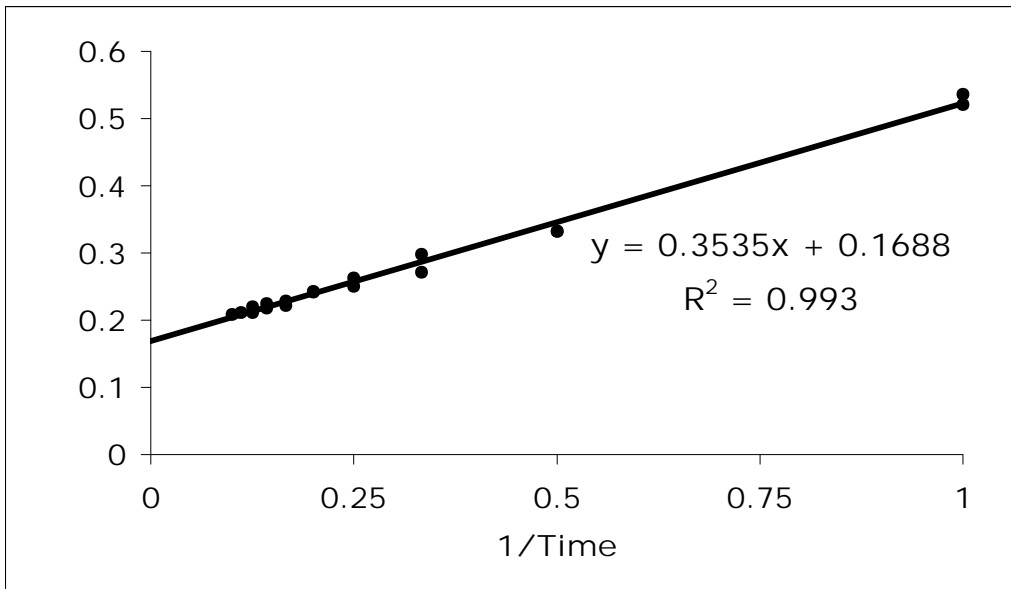


Figure 3. Double reciprocal plot of mean daily pit volume and time used to extrapolate maximum pit volume ($F_{1, 16} = 2264.542$, $n=18$, $p < 0.001$). Maximum pit volume (5.92 cm^3) is equal to the inverse of the y-intercept.

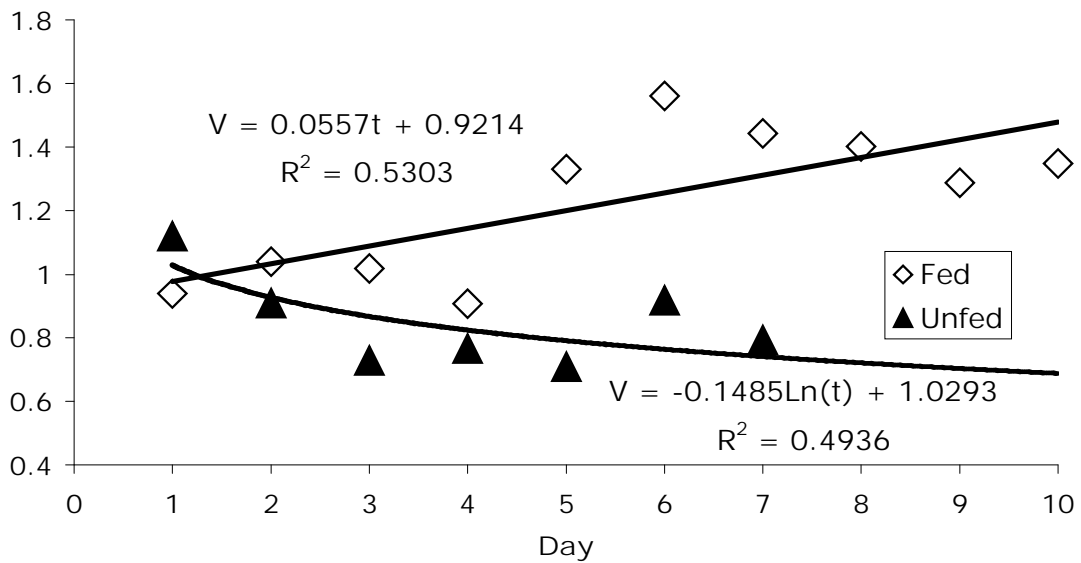


Figure 4. Mean initial pit volume of fed ($F_{1, 8} = 9.033$, $p = 0.017$) and unfed ($F_{1, 5} = 4.166$, $p = 0.097$) wormlions over a 10-day period in which wormlion holes were disturbed daily.