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Sub-optimal pit construction in predatory ant lion larvae (*Myrmeleon* sp.)

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ABSTRACT

The impacts on energy gains of two aspects of ant lion pit architecture were investigated in a natural population of pit-building ant lion larvae (*Myrmeleon* sp.) in Costa Rica. Field and laboratory settings were used to examine the impacts of circumference and depth of the pit on net energy gain rate. An optimization model predicted a point optimum circumference and angle of depression in an unconstrained system, and positive correlations between body mass, pit circumference, and pit angle of depression in the presence of physiological constraints on both measures. Such a physiological constraint is possible in this system due to a large one-time construction cost. All of these correlations were observed in a lab setting with filtered substrate and no competition; though none were significant in the field. Individuals additionally constructed wider, shallower pits in the field. These results are consistent with an angle of depression that is limited by the angle of repose of the substrate in the field, rather than physiology. These results provided suggestive evidence for sub-optimal pit dimensions in *Myrmeleon* sp., and for the importance of substrate type in understanding the architecture of natural ant lion pits. The model predicted that the frequency of relocation would not affect the optimal angle of depression, but it would affect the optimal pit circumference to a degree proportional to the square root of the change in the average time an ant lion occupies a single pit. These findings challenge the widely held assumption of adaptive optimality in animal foraging.

1. Introduction

Ant lions of the sub-family Myrmeleontidae (Neuroptera: Myrmeleontidae) are well known sit-and-wait predators that construct conical pits during their larval stage in order to capture passing prey (Griffiths, 1986; Fertin and Casas, 2006; Scharf and Ovadia, 2006; Swenson et al., 2007). Loose, finer substrate particles lining the walls of the pits, along with sand throwing by the ant lions result in prey losing traction and sliding toward the bottom of the pits where they are attacked (Fertin and Casas, 2006; Swenson et al., 2007). As a result, pits are constructed preferentially in fine, dry substrate, and substrate particle size has been well-documented to affect both capture success and construction behaviour (Loiterton and Magrath, 1996; Botz et al., 2003; Farji-Brener, 2003; Farji-Brener et al., 2008; Devetak et al., 2005). Ant lions are largely sessile following initial pit construction (Swenson et al., 2007), though they are known to relocate in response to intraspecific competition (Griffiths, 1993; Day and Zalucki, 2000; Scharf et al., 2008) and low food availability (Eltz, 1997), which can both additionally have an effect on pit architecture (Inacio et al., 1993; Gotelli, 1997; Swenson et al., 2007).

Ant lion pits present an ideal system in which to study optimal trap architecture as their pits are known to deviate very little from perfect conicity (Fertin and Casas, 2006), and their relocation habits seem to be largely dependent on extrinsic factors (competition and food availability: Griffiths, 1993; Day and Zalucki, 2000; Scharf et al., 2008) that can be controlled in the lab. Furthermore, as organisms that consume a large majority of their resources during their larval stage (Swenson et al., 2007), their fecundity is expected to correlate with the net energy gained (total energy−energy expenditure) over the course of this period. Field evidence supports this prediction showing a strong positive correlation between larval body size and adult fecundity (Griffiths, 1985). As a result, one might expect a fitness maximizing pit-building strategy to maximize the average net-energy gained in each pit in which the ant lion resides.

Both the energetic gains an ant lion receives from its pit and its energetic expenditures are likely to be impacted by the circumference of the top of the pit and the slope (Griffiths, 1986; Fertin and Casas, 2006) of the pit. The former will determine the rate of prey entry into the pit, and the latter will affect the ability of prey to escape once they have entered. Both of these aspects can presumably be determined by the larval individual based on the costs of construction and maintenance and the abundance of prey. In addition, two extrinsic factors—the density of nearby (competing) pits (Griffiths, 1993; Day and Zalucki, 2000; Scharf et al., 2008), and the substrate particle size (Loiterton and

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Magrath, 1996; Farji-Brener, 2003)—can affect capture rates. The shape of the fitness surface as a function of all of these parameters is expected to generate empirical relationships between the parameters, some of which have previously been observed (Griffiths, 1986; Devetak et al., 2005; Fertin and Casas, 2006; Farji-Brener et al., 2008). Substrate type and conspecific density can be controlled in a lab setting, which allows for a closer examination of the relationship between the intrinsic variables: pit circumference and slope. Manipulating the extrinsic variables additionally allows for an assessment of the behavioural plasticity present in pit construction.

Past empirical evidence has suggested a positive correlation between the size of constructed pits and ant lion body size (Griffiths, 1986; Swenson et al., 2007), as well as a negative correlation between particle size and angle of repose in the substrate (the maximum architecturally stable slope angle) (Lucas, 1982; Botz et al., 2003). In this study, the relationships between pit slope, pit circumference, body mass, and pit density were examined in a natural population of ant lions (*Myrmeleon* sp.) in Las Cruces, Costa Rica, both in the field and in a laboratory setting with no competition, controlling for density and substrate type. A simple model was developed to estimate the net energy gain an ant lion receives from a single pit over the course of its average pit residency time as a function of the slope (measured as the angle between the horizontal and the pit wall, referred to hereafter as the angle of depression) and the circumference of the entrance to the pit. This model predicts, in the absence of competition, the existence of a point optimum pit circumference and angle of depression that maximizes net energy gain over the residence period in a single pit. However, the fact that a majority of the energetic costs are incurred at one time, during pit construction (Swenson et al., 2007; Griffiths, 1986), may represent a constraint that is dependent on the size and hunger level of the organisms (Heinrich and Heinrich, 1984; Hauber, 1999) resulting in sub-optimal pit dimensions (Griffiths, 1986). Such physiological constraints have previously been observed to result in sub-optimality of other aspects of ant lion foraging as well (Scharf and Ovadia, 2006). If this is the case, the model predicts a positive correlation between pit circumference and angle of depression, somewhat contradictory to the findings of Griffiths (1986), in which third-instar larvae were observed to construct larger, shallower pits than first two larval instars. The predictions of the model presented in this study were tested empirically in both a laboratory and field setting.

2. Methods

2.1. Experimental methods

All field and laboratory observations were made at Las Cruces Biological Station in Costa Rica (8°47′N, 82°57′W, 1000–1385 m elevation) in February 2008 (during the dry season). 18 pits from a natural population of *Myrmeleon* sp. found in Wilson Botanical Garden were located, and diameter and depth were both measured to a resolution of 1 mm using callipers. From these measures, circumferences ($C = \pi * \text{diameter}$) (accuracy of $\pm (\pi/2)$ mm) and angles of depression ($\theta = \arctan(\text{depth}/(\text{diameter}/2))$) (accuracy of $\sim\pm 1.3^\circ$ (based on calculations using the average depth and diameter over all measurements)) were calculated. For each pit, the distances to nearby pits were measured using a ruler, and the total number of surrounding pits within 25 cm was recorded. Each pit was numbered in order to keep track of individuals. Ant lions were then extracted carefully from their pits using tweezers and placed individually in roughly cylindrical plastic cups (100 mm (diameter) × 110 mm (depth)) filled with substrate from the field site in which the natural population was found. The substrate used had been filtered with a sieve to remove larger particles. These cups were then placed on a tray and left for 24 h in a high-sun, rain-protected area outside to allow time for the ant lions to rebuild their pits. At the end of this period, nine of the original 18 ant lions were found to have constructed new pits, and these pits were again measured in diameter and depth to a resolution of 1 mm, from which circumferences and angles of depression were calculated. All 18 ant lions were then extracted, killed using a cyanide kill-jar, and weighed to a resolution of 0.001 g using a fine balance.

2.2. Model

I constructed a simple analytical model of the energy trades-offs faced by an ant lion with respect to pit circumference (C) and angle of depression (θ) under the assumption that the pits were conical (see Fertin and Casas, 2006). Net energetic gain (E_{NET}) over the average residence period in a single pit (τ) was used as a contextual measure of fitness and assumed to be equal to the energetic gains during the residence period (E_{IN}) minus the one-time energetic expenditure (E_{OUT}) of construction.

Energetic gains during the residence period were assumed to be equal to the total number of visitors (prey entering the pit) in that time multiplied by the average net energy gain per visitor. The number of visitors per unit time was assumed to be proportional to the pit circumference (Griffiths, 1986), making the total number of visitors proportional to the pit circumference multiplied by the length of the average residency period ($C\tau$). Net energy gain per visitor was assumed to be a function of the angle of depression ($f(\theta)$), since the angle of the pit is important in both capture success and costs associated with capture (e.g. sand-throwing behaviour, frequency of avalanches) (see Griffiths, 1986; Fertin and Casas, 2006). The capture rate is also affected by substrate type (Lucas, 1982; Botz et al., 2003), but because the substrate was kept constant in the lab, and all field data was collected from one site, this effect was not considered explicitly in the model. Adding a proportionality constant (c_1), the following equation for the average energy gained during each pit residency (E_{IN}) was generated:

$$E_{IN} = c_1 f(\theta) C\tau \tag{1}$$

The function, $f(\theta)$, was hypothesized to be piecewise, characterized by a bell-shaped function of θ reaching a maximum value, which for simplicity was standardized to 1 (this could be accomplished in a real scenario by adjusting the value of c_1), at a certain angle, θ_{MAX}, which optimizes the trade-off between capture success and maintenance costs, which should both increase with θ. This function will be denoted by $g(\theta)$, where $g'(\theta) > 0$ for all $\theta < \theta_{MAX}$, and $g''(\theta) < 0$ except for very small values of θ if S-shaped. However, there should also be an angle of repose dependent on the substrate (denoted by θ_{LIM}) beyond which the pit is no longer architecturally stable (Lucas, 1982; Botz et al., 2003), and $f(\theta)$ was concordantly set equal to zero for $\theta > \theta_{LIM}$, giving the following general equation for $f(\theta)$:

$$f(\theta) = \begin{cases} g(\theta), & 0 \le \theta \le \theta_{LIM} \\ 0, & \theta > \theta_{LIM} \end{cases} \tag{2}$$

The energy expenditure resulting from the construction of the pit was hypothesized to be proportional to the amount of substrate displaced, equal to the volume of the pit (V), where the proportionality constant (denoted by c_2) can also be a function of the substrate type. However, the model did not consider substrate type as a variable since it was controlled in this study. Thus, the following equation was used to represent the energy expenditures (E_{OUT}):

$$E_{OUT} = c_2 V \tag{3}$$

This equation was then reparametrized in terms of C and θ according to the following equalities:

$$V = \frac{\pi r^2 h}{3} = \frac{c(r^2)\tan(\theta)}{6} = \frac{1}{24(\pi^2)} C^3 \tan(\theta) \tag{4}$$

From Eqs. (1), (3), and (4), the net energy gained during residency in a particular pit (E_{NET}) as a function of C and θ was given by

$$E_{NET} = c_1 f(\theta) C \tau - c_2 \frac{1}{24(\pi^2)} C^3 \tan(\theta) \tag{5}$$

It should be noted that the costs of pit maintenance were not fully accounted for in this model. While the costs associated with pit angle and prey visits were incorporated into $f(\theta)$, it was also hypothesized that maintenance costs would depend on the surface area of the pit and the density of pits in the area (Day and Zalucki, 2000). These terms were omitted from the model for the following reasons. Competition effects were absent from the lab portion of this study, meaning that a term representing competition-related costs would only be relevant in the field study. Furthermore, it is not known whether this term would be dependent at all on the dimensions of the pit. If it was not, it would not be relevant to the optimal pit dimensions. However, even if one were to assume that it was, the specific nature of this term would be difficult to predict without extensive empirical evidence that is not currently available. This question requires further study. An analogous problem of missing information exists for changes in surface area. In addition, since the assumption is that increasing surface area increases costs, the model is likely a good approximation without this term. This arises because an increase in surface area corresponds to an increase in volume, angle, or both, all of which already lead to increased costs in the model.

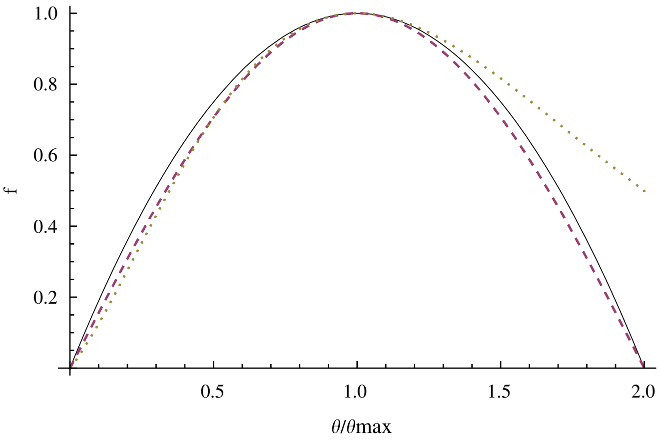

Fig. 1. A graphical depiction of all functions, $g(\theta)$, presented from the model (solid: $g(\theta) = 2(\theta/\theta_{MAX})–(\theta/\theta_{MAX})^2$; dashed: $g(\theta) = \sin(\theta\pi/2\theta_{MAX})$; dotted: $(g(\theta) = (\theta/\theta_{MAX})^{(1(\theta/\theta_{MAX}))})$ from 0 to $2\theta_{MAX}$. In the model, θ_{MAX} denotes the angle of depression which optimizes the trade-off between capture success and maintenance costs with respect to angle. The resulting function of θ is bell-shaped and reaches a maximum of 1 at θ_{MAX}. At an angle of θ_{LIM} (the maximum angle of depression at which the pit is architecturally stable, or angle of repose), the function $f(\theta)$ will truncate (it assumed that $\theta_{MAX} > \theta_{LIM}$), falling to zero.

2.3. Model analysis

The model was analysed numerically using Maple 10 (Maplesoft 2006) and Mathematica 6.0 (Wolfram Research 2007). In the analyses presented here, the function $g(\theta)$ was assigned a form, $g(\theta) = \sin(\theta\pi/2\theta_{MAX})$, which was consistent with the model's specifications (Fig. 1). Two other functions that met the model's specifications for $g(\theta)$ were also used in analyses; one exponential $(g(\theta) = (\theta/\theta_{MAX})^{(1(\theta/\theta_{MAX}))})$, and one quadratic $(g(\theta) = 2(\theta/\theta_{MAX})–(\theta/\theta_{MAX})^2)$ (Fig. 1). However, the results were qualitatively identical in all cases suggesting the shape of $g(\theta)$ to be more important than its mathematical representation (see Table 1). The parameter θ_{MAX} was set equal to 1, such that all values of θ were expressed as fractions of θ_{MAX}. Since θ_{LIM} represents a truncation of the gain function (as demonstrated in Fig. 4), its qualitative effects can be predicted graphically with ease at any value without explicit calculation from a representation of the model that assumes it is large. This representation is given in Figs. 2 and 3. The values of τ, c_1, and c_2 were manipulated, and found to not affect the general shape of the model, though they did have an effect on the location of the optimum. This effect was calculated by analysing the model symbolically with no specific form assigned to $f(\theta)$ (the most general case). Since the analysis was primarily concerned with relative predictions, these constants were all set equal to 1 for the sake of simplicity in the version that was presented (Figs. 2–4). Consequently, it should be noted that the results of this analysis mostly present highly general predictions with respect to relative parameter relationships (Fig. 3) rather than specific numerical values. The model was optimized graphically with respect to C and θ by plotting the points where the magnitude of each component of the gradient vector $((\delta E_{NET}/\delta\theta)$ and $(\delta E_{NET}/\delta C))$ is equal to 0 in state space. Regions in which these components were positively correlated and negatively correlated were determined (Figs. 3 and 4). The

Table 1
A comparison of the three forms used in the model for $g(\theta)$.

Function ($g(\theta)$)	First derivative ($g'(\theta)$)	Second derivative ($g''(\theta)$)	Optimal (E_{NET}-maximizing) θ/θ_{MAX}
$\sin\left(\frac{\theta\pi}{2\theta_{MAX}}\right)$	$\frac{\pi\cos\left(\frac{\theta\pi}{2\theta_{MAX}}\right)}{2\theta_{MAX}}$	$-\frac{(\pi^2)\left(\sin\left(\frac{\theta\pi}{2\theta_{MAX}}\right)\right)}{4\theta_{MAX}^2}$	0.744
$\left(\frac{\theta}{\theta_{MAX}}\right)^{1-(\theta/\theta_{MAX})}$	$\left(\frac{\theta}{\theta_{MAX}}\right)^{1-(\theta/\theta_{MAX})}\left(\left(\frac{1-\left(\frac{\theta}{\theta_{MAX}}\right)}{\theta}\right)-\left(\frac{\log\left(\frac{\theta}{\theta_{MAX}}\right)}{\theta_{MAX}}\right)\right)$	$\left(\frac{\theta}{\theta_{MAX}}\right)^{1-(\theta/\theta_{MAX})}\left(\left(-\frac{Z}{\theta_{MAX}\theta}\right)-\left(\frac{1-\left(\frac{\theta}{\theta_{MAX}}\right)}{\theta^2}\right)\right)$ $+\left(\frac{\theta}{\theta_{MAX}}\right)^{1-(\theta/\theta_{MAX})}\left(\left(\frac{1-\left(\frac{\theta}{\theta_{MAX}}\right)}{\theta}\right)-\left(\frac{\log\left(\frac{\theta}{\theta_{MAX}}\right)}{\theta_{MAX}}\right)\right)^Z$	0.734
$2\left(\frac{\theta}{\theta_{MAX}}\right)-\left(\frac{\theta}{\theta_{MAX}}\right)^Z$	$\left(\frac{2}{\theta_{MAX}}\right)-\left(\frac{2\theta}{\theta_{MAX}}\right)$	$-\frac{2}{\theta_{MAX}}$	0.693

In the most general case of the model (where no form for $g(\theta)$ is specified), the optimal pit angle depended only on the function $f(\theta)$, which means that this angle was a constant fraction of θ_{MAX} for each form of the function $g(\theta)$. The second derivatives are negative always between 0 and θ_{MAX} in the first and third functions and negative at values between $0.229\theta_{MAX}$ and θ_{MAX} in the second function.

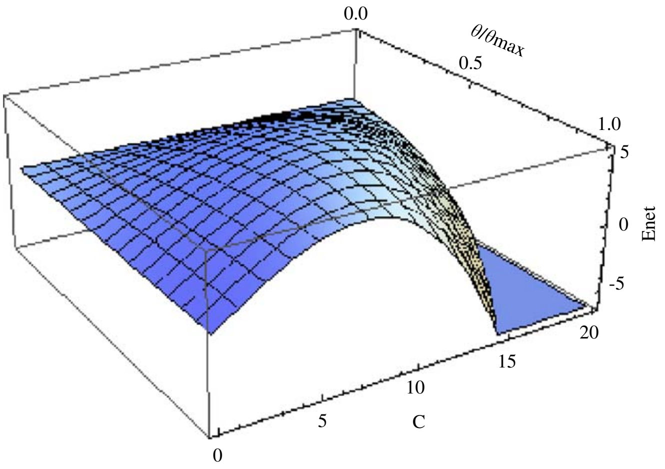

Fig. 2. A 3D plot of the fitness surface predicted by the model (with $g(\theta)=\sin(\theta\pi/2\theta_{MAX})$) if $\theta_{LIM}=\theta_{MAX}$ (with E_{NET} on the z-axis as a function of C and θ). The model predicts the existence of a point fitness maximum value that is an evolutionary attractor. Here, θ is measured as a fraction of θ_{MAX}, and the units of C depend on the values of c_1 and c_2, which are unknown constants in the model. In the more realistic case in which $\theta_{LIM}<\theta_{MAX}$, this fitness surface will truncate at $\theta=\theta_{LIM}$, where $f(\theta)$ falls instantaneously to zero. Since the optimum occurs at a smaller angle than θ_{MAX} in all versions of the model (this makes sense because θ_{MAX} optimizes a function of θ that does not include the construction cost term, which increases with θ), cases with $\theta_{LIM}>\theta_{MAX}$ will result in the same optima as with $\theta_{LIM}=\theta_{MAX}$.

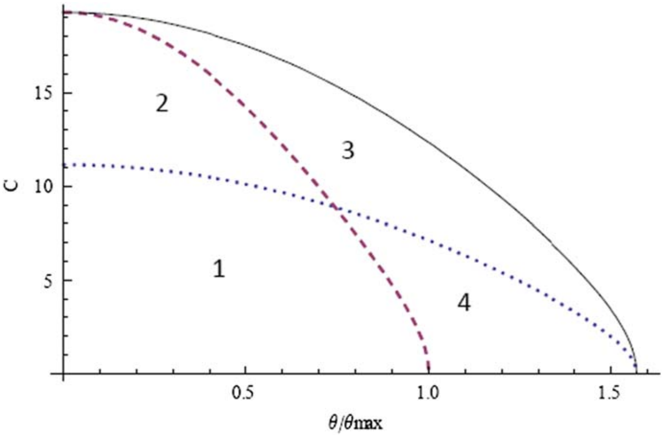

Fig. 3. A state-space plot of the C and θ from the model shows regions where the direction of the C and θ components of the gradient vector of E_{NET} ($(\delta E_{NET}/\delta C)$ and $(\delta E_{NET}/\delta\theta)$, respectively) have a positive correlation (regions 1 and 3) and regions where they have a negative correlation (regions 2 and 4). Since the gradient represents the direction of the largest increase in E_{NET} (our measure of fitness), the model predicts C and θ to evolve in the same direction in regions 1 and 3 and in opposite directions in regions 2 and 4, eventually approaching a fitness maximum at the point where the lines intersect. Here, θ is measured as a fraction of θ_{MAX}, and the units of C depend on the values of c_1 and c_2, which are unknown constants in the model. The lines represent $(\delta E_{NET}/\delta C)=0$ (dotted), $(\delta E_{NET}/\delta\theta)=0$ (dashed), and $E_{NET}=0$ (solid). Each of these values is positive below/to the left of its corresponding line, and negative above and to the right. As a result, it is easy to see from the graph that the optimum point is an evolutionary attractor. The total region under the solid curve represents the region where $E_{NET}>0$.

curve $E_{NET}=0$ was added to this plot to highlight the overall region of positive net energy gain in state space (Figs. 3 and 4).

2.4. Data analysis

In both the field data and the lab data, all possible combinations of pit circumference, angle of depression, and ant lion mass were tested for correlation using Spearman Rank tests. Each of these measures was additionally tested for correlation with density in the field data (again using Spearman rank tests). Pairwise comparisons of pit circumference and angle of depression between the field and the lab in individuals that constructed pits in both environments were conducted using Wilcoxon signed-rank tests. These differences were then tested for correlation with body mass using Spearman Rank tests. An outlier was removed from the lab data analysis concerned with the angle of depression (the residual was found to be greater than the median residual plus 1.5 IQR (see Moore and McCabe, 2006)).

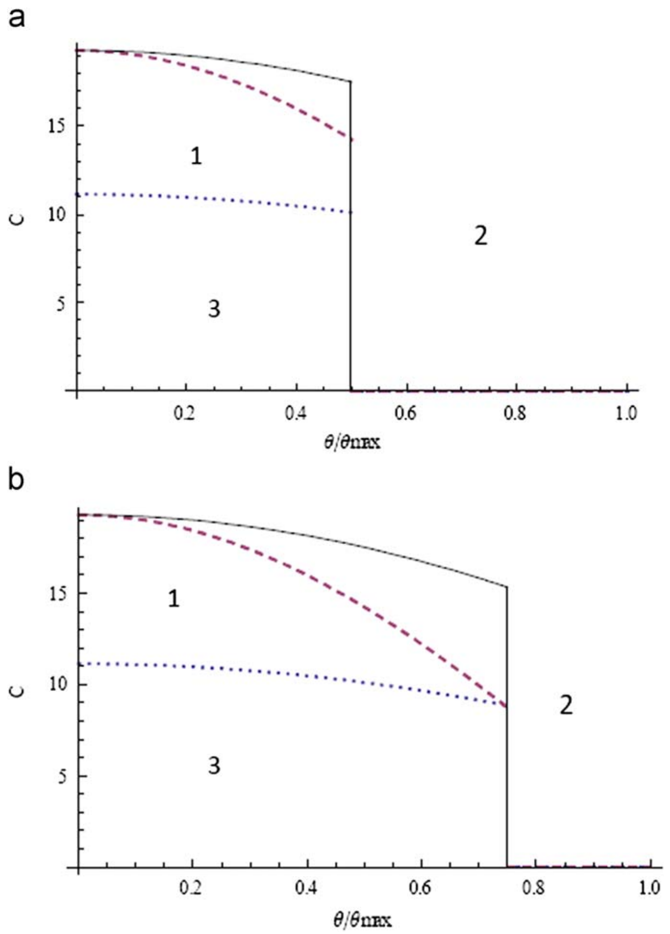

Fig. 4. The truncation of the gain function resulting from two different values of θ_{LIM}: (a) $\theta_{LIM}=0.5\theta_{MAX}$ and (b) $\theta_{LIM}=0.75\theta_{MAX}$. The location of the optimum is unaffected in (b), occurring at $0.744\theta_{MAX}$, but θ_{LIM} becomes limiting in (a) resulting in a new optimum at $\theta=\theta_{LIM}$ with a higher C value. Once again, region 3 represents the points in state space where the C and θ components of the gradient are both positive, meaning that they will evolve towards the optimum dimensions. The lines represent $(\delta E_{NET}/\delta C)=0$ (dotted), $(\delta E_{NET}/\delta\theta)=0$ (dashed), and $E_{NET}=0$ (solid), and the black line is added to join the two ends of each curve at their point of discontinuity, and to illustrate the new optimum in a) at its point of intersection with $(\delta E_{NET}/\delta C)=0$ (dotted).

3. Results

3.1. Model

The model developed in this study predicted the existence of a point fitness-maximizing pair of C and θ values (Figs. 2 and 3). The optimum angle depended only on the form of the function $g(\theta)$, and the values of θ_{LIM} and θ_{MAX}. It was found to be independent of the values of c_1, c_2, and τ. This was confirmed computationally by evaluating it repeatedly over an array of values in each of these parameters, and can be seen from Eqs. (8) and (9). Depending on which form of the function $g(\theta)$ was used, the optimal angle varied between $0.69\theta_{MAX}$ and $0.75\theta_{MAX}$. The optimal circumference was predicted to increase proportionally with increases in the square root of the average residency time, τ, as well as the square root of the constant ratio, (c_1/c_2), using the constants from Eq. (5). These relationships can be seen from the first-order necessary conditions for a maximum.

$$(\delta E_{NET}/\delta C)|_{(C=C^*,\theta=\theta^*)} = c_1 f(\theta^*)\tau - c_2 \frac{1}{8(\pi^2)} C^{*2} \tan(\theta^*) = 0 \tag{6}$$

$$(\delta E_{NET}/\delta \theta)|_{(C=C^*,\theta=\theta^*)} = c_1 f'(\theta^*) C^* \tau - c_2 \frac{1}{24(\pi^2)} C^{*3} \sec^2(\theta^*) = 0 \tag{7}$$

From these equations, it can easily be shown that,

$$C^* = \sqrt{\frac{8\pi^2 c_1 f(\theta^*)\tau}{c_2 \tan(\theta^*)}} = \sqrt{\frac{24\pi^2 c_1 f'(\theta^*)\tau}{c_2 \sec^2(\theta^*)}} \tag{8}$$

and for any given $f(\theta)$, θ^* will be the value that satisfies,

$$f(\theta^*) = \frac{3f'(\theta^*) \tan(\theta^*)}{\sec^2(\theta^*)} \tag{9}$$

The model further predicted the possibility of an adaptive correlation between C and θ, if a constraint existed on pit construction that resulted in obligately sub-optimal pit architecture, that would be positive (Fig. 3). If such a constraint was present, it is hypothesized that larger ant lions would be able to better approach the optimal dimensions, resulting in positive correlations between body mass, pit circumference, and angle of depression. However, if such a physiological constraint existed, but the value of θ_{LIM} (the angle of repose) was sufficiently small so as to be limiting to a greater extent than physiology, it is hypothesized that one would see a positive correlation between pit circumference and body mass, but angle of depression would be independent of both because most individuals would construct pits with an angle of depression equal or close to the angle of repose (θ_{LIM}). These statements, of course, rely on the assumption that sub-optimal pits would be smaller and/or shallower than the optimum, which is consistent with a physiological constraint (Griffiths, 1986).

3.2. Lab data

Strong positive correlations were observed between pit angle of depression and both pit circumference ($\rho = 0.86$, $p < 0.01$) and ant lion mass ($\rho = 0.96$, $p < 0.01$) in the lab. Pit circumference and body mass were significantly positively correlated ($p = 0.008$, $R^2 = 0.6521$) as well ($\rho = 0.81$, $p = 0.02$).

3.3. Field data

Individuals who constructed pits in both the field and the lab constructed approximately 32% shallower ($S = 0$, $p \leqslant 0.01$) and 78% larger ($S = 0$, $p \leqslant 0.01$) pits in the field (Fig. 5), though the magnitudes of these differences did not significantly correlate with their body mass (difference in circumference: ($\rho = -0.43$, $p > 0.2$), difference in angle of depression: ($\rho = 0.14$, $p > 0.2$)), or each other ($\rho = -0.57$, $p > 0.1$). Angle of depression of pits constructed in the field did not significantly correlate with body mass ($\rho = 0.40$, $p = 0.1$), pit density ($\rho = 0.07$, $p > 0.2$), or pit circumference ($\rho = -0.07$, $p > 0.2$). Pit circumference did not significantly correlate with body mass ($\rho = 0.38$, $p > 0.1$), or pit density ($\rho = -0.37$, $p > 0.1$) either. There was also no significant correlation between body mass and pit density ($\rho = -0.08$, $p > 0.2$).

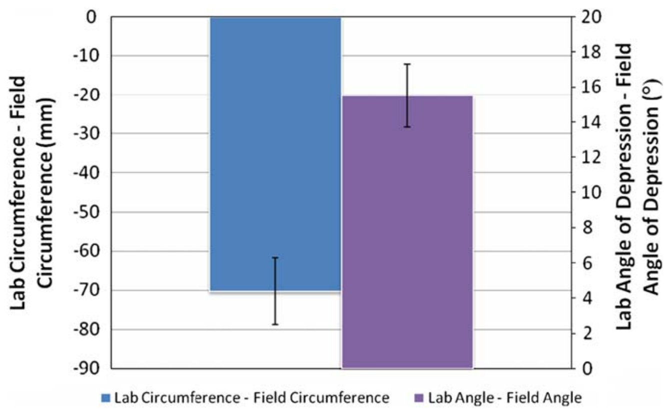

Fig. 5. The mean values of the differences between individuals' pit circumference and pit angle of depression in the field vs. the lab. Individuals constructed significantly shallower pits ($S = 0$, $p \leqslant 0.01$) with significantly larger circumferences ($S = 0$, $p \leqslant 0.01$) in the field. Neither of these differences correlated with ant lion mass (circumference: $\rho = -0.43$, $\rho_{\text{critical},\alpha = 0.05} = -0.74$; angle of depression: $\rho = 0.14$, $\rho_{\text{critical},\alpha = 0.05} = 0.74$).

4. Discussion

Both the field and lab results can potentially be explained, at least in part, using the model. The lab results in this study provide evidence in support of the model given a physiological constraint on pit construction resulting in more sub-optimal dimensions for pits constructed by smaller ant lions (see Griffiths, 1986). In a controlled setting with filtered substrate, and without competition or disturbance, positive correlations between pit circumference, body mass, and angle of depression in *Myrmeleon* sp. were observed. This result contradicts an earlier study by Griffiths (1986) using *Macroleon quinquemaculatus* larvae that found the angle of depression to be negatively correlated with both pit diameter (which is proportional to pit circumference) and body mass. One notable potential source for this discrepancy is the difference in study species. Griffiths (1986) noted that *M. quinquemaculatus* larvae were more efficient at capturing different prey species depending on their own body size. Larger ant lions were more efficient at capturing a larger prey species (*Polyrachis schistacea*), while smaller ant lions were more efficient at capturing a smaller, more agile prey species (*Camponotus* sp.) (Griffiths, 1986). Griffiths (1986) also noted that, for large individuals, prey capture rate depended less on the angle of depression than on the strength of the ant lion, suggesting that these larger ant lions should opt for larger, shallower pits than smaller ant lions. It is possible that angle had a larger effect on prey capture success in the species studied here, although time constraints prevented the experimental exploration of this possibility. Further research is needed experimentally looking at the relationship between the angle of depression and capture efficiency ($f(\theta)$) in *Myrmeleon* sp. so that the model can be refined to make more accurate predictions.

In the field study, pits were significantly shallower and wider than those constructed by the same individuals in the lab. The difference in angle may have been due to the filtration of the substrate in the lab study resulting in a higher angle of repose. Farji-Brener (2003) found angle of depression to decrease with increasing particle size, and Lucas (1982) and Botz et al. (2003) both found the angle of repose (θ_{LIM}) of a substrate to be smaller when the particle size was larger. Botz et al. (2003) further found the pit angles in their study to be statistically indistinguishable from the angles of repose of their substrates. A lower angle of repose in the field (resulting from larger particles) may have restricted the optimal dimensions, allowing more ant lions to reach the best possible angle. This is consistent with the observed lack of correlation between the angle of depression and other parameters in the field mentioned above. The model does predict a slightly higher optimal pit circumference when θ_{LIM} is lower (Figs. 3 and 4), but this certainly does not amount to anything close to the 78% difference observed with the forms of $g(\theta)$ used in the analyses presented here. One other possible explanation from the model is that the act of removing the ant lions from their natural pits, and trans-locating them to the lab represented a perceived decrease in average residency time, which could result in a dramatically decreased optimal circumference in the model, whereas the optimal angle of depression would be unaffected. It is also possible that intraspecific competition resulting from higher densities creates an added selection pressure favouring wide pits (Inacio et al., 1993) in the field. However, pit diameter (proportional to circumference) is often found in empirical data to negatively correlate with density (Day and Zalucki, 2000), and no significant correlation was observed in this study, making this explanation somewhat unlikely. Unfortunately, the experimental results of this study cannot disentangle the effects of density and substrate type because both were effectively altered simultaneously between the two treatments. Further research is needed on this in order to refine the model.

Though the model in this study provides some qualitative and mechanistic insight into the possible effects of substrate variation, further research is also needed to put the predictions of the model into empirical perspective, specifically concerning the nature of $g(\theta)$, approximate values for θ_{MAX} (if it exists), and perhaps most importantly, the approximate values of ratio $\theta_{LIM}/\theta_{MAX}$ in different substrates, which would have an impact on whether the nonlinearity of the function $g(\theta)$ is important to the model's predictions (if this ratio were small enough, $f(\theta)$ would be effectively linear until it truncated at θ_{LIM}). There is some empirical evidence placing the angles of repose of substrates in which ant lions construct pits between 40° and 50° (Botz et al., 2003). The maximum value θ_{MAX} could have is 90°, and the findings of Botz et al. (2003) suggest it is at least sometimes larger than or equal to θ_{LIM}. This places the ratio of $\theta_{LIM}/\theta_{MAX}$ in cases of interest most likely somewhere between 0.5 and 1 (θ_{LIM} would not be relevant to pit dimensions if it exceeded θ_{MAX}), with the exact value varying between substrates. In substrates where this ratio is greater than the E_{NET}-maximizing θ divided by θ_{MAX}, the angle of repose should not affect the pit dimensions either, and we should see pit walls that are shallower than θ_{LIM}. It would be interesting to repeat the comparison of pit angle of depression and angle of repose from Botz et al. (2003) in a wider range of substrate particle sizes to see if this can be observed empirically.

While no significant correlations were found in the field between mass, density, angle of depression, and circumference, the conclusiveness of these findings is slightly suspect in light of the sample size. Conducting field observations in uncontrolled environments often results in more noise than controlled laboratory experiments, which might account for the differences in significance in the field results compared those in the lab. With this in mind, it should be noted that positive correlations between mass and both angle ($\rho = 0.40$) and circumference ($\rho = 0.38$) would have been significant or nearly significant at a 0.1 level of significance ($\rho_{\text{critical},\ n=18,\ \alpha=0.1} = 0.40$). A similar case could be made for a negative correlation between density and pit circumference ($\rho = -0.37$), if one were to repeat this experiment with a larger sample size. Such a repetition of this experiment should definitely be done. It is also possible, however, that extrinsic factors such as frequency of disturbance and angle of repose significantly limited the optimal dimensions in the field to a point where they were less physiologically constrained, or not constrained at all. If this were the case, the model would predict a lack of correlation between these parameters.

To fully understand the trade-offs influencing pit construction in *Myrmeleon* sp., this study shows that body mass, and substrate type are nearly always factors, and conspecific density is also likely to be important. This study further shows that simple models of these trade-offs can be successful in making predictions about optimal dimensional relationships in ant lion pit construction. The model developed in this study provides precise, falsifiable predictions concerning the effects of varying the average residency time on pit circumference (it should vary positively with average residency time to an amount proportional to the square root of the change in average residency time) and angle of depression (there should be no effect of residency time) that present ideal opportunities for future empirical research. The model additionally provides implicit evidence, in combination with the experimental results of this and other studies (Griffiths, 1986; Swenson et al., 2007), for the existence of a physiological constraint on pit construction in ant lions resulting in suboptimality of pit dimensions whose severity depends on body size and hunger level (Heinrich and Heinrich, 1984; Hauber, 1999). Further research explicitly demonstrating this constraint, as well as on its nature and severity, should it exist, is called for.

More generally, this kind of evidence for obligate suboptimality in the foraging behaviour of a species challenges an assumption, that evolution has already led to perfect (or near perfect) adaptation, which is used often in ecological literature attempting to explain and contextualize natural phenomena. This assumption should perhaps be re-examined on a case-by-case basis.

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