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蟻蛉幼蟲的覓食行為

Foraging Behavior of Antlion Larvae



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## 中文摘要

蟻蛉幼蟲（即蟻獅）是會構築陷阱來捕捉獵物的昆蟲。至今與蟻獅構築沙阱行為相關之研究包羅萬象，但隱含於其行為背後的決策機制仍鮮少被探究。本篇論文分為三個章節，第一章包含蟻獅的生活史簡述與研究對象臀腋蟻蛉（*Myrmeleon persimilis*）的基本介紹。第二及第三章分別由兩個層面探討蟻獅構築沙阱之行為機制。

第一個探討層面即蟻獅覓食策略的轉換機制。觀察發現，蟻獅採取兩種不同的覓食策略，即構築沙阱覓食（pit-trapping strategy）與伏擊獵物（ambush strategy）。然而兩策略間轉換的機制目前尚未被瞭解透徹。在第二章中我運用動態最適化模型（dynamic optimization model），在模擬的各種生態環境（ecological conditions）變化下發現：蟻獅於兩種覓食方式間轉換之行為是最適覓食策略。該模型預測蟻獅在自身能量較高時應採取伏擊策略、能量較低時應構築沙阱來覓食。以上預測與一重要假設相關，即蟻獅在決定覓食策略時面臨生態上的取捨（ecological tradeoff）：構築沙阱一方面能增加成功捕捉獵物的機率，但另一方面（因沙阱所提供的線索）也增加被天敵攻擊的機會。透過實驗，該模型的預測和重要假設均被驗證。綜合各項結果：蟻獅取捨於構築沙阱及伏擊的利與弊，動態地選擇將其適存值（fitness）最大化的策略。

第二個探討層面為蟻獅沙阱的空間分布。野外觀察發現，蟻獅的沙阱常聚集在一起，然而該現象的缺點顯而易見（如易被天敵發現及種內競爭），因此蟻獅的聚集現象仍為生態學上一未解的難題。第三章中，我以賽局理論（game theory）的觀點，提供了對於蟻獅聚集現象的可能解釋。運用空間直觀性個體基準模型（spatially explicit individual based model），我建構出一模擬的空間，該空間由兩隻蟻獅個體以及提供牠們覓食的生態環境所組成。結果指出：當族群中的蟻獅個體採取一演化穩定策略（evolutionarily stable strategy）—和其他個體相鄰時降低換位（relocation）機率，將促使聚集現象形成。為測試由模型得到的結果，我以擲沙粒行為模擬鄰近個體的存在，並設計實驗來檢測蟻獅是否會表現出上述之演化穩定策略。實驗發現，接收到擲沙粒訊息的個體降低了牠們換位的機率。綜合各項結果：因鄰近個體能提供環境中可利用資源（如獵物）的重要訊息，在演化作用下，當與其他個體相鄰時減少換位為一穩定策略，

蟻獅個體因而聚集在一起。

**關鍵詞：**蟻蛉幼蟲、蟻蛉屬、覓食行為、生態取捨、聚集、演化賽局理論、換位



## Abstract

Antlions are trap-building insects, but their foraging behavior does not simply consist of the pit construction. To date, a number of aspects of the pit-trapping behavior in antlions have been examined; however, the decision-making mechanisms underlying the observed behavioral responses remain largely unknown. In this thesis, I examined two aspects of the pit-foraging behavior of antlions. A common antlion species in Taiwan, *Myrmeleon persimilis*, was used as the model organism. In Chapter 1, brief descriptions of the natural history of antlions and the focal species are presented.

The first aspect of the pit-foraging behavior examined in this thesis is the act of pit foraging itself. That is, although antlions are typically considered to forage with pits, they can also ambush prey without using pits. Why antlions switch between the two strategies is not fully understood. In Chapter 2, using a dynamic optimization model, I show that the strategy-switching behavior is the optimal foraging strategy under a variety of ecological conditions. In particular, the model predicts that antlions should exhibit the pit-trapping strategy when their energy status is low and should use the ambush strategy when their energy status is high. One of the key assumptions leading to this result is an ecological tradeoff associated with the pit-foraging strategy where pit-foraging increases prey capture success but also increases predation risk. The prediction and the assumption of the model were empirically verified. These results suggest that antlions dynamically choose their strategies to maximize fitness by balancing the cost and benefit of the pit-trapping vs. ambush strategies.

The second aspect concerns a spatial aspect of pit-foraging. Antlion pits are commonly found in aggregations in the field, but finding disadvantages of the aggregation (e.g., predation risk and competition) is easier than finding an advantage of it. Thus the pit aggregation is an ecological conundrum. In Chapter 3, I offer an

explanation for the aggregation behavior from a game theoretical point of view. By using a spatially explicit individual based model, an ecological scenario where two antlions forage in the common environment was simulated, and how different relocation strategies affect their fitness was examined. The results confirmed that a strategy leading to aggregations (i.e., relocate less when other individuals are nearby) can be the unique evolutionarily stable strategy. To validate the theoretical result, whether antlions follow the evolutionarily stable strategy was empirically examined. The presence of neighbors was simulated by sand tossing, and antlions that received the simulated sand tossing decreased their tendency to relocate. These results suggest that antlions aggregate because the presence of neighbors contains important information about the site quality, and the behavior has been selected through the evolutionary game.

**Key words:** antlions, *Myrmeleon*, foraging behavior, ecological tradeoff, aggregation, evolutionary game theory, relocation



## Table of contents

Acknowledgement .....	i
Chinese abstract .....	ii
Abstract .....	iv
Table of contents .....	vi
List of tables.....	viii
List of figures.....	ix
Chapter 1. Antlions and their pit-trapping behavior: the thesis introduction.....	1
1.1. Introduction .....	1
1.2. Natural history of antlions.....	2
1.3. Species description.....	3
Chapter 2. Adaptive foraging strategy switches in the antlion larva, <i>Myrmeleon persimilis</i> (Neuroptera: Myrmeleontidae) .....	7
2.1. Introduction .....	7
2.2. Materials and methods.....	9
2.2.1. Study animals .....	9
2.2.2. Dynamic optimization model.....	9
2.2.3. Laboratory experiments .....	11
2.2.3.1. <i>Effects of prey on pit-trapping individuals</i> .....	12
2.2.3.2. <i>Effects of prey on ambushing individuals</i> .....	13
2.2.3.3. <i>Effects of foraging strategy on cannibalism risk</i> .....	13
2.2.3.4. <i>Data analysis</i> .....	14
2.2.4. Field observation .....	14
2.3. Results.....	15
2.3.1. Dynamic optimization model.....	15
2.3.2. Laboratory experiments .....	16
2.3.2.1. <i>Effects of prey on pit-trapping individuals</i> .....	16
2.3.2.2. <i>Effects of prey on ambushing individuals</i> .....	17
2.3.2.3. <i>Effects of foraging strategy on cannibalism risk</i> .....	17
2.3.3. Field observation .....	17
2.4. Discussion.....	18



## Table of contents (continued)

Chapter 3. Use of social information in relocation decisions of the antlion larva, <i>Myrmeleon persimilis</i> (Neuroptera: Myrmeleontidae) .....	29
3.1. Introduction .....	29
3.2. Materials and methods .....	31
3.2.1. Individual based model.....	31
3.2.1.1. <i>General flow</i> .....	31
3.2.1.2. <i>Environment</i> .....	31
3.2.1.3. <i>Ants</i> .....	32
3.2.1.4. <i>Antlions</i> .....	33
3.2.1.5. <i>Analysis</i> .....	35
3.2.2. Laboratory experiment .....	36
3.2.2.1. <i>Study animals</i> .....	36
3.2.2.2. <i>Effects of prey supply and sand tossing on relocation</i> .....	37
3.2.2.3. <i>Statistical analysis</i> .....	38
3.3. Results.....	38
3.3.1. Individual based model.....	38
3.3.2. Effects of prey supply and sand tossing on relocation .....	39
3.4. Discussion .....	40
References .....	49



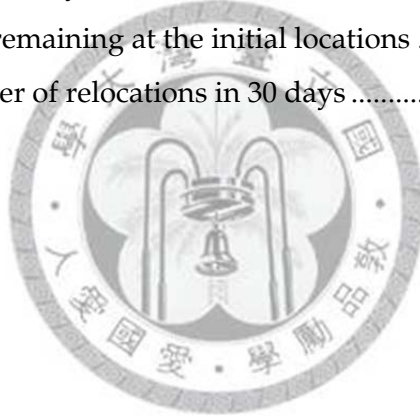
## List of tables

Table 3-1. Parameters of the individual based model, their definitions and default values.....	43
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## List of figures

Fig. 1-1. Characteristics of the adults and larvae of <i>Myrmeleon persimilis</i> .....	5
Fig. 2-1. Two foraging strategies of <i>Myrmeleon persimilis</i> larvae.....	22
Fig. 2-2. Optimal behavioral strategy solutions obtained by the dynamic optimization model.....	23
Fig. 2-3. Proportion of pit-trapping individuals switched to exhibit the ambush strategy .....	24
Fig. 2-4. Proportion of ambushing individuals switched to exhibit the pit-trapping strategy .....	25
Fig. 2-5. Box plots showing weight loss during starvation in <i>Myrmeleon persimilis</i> .....	26
Fig. 2-6. Relationship between the weights and pit diameters of antlions.....	27
Fig. 3-1. Aggregations formed by <i>Myrmeleon persimilis</i> larvae.....	44
Fig. 3-2. Average energy attained by antlions at the end of a simulation run.....	45
Fig. 3-3. Proportion of larvae remaining at the initial locations .....	46
Fig. 3-4. Boxplots of the number of relocations in 30 days .....	47



# Chapter 1

## Antlions and their pit-trapping behavior: the thesis introduction

### 1.1. Introduction

Trap building is a unique foraging method adopted by sit-and-wait predators. Less than 1% of terrestrial animals build traps to capture prey in nature (Ruxton and Hansell 2009). Besides human beings, all other trap-building animals are invertebrates, and their trap-building behavior can be categorized into two types (Hansell 2008). The organisms of the first type, such as glowworms (Broadley and Stringer 2001) and many spider species, make use of self-secreted materials. The second type animals, on the other hand, do not use self-secreted materials but utilize external substances (e.g., sand or soil particles) to construct pitfall traps, which is considered less costly compared to the first type (Lucas 1985). There are only two kinds of invertebrates adopting the second method: snipe fly larvae (wormlions; Diptera: Rhagionidae and Vermileonidae) and antlion larvae (antlions; Neuroptera: Myrmeleontidae) (Ruxton and Hansell 2009).

Even though antlions are trap-building animals, their foraging behavior does not simply consist of the pit construction, and many aspects of the trap-foraging are finely adjusted. For example, antlions vary their pit architecture (e.g., pit diameter and pit depth) with respect to abiotic factors such as microclimatological factors (Youthed and Moran 1969; Scharf et al. 2008b), sand particle size (Farji-Brener 2003), photoperiod (Scharf et al. 2008b) and biotic factors such as prey availability (Youthed and Moran 1969; Hauber 1999) and competitor density (Youthed and Moran 1969).

Although many factors that affect antlions' pit-trapping behavior are known, some observations on the behavior still deserve explanations. My thesis aims to offer concrete explanations for two unresolved observations. First, antlion larvae sometimes do not construct pits to capture prey and instead ambush prey without

pits. The decision rule that antlions use to decide whether to pit-forage or ambush is not known. This question is addressed in Chapter 2. The other unresolved observation is about the pit-site selection. Antlion pits are found in aggregations despite the obvious costs such as increased competition for resources. Thus, pit aggregation is an ecological puzzle. In Chapter 3, I present an explanation for this question from a game theoretical point of view.

This thesis consists of three chapters. Chapter 2 and Chapter 3 were written as independent manuscripts, and thus some of the contents (e.g., information on the species) are intentionally redundant. In the rest of this chapter, I briefly review the natural history of antlions and describe the focal species of the thesis. The species description given in this chapter is more detailed than those in Chapter 2 and Chapter 3.

## 1.2. Natural history of antlions

There are over 2000 known species of antlions (Neuroptera: Myrmeleontidae) worldwide (Nardi 2007). Three major subfamilies in Myrmeleontidae include Stilbopteryginae, Palparinae, and Myrmeleontinae (myrmex = ant; leo = lion) (Stange 1994). All antlion species in Taiwan belong to the largest subfamily Myrmeleontinae (Stange et al. 2002).

Adult antlions look like damselflies but their antennae are in a clavate form and are weak fliers. Female adults insert their abdomens into the sand for texture testing when laying eggs, and the oviposited eggs are coated with sand particles for camouflage (Stange et al. 2002). Larval antlions have three long instar stages (e.g., up to two years) followed by pupation. Several weeks after pupation, mobile pupae cut open the cocoons with mandibles, climbing out onto the sand surfaces and dry their body parts on available objects (Stange et al. 2002). The body of a larval antlion is covered with thousands of sensory bristles that are sensitive to vibration (Nardi 2007).

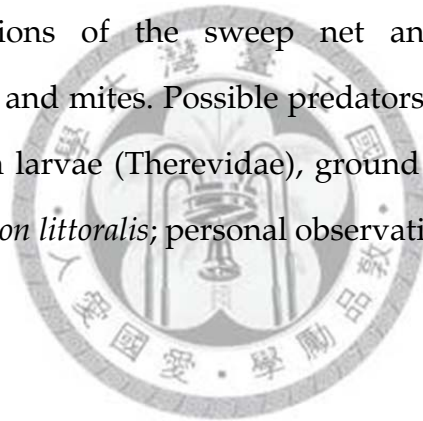
Pit-building antlions are commonly categorized as sit-and-wait predators (Wilson 1974; Scharf and Ovadia 2006) that remain at fixed locations for prolonged periods, usually building traps to capture mobile prey. Antlions construct conical pits to trap invertebrates in the following steps (described by Youthed and Moran (1969) in addition to our personal observations). When constructing a pit, the larva flicks sand particles outwards with its head and usually excavates a small pit at first. Subsequently, it creates a circular furrow and spirals inwards by tossing sands, increasing the depth of the furrow. Finally, it buries itself at the bottom of the pit. Owing to the pit structure, small invertebrates which encounter pits often slip down into the jaws of the awaiting larvae. Once an antlion larva seizes a falling prey by its mandibles, digestive juice is secreted (Nardi 2007). The antlion then extracts the digested prey through hollow jaws which consist of maxillae interlocked to the grooves in mandibles (Griffiths 1980). After consuming a prey, the larva places the corpse on the head and throws it out of the pit. Ants (Matsura 1987) and larval insects that live underneath the sand (Stange et al. 2002) are typical prey of antlions.

### 1.3. Species description

The antlion species used in this thesis is *Myrmeleon persimilis* (Fig. 1-1A), an endemic and the most widespread coastal species of the genus *Myrmeleon* in Taiwan (Stange et al. 2002). The length of the forewings of *M. persimilis* adult ranges from 22 to 29 mm, and the body color is dark brown. A few morphological characteristics of *M. persimilis* can be used to distinguish it from other closely related species (Stange et al. 2002). First, the male adult *M. persimilis* has large pilura axillares on its hind wings (Fig. 1-1B). Second, the knob part of antenna is much wider than the pedicel part and is covered with mat-like setae which are much shorter than the knob width (Fig. 1-1C). Third, there is one pair of submedian round dark-brown spots (nearly touching at the midline of the head) on the ventral head capsule (Fig. 1-1D). *M. persimilis* larvae, like other antlion species, have three instar stages and usually

pupate inside sand cocoons. At the time of pupation, their weights reach about 50 mg. The pupal period is about 26 days (Stange et al. 2002). Eclosions take place mainly in February to May in northern parts of Taiwan (personal observation).

In coastal habitats of northern Taiwan, *M. persimilis* larvae usually make pitfall traps under bushes (but see Stange et al. (2002) for a different observation) but sometimes in open fields to capture small invertebrates. I used pitfall traps and sweep net samplings to examine the possible prey of the antlion in the field and found that the most common potential prey (invertebrates less than 0.5 cm) in the habitat was the ant, *Pheidole megacephala* (97.3% in the pitfall trap samples and 13.6% in the sweep net samples). Other potential prey included leafhoppers (74.3% in the sweep net samples) and dipteran insects (4.7% in the sweep net samples). The remaining small proportions of the sweep net and pitfall samples include hemipterans, coleopterans, and mites. Possible predators of larval *M. persimilis* in the study site include dipteran larvae (Therevidae), ground beetles, and larvae of other antlion species (e.g., *Distoleon littoralis*; personal observations).



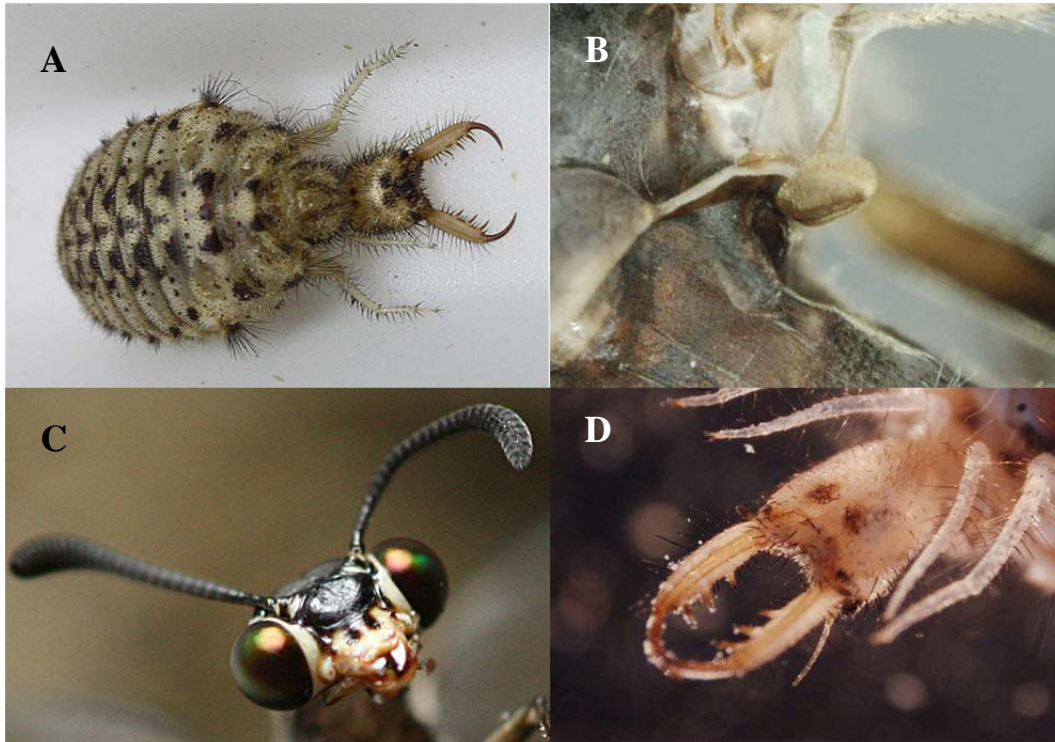


Fig. 1-1. Characteristics of the adults and larvae of *Myrmeleon persimilis*. A: Appearance of a third instar larva. B: The large pilura axillary on a hind wing. C: The antennae covered with fairy setae; the knob part is wider than the pedicel part. D: One pair of dark brown spots nearly touching the midline of the ventral head capsule.





## Chapter 2

### Adaptive foraging strategy switches in the antlion larva, *Myrmeleon persimilis* (Neuroptera: Myrmeleontidae)

#### 2.1. Introduction

Many animals exhibit distinct foraging strategies (Helfman 1990; Schmitz 2005). Sit-and-wait foraging and active foraging, for example, are two distinct strategies, and their economics have been widely studied in a variety of ecological contexts (Helfman 1990; Perry 1999; Scharf et al. 2006). There are species that specialize on exhibiting one foraging strategy whereas other species flexibly switch among different strategies. For example, some lizard species specialize on either active foraging or sit-and-wait foraging (Huey and Pianka 1981). On the other hand, many species of fish and invertebrates switch between active and sit-and-wait tactics (Inoue and Matura 1983; Formanowicz and Bradley 1987; Hirvonen 1999). Foraging strategies adopted by predators influence behavioral responses of their prey (Sih et al. 1998; Butler 2005; Loria et al. 2008), affecting properties of food webs and ecosystem functions (Schmitz and Suttle 2001; Schmitz 2008). Understanding how animals make their foraging decisions is important not only for the study of behavior but also examining larger scale ecological processes such as community and ecosystem level dynamics (Bolker et al. 2003; Abrams 2010; Schmitz 2010).

Antlion larvae (Neuroptera: Myrmeleontidae) are commonly known as sit-and-wait predatory insects that capture small invertebrates in sandy environments using conical pits (Wilson 1974; Griffiths 1980; Lucas 1982; Griffiths 1986; Devetak 2005; Devetak et al. 2005; Fertin and Casas 2006; Nardi 2007; Ruxton and Hansell 2009). Some antlion species can also capture prey without constructing pits (we call it ambush strategy hereafter) (Miller et al. 1999). In other words, those species can flexibly switch between the pit-trapping strategy and the ambush strategy. The pit-trapping strategy enjoys higher prey capture successes than the

ambush strategy with limited hunting range (Heinrich and Heinrich 1984; Griffiths 1986; Cain 1987; van Zyl et al. 1997; Elimelech and Pinshow 2008). In addition, previous studies that investigated the energetic cost of the pit-trapping strategy found that the pit maintenance cost is small even considering the low basal metabolism of the antlion (Lucas 1985; van Zyl et al. 1997). Thus, the energetic tradeoff does not appear as the primary factor for antlions to switch between the strategies.

Predation risk is an important factor that affects the foraging behavior of many organisms (Kats and Dill 1998; Lima 1998; McPeck and Peckarsky 1998; Caro 2005), and antlions are no exception. For example, Florida scrub-jays locate *Myrmeleon carolinus* antlion larvae from the pits and preferentially predate on larvae with large pits (Hauber 1999). Considering the poor mobility of antlions (Farji-Brener 2003), pits can impose high predation risk on the individuals that maintain them. Lucas (1985) found that antlions usually construct pits in dusk for preventing attacks by predators. Furthermore, Loria et al. (2008) found that antlions decrease the pit-building activity when potential predators exist in their experiments. Despite these findings, antlion larvae still exhibit large behavioral variation, e.g., under the enemy free environment in the laboratory condition and within the same area in the field (personal observation). In other words, some individuals forage with pits while others ambush even in the same environment. Thus, although predation risk appears to be an important factor for antlions to switch between the pit-trapping and the ambush strategies, the behavioral rule that antlions use to switch foraging strategy is not well understood.

In this study, we examined how the antlion larva *Myrmeleon persimilis* switches its foraging strategies. The key factor we focused was the tradeoff between the pit-trapping strategy and the ambush strategy discussed above where the pit-trapping strategy results in a higher prey intake rate but also faces higher predation risk. We show that antlions switch between the two foraging strategies

even when the predation risk of the environment is constant (e.g., laboratory condition) using an optimal foraging model whose predictions and an assumption were empirically validated. As will be discussed below, because the results imply that the physiological status of the antlion is an important factor for the behavioral expression, supplementary field observations were also conducted to evaluate the natural physiological conditions of antlions.

## 2.2. Materials and methods

### 2.2.1. Study animals

The antlion species used in this study is *Myrmeleon persimilis* (Neuroptera: Myrmeleontidae), an endemic and the most widespread coastal species of genus *Myrmeleon* in Taiwan (Stange et al. 2002). *M. persimilis* larva, like other antlion species, has three instar stages and usually eclose during February to May (unpublished data). For a more detailed description of the species, see Chapter 1.

*M. persimilis* larvae were collected at a coastal habitat in Shimen District, New Taipei City (25°18'N, 121°32'E). It is a sandy region with abundant rainfall. When it rains, *M. persimilis* larvae burrow a few centimeters under the sand surface (directly beneath the original pit site) and come out when the sand is dried. The common plant species in the habitat include wormwoods (*Artemisia capillaries*), tree heliotropes (*Tournefortia argentea*), Hosobawadan (*Crepidiastrum lanceolatum*), and Indian Blankets (*Gaillardia pulchella*) (personal observations). Pit-foraging individuals usually make the pit traps under bushes but sometimes in open field to capture small invertebrates such as ants (*Pheidole megacephala*) and larvae of darkling beetles. Potential predators of larval *M. persimilis* in this habitat include dipteran larvae (Therevidae), ground beetles, and larvae of other antlion species (e.g., *Distoleon littoralis*).

### 2.2.2. Dynamic optimization model

A dynamic optimization model was constructed to examine how an antlion

chooses its foraging strategy based on its states (i.e., energy state and time) to maximize its fitness. The model considers the situation where an antlion aims to survive for a specific time duration  $T$  (e.g., the larval stage). In each time step (discussed below), the larva makes a decision about its foraging strategy. There are two behavioral options: pit-foraging strategy or ambush strategy. When the larva adopts the pit-trapping strategy, it enjoys a greater prey capturing success (Griffiths 1991; Nardi 2007; Elimelech and Pinshow 2008) but also suffers higher predation risk (Hauber 1999) with respect to the ambush strategy. There are three parameters for each strategy in the model:  $f_Q$  (foraging success),  $d_Q$  (predation risk), and  $c_Q$  (metabolic cost). The subscript ( $Q = P$  or  $A$ ) describes the behavioral option. For example,  $f_P$  and  $f_A$  are the foraging success for an individual with the pit-trapping strategy and with the ambush strategy, respectively.

The larva is associated with two state variables: energy state  $x$  and time  $t$ . The energy state varies from 1 to  $x_{\max}$ , and the time step varies from 1 to  $T$ . Suppose, at time  $t$ , the larva (whose energy state is  $x$ ) chooses the behavioral option  $Q$ , its expected fitness is

$$W_Q = (1 - d_Q)[f_Q F(x + 1, t + 1) + (1 - f_Q)(1 - c_Q)F(x, t + 1) + (1 - f_Q)c_Q F(x - 1, t + 1)]$$

where  $F(x, t)$  is the maximum expected fitness of the larva at time  $t$  whose energy state is  $x$ . (How to obtain the values for  $F$  is discussed below.) In explaining the above equation, if the larva is predated (the probability is  $d_Q$ ), its fitness is zero. If the larva escapes from predation risk ( $1 - d_Q$ ), it may forage successfully (the probability is  $f_Q$ ) or miss its prey ( $1 - f_Q$ ). The larva which forages successfully improves its energy state to a higher level. On the other hand, if the larva fails to capture prey, it may lose its energy owing to metabolic cost (the probability is  $c_Q$ ), or maintaining its energy state ( $1 - c_Q$ ). Regardless of the foraging option ( $Q = P$  or  $A$ ), the general mechanics are the same. However, there are tradeoffs in the parameters. The model predicts that the option  $P$  (pit-trapping) is the optimal strategy if  $W_P > W_A$ ; the option  $A$

(ambushing) is the optimal strategy when  $W_A > W_P$ .

We are interested in how the ecological tradeoff (i.e., maintaining a pit increases predation risk while also increasing foraging success) influences the behavioral decision. Thus  $d_P > d_A$  and  $f_P > f_A$  are assumed. To analyze the model, we need to determine the six parameter values:  $d_Q, f_Q, c_Q$  ( $Q = P$  or  $A$ ), and the state conditions:  $x_{\max}$  and  $T$ . In addition, the terminal fitness must be decided (Mangel and Clark 1988). The terminal fitness describes the fitness of the individual with energy  $x$  at the last time step. For the results we describe below, the terminal fitness is assumed to be the energy state  $x$ . In other words, the greater the energy state, the greater the fitness is. However, changing the detail (e.g., the fitness increases acceleratingly or deceleratingly with the energy state) does not alter the qualitative conclusion. We set  $x_{\max} = 10$  and  $T = 30$ , but the qualitative results are also robust to these settings (details are mentioned in *Results*). Once the details are specified, the optimal solutions of the model can be derived using the backward iteration method (Mangel and Clark 1988).

To validate that the results are not specific to the particular parameter values, the parameter values were varied for the entire range. That is, because each parameter is a probability,  $d_Q$  and  $f_Q$  were varied from 0 to 1 with an increment of 0.1, and all the combinations satisfying the assumptions were examined. The metabolic costs  $c_Q$  were assumed to be the same because of the low cost of pit-maintenance in antlions (Lucas 1985; van Zyl et al. 1997).

### 2.2.3. Laboratory experiments

As will be described below, the dynamic optimization model predicts that the optimal strategy is the pit-trapping strategy when the energy status is low (e.g., starved) and is the ambush strategy when the energy status is high. Laboratory experiments were conducted to examine whether antlions forage according to the optimal foraging predictions. In addition, an assumption of the model (i.e.,  $d_P > d_A$ ,

the probability of death due to predation is higher for the pit-trapping strategy) was also tested to strengthen the validity of the model.

### 2.2.3.1. Effects of prey on pit-trapping individuals

In this experiment, whether pit-trapping antlions change their strategy to the ambush strategy when their energy states improve was examined. The ambush strategy was defined as hiding on the sand surface with only mandibles exposing outside, sometimes with a shallow cavity (Fig. 2-1A) (Heinrich and Heinrich 1984). If there was a shallow cavity, its diameter (though may not be a circular shape) was smaller than 1 cm. The pit-trapping strategy was defined as having a conical pitfall trap with the diameter greater than 1 cm (Fig. 2-1B). The pit-trapping individual usually stayed at the bottom of the pit, opening its mandibles and waiting for falling prey.

Antlions used in the experiment were individually housed in containers filled with sands (44.5 cm by 34.7 cm, sand depth 4 cm) and were maintained in a controlled environment: temperature ( $25 \pm 2^\circ\text{C}$ ), humidity ( $40 \pm 5\%$ ), and L:D 14:10 cycle. Second instar antlions ( $n = 37$ ) were fed with flour beetle larvae, *Tribolium confusum*, until they stopped consuming a prey. Subsequently they were starved for four weeks to standardize the starvation levels of the study subjects. At this point, all individuals exhibited the pit-trapping strategy. The starved larvae were randomly allocated to three treatment levels: 0, 1, or 6 prey items (third instar *T. confusum* larvae were used as the prey). The low treatment levels (i.e., 1 and 0 prey) were intended to affect the satiation levels of the larvae only little to none, while the high prey level (i.e., 6 prey) was intended to increase the satiation level substantially. Prey larvae were placed by pits in such a way they walked into the pits by themselves. In the multiple prey treatment level, one prey was given at a time, and the subsequent prey was introduced after the preceding prey was consumed. Whether the pit-trapping individuals switched their strategies to the ambush strategy was



recorded after 24 h.

#### 2.2.3.2. *Effects of prey on ambushing individuals*

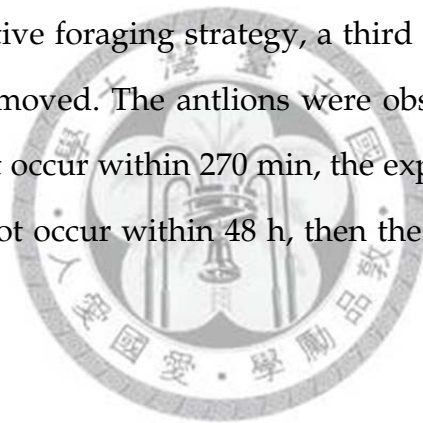
The purpose in this experiment is to test another prediction of the model; ambushing individuals change their foraging mode to the pit-trapping strategy in response to a shortage of prey (i.e., low energy status in the model). As in the previous experiment, antlions used in the experiment were individually housed in containers filled with sands (44.5 cm by 34.7 cm, sand depth 4 cm) and were maintained in a controlled environment: temperature ( $25 \pm 2^\circ\text{C}$ ), humidity ( $40 \pm 5\%$ ), and L:D 14:10 cycle. To conduct the experiment, we needed to prepare antlions exhibiting the ambush strategy. Because the first experiment described above showed that the prey supply makes them exhibit the ambush strategy (see *Results* for details), second instar antlions were fed continuously until exhibiting the ambush strategy. Ambushing individuals were randomly allocated to two treatment levels: no prey ( $n = 35$ ), two prey items ( $n = 35$ ) (third instar *T. confusum* larvae were used as the prey). Unlike the previous experiment, the ambushing larvae were generally more satiated so that the large treatment effects could not be established. Furthermore, in the two prey treatment level, three (of the 35 replications) antlions ate only one larvae even though two larvae were provided (i.e., did not eat the second prey item). Thus for the data analysis, these three replications were considered as a new treatment level (i.e., one prey). As in the previous experiment, the purpose of the treatment was to create differences in the energy state of the study subjects. Subsequently, whether the ambushing antlions switched their strategies to the pit-trapping strategy was recorded after 24 h.

#### 2.2.3.3. *Effects of foraging strategy on cannibalism risk*

The purpose in this experiment was to test an assumption of the model; the probability of death due to predation is higher with the pit-trapping strategy than the

ambushing strategy. Previous studies have shown that smaller antlion larvae were more likely to be cannibalized by larger larvae especially when the individual density was high (Matsura and Takano 1989; Griffiths 1992; Gotelli 1997). Therefore, in this experiment, starved third instar antlions (starved more than one month) were used as predators.

In a plastic cup (diameter: 8.4 cm; sand depth: 3.5 cm; volume of sand: 194 cm<sup>3</sup>), three equal pie-shaped areas were created with plastic plate partitions. One trap-building second instar larva, one ambushing second instar larva, and one third instar larva were randomly introduced: one in each area. The second instar larvae were introduced first. The foraging strategies of the second instar larvae were manipulated by controlling their starvation status as described above. After each larvae assumed the respective foraging strategy, a third instar larva was introduced, and the partitions were removed. The antlions were observed every 30 min for 270 min. If cannibalism did not occur within 270 min, the experimental trial was checked again after 24 h. If it did not occur within 48 h, then the experiment was terminated regardless of the outcome.



#### 2.2.3.4. Data analysis

When testing the effects of prey on pit-trapping and ambushing individuals, Binomial Generalized Linear Model (GLM) was used to analyze the probability of switching to the other strategy (either pit-trapping or ambush strategy). The predictor variable is the number of consumed prey item (i.e., treatment), and whether the larva switches to another strategy is the binary response variable. The Binomial test was used to test whether third instar larvae preferentially forage on trap-building or ambushing second instar larvae in the cannibalism experiment.

#### 2.2.4. Field observation

Again, as will be described below, the model predicts that an important factor

for an antlion to decide its foraging strategy is its energy state. To gain some information on this variable, we examined the starvation status of antlions in the field.

All field observations were conducted between 0900 hours and 1800 hours. When we observed a pit in the field, the diameter of the pit was recorded with a caliper. Then, the larva was dug out, and its weight and head width were recorded in the laboratory within a few hours of the collection. These measurements represent the conditions of larvae in the field. Subsequently, larvae were kept in plastic cups (5.2 cm in diameter which is enough for larvae in each stage can construct a pit) filled with sand collected from the same habitat and were maintained in a controlled room whose condition is described above. Immediately after the initial measurement, each larva was fed sufficient until it stopped consuming a prey; flour beetle larvae (*T. confusum*) were used as prey. This procedure usually took 7 h and larvae consumed 3 to 6 flour beetle larvae to attain the satiation (take the second instar larva for example). After they reached satiation, their weights were recorded again. These weights represent the weights at satiation. At this point, we have the field observed weight and the satiation weight from each larva. Subsequently, the larvae were starved for four weeks and their weights during starvation were recorded weekly.

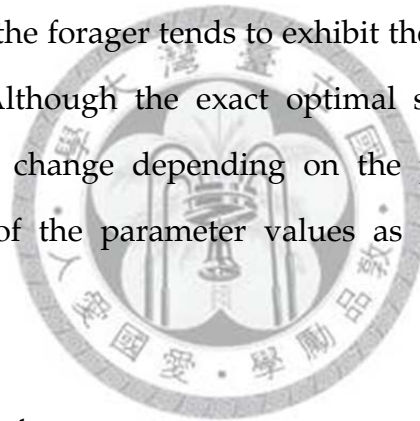
Initially, we planned to quantify the starvation status of antlions in the field based on the weight loss profile characterized in the laboratory (Jakob et al. 1996; Bilde and Toft 1998). However, because the majority of the antlions in the field had much smaller weights than the weights after 28 days of starvation (details are described in *Results*), the extrapolation was not conducted.

## **2.3. Results**

### **2.3.1. Dynamic optimization model**

Depending on the parameter values, there are three possible outcomes: always (i.e., regardless of the state variables  $t$  and  $x$ ) ambush, always pit-forage, and change

the strategy depending on the state variables. Given the parameter constraints (i.e.,  $d_P > d_A$  and  $f_P > f_A$ ), the tradeoff must be sufficiently large for the state-dependent strategy (i.e., switching strategy) to emerge. For example, the parameter combination ( $d_P = 0.2, d_A = 0.1, f_P = 0.2, f_A = 0.1, c_P = 0.1, c_A = 0.1$ ) will result in a situation where the ambush strategy is always optimal despite the existence of the tradeoff. However, further increasing  $f_P$  (e.g., an increase of the tradeoff size) makes the pit-foraging optimal depending on the state variables (Fig. 2-2). When this occurs, the exact state variable combinations in which pit-foraging is optimal will change, but a qualitative pattern is the same. The pattern is that for a given time point  $t$ , if the optimal strategy varies depending on the energy state, the optimal strategy is pit-trapping if  $x \leq x^*$  and ambush if  $x > x^*$  where  $x^*$  is the critical energy state that separates the behavioral strategies. In other words, the forager tends to exhibit the pit-trapping strategy when its energy state is low. Although the exact optimal solution for a specific state variable combination will change depending on the parameters, this qualitative pattern holds regardless of the parameter values as long as the constraints are imposed.



## 2.3.2. Laboratory experiments

### 2.3.2.1. Effects of prey on pit-trapping individuals

There was a positive relationship between the probability of switching to the ambush strategy and the number of prey given to them (Fig. 2-3). The estimated model is  $\text{logit}(p) = -1.944 + 0.482x$  where  $p$  is the probability and  $x$  is the number of prey (Binomial GLM,  $p$ -values for the intercept and the slope are 0.001 and 0.002, respectively based on the Wald test). The positive (i.e., 0.482) and significant treatment coefficient suggests that increasing one prey will increase the odds of switching to the ambush strategy by 61%.

### 2.3.2.2. Effects of prey on ambushing individuals

The prey supply had a negative effect on the probability of switching to the pit-trapping strategy (Fig. 2-4). In other words, when prey were not given to the antlions, those antlions were more likely to begin to exhibit the pit-trapping strategy. The estimated model is  $\text{logit}(p) = -0.208 - 1.092x$  where  $p$  is the probability of switching to the pit-trapping strategy, and  $x$  is the number of prey (Binomial GLM,  $p$ -values for the intercept and the slope are 0.536 and 0.002, respectively based on the Wald test). The negative (i.e.,  $-1.092$ ) and significant treatment coefficient suggests that increasing one prey will decrease the odds of switching to the pit-trapping strategy by 66%.

### 2.3.2.3. Effects of foraging strategy on cannibalism risk

Cannibalism events were rare. Among 106 experimental trials, only nine trials resulted in cannibalism events in the given experimental duration (i.e., 48 h). However, given that cannibalism occurred, third instar individuals cannibalized pit-trapping individuals (eight cannibalism events) more than ambushing individuals (one cannibalism event). The result suggests that the pit-trapping strategy is more vulnerable than the ambush strategy (Binomial test:  $p = 0.045$ ).

### 2.3.3. Field observation

Figure 2-5 shows the trends of the weight decline since satiation under starvation. Even when antlions were starved for four weeks, the weight losses were not substantial relative to the body weights. The weights of the antlions in the field were generally lower than the weights of them in the laboratory after 28 days of starvation. The average ( $\pm$  SD) weights of the second instars ( $n = 49$ ) and third instars ( $n = 46$ ) after 28 days of starvation were  $9.00 \pm 2.36$  mg and  $23.38 \pm 6.84$  mg, respectively. The average ( $\pm$  SD) weights of the second instars and the third instars in the field were  $7.96 \pm 2.50$  mg and  $19.05 \pm 6.20$  mg, respectively. Based on the within individual

comparison, of 49 second instar individuals, the field weights were lower than the weights at 28th days of starvation for 37 individuals (76%). Of 46 third instar individuals, the same was true for 40 individuals (87%). These results suggest that antlions in the field are unlikely to attain satiation.

The weights of antlions and their pit diameters in the field were positively correlated for the third instar (Wald test,  $p < 0.001$ ) (Fig. 2-6), but no significant trend was observed for the second instar (Wald test,  $p = 0.63$ ).

## 2.4. Discussion

In this study, theoretical and empirical approaches were used to understand how an antlion changes foraging strategy. The model predicted that the optimal strategy is the ambush strategy when the energy status is high and is the pit-trapping strategy when the energy status is low. The model predictions as well as an assumption of the model were confirmed by laboratory experiments. These results suggest that the model captures important dynamics in the antlion foraging scenario and thus suggest that antlions choose their strategy to maximize their fitness by balancing the cost and benefit of the pit-trapping vs. ambush strategies.

The dynamic optimization model predicts that the optimal strategy is the pit-trapping when the energy state is relatively low and is the ambushing when the energy state is high (Fig. 2-2). This result can be understood based on the strong selective pressure that death has on the fitness of an individual (Hamilton 1964; Williams 1966). When the energy state is sufficiently high, the antlion should choose the safer strategy (i.e., ambushing) and survive. In other words, individuals with high energy levels can afford to lose the energy. However, when the energy state is relatively low, the individual can also die due to starvation. Thus, energy deprived individuals should take the higher risked strategy (i.e., pit-trapping strategy). Risk-sensitivity theory also makes the similar prediction where organisms in poor condition tend to take higher risked strategies (Caraco et al. 1990).

In a model validation experiment, *M. persimilis* larvae switched from the pit-trapping strategy to the ambush strategy after consuming more prey (Fig. 2-3). Similar results were also found in other studies. For example, a desert burrowing spider decreased its investment in web construction after consuming enough prey items (Lubin and Henschel 1996). Elimelech and Pinshow (2008) found that an antlion *Myrmecaelurus* sp. that can adopt both the pit-trapping and the ambush strategies decrease the period of maintaining the pit in response to an increase in the prey encounter rate. These results from another species as well as a different taxon suggest that the results found in this study may be general, and the similar selective pressure (e.g., risk of predation) operates on a variety of organisms with trap-foraging strategies.

A model assumption that pit-foraging individuals face higher predation risk than ambushing ones was tested experimentally. It is an issue being discussed but seldom tested experimentally (but see Loria et al. 2008). We found that the pit-trapping strategy resulted in higher cannibalism risk than the ambush strategy although the cannibalism rate was generally low. During the experiment, we observed that third instar larvae stayed near the pits of pit-trapping larvae and sometimes even ruined or replaced the pits. These observations suggest that third instar larvae can perceive the presence of pits. However, we cannot conclude that whether third instar larvae attacked pit-trapping individuals more because pit-trapping individuals are easier to be detected and/or easier to be attacked (e.g., third instar larvae detected the presence of both pit-trapping and ambushing individuals). Although cannibalism was considered in this study due to the convenience, there are many other potential natural enemies of *M. persimilis* larvae, which include the larvae of other antlion species (e.g., ambushing species, *Distoleon littoralis*; personal observation) and Therevidae larvae (parasitoids of antlions in Taiwan, (Stange et al. 2002)). Thus, the predation risk that the antlion faces in the field can be very high, which should be examined in future studies.

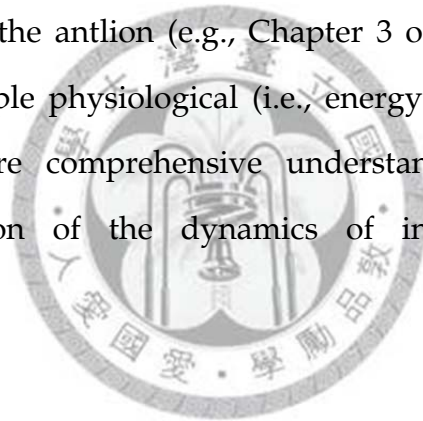


Our field observations show that *M. persimilis* larvae were generally starved. However, almost all of the antlions we observed and collected in the field were ones that were pit-trapping because it is difficult to detect ambushing antlions in the field. If the model predictions were valid, we would expect that individuals in prey abundant locations are more likely to exhibit the ambush strategy than ones in prey scarce environments. However, the consistent high degrees of food deprivation (Fig. 2-5) suggest that satiation seems hard to be achieved in the field.

Although the model does not make any prediction about the pit diameter, it is known that antlions enlarge their pits in time (e.g., unsuccessful capture experience would result in larger pits) (Guillette et al. 2009; Scharf et al. 2010). Therefore, the field observation and the model prediction appear contradictory. We should see a negative correlation between the weights of the antlions and their pit sizes. This is because individuals with higher weights (higher energy levels) tend to ambush more and thus should have shorter periods of pit maintenance (smaller pits). This contradictory result may be explained by the differences in their life stages. For example, the model predicts that individuals at the end of the time (e.g., the end of the larval period) tend to exhibit the pit-trapping strategy given an energy state (Fig. 2-2). The reason why the third instar larva keeps enlarging its pit might be owing to the need of energy gained for pupation (higher body mass before pupation results in higher adult body size (Gotelli 1997; Scharf et al. 2008a). Thus, paying more effort on maintaining or enlarging the pit is valuable, even though the increasing pit size might also increase the attack of predators (Hauber 1999). In fact, although not statistically significant, the second instar individuals show a negative trend (Fig. 2-6). However, to understand the results with respect to the pit size, we need to understand how the pit size actually relates to predation risk, which we know very little and is likely to substantially vary among predators (e.g., birds vs. ground dwelling predators).

By understanding the behavioral mechanism, we might further examine the

community and ecosystem level consequences of the behavior. For example, the different foraging strategies would impose different predation risk on their prey (such as ant populations) (Schmitz and Suttle 2001). The importance of the foraging strategy in ecosystem function has been revealed. For example, prey species consumed by predators with different foraging strategies might exhibit variable phenotypes, then affecting the composition of plant species in the environment (Schmitz 2008). Our study suggests that antlions maximize their fitness by balancing the cost and benefit of each strategy, which results in the context-dependent flexible foraging behavior. Thus, behavioral expressions of antlions can have important effects on the community and ecosystem dynamics of the environment in which they reside. Furthermore, such large scale dynamics may in turn also influence the behavioral expressions of the antlion (e.g., Chapter 3 of this thesis). Although this study focused on the simple physiological (i.e., energy state) and behavioral level dynamics, to obtain more comprehensive understanding about the behavior, simultaneous consideration of the dynamics of interacting species will be worthwhile.



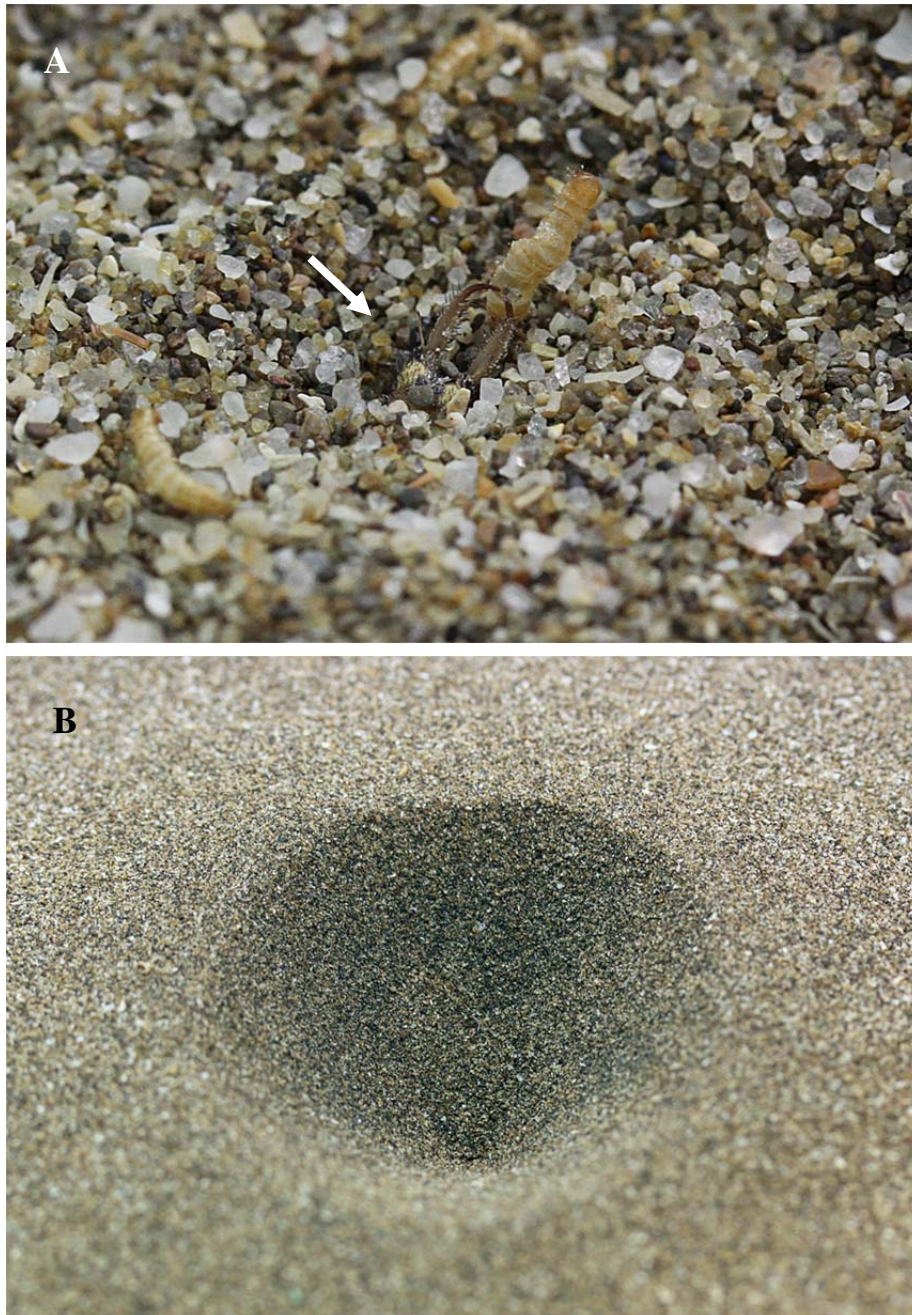


Fig. 2-1. Two foraging strategies of *Myrmeleon persimilis* larvae. A: Ambush strategy defined as hiding beneath the sand surface with only the mandibles protruding. An ambushing individual (arrow) is consuming a flour beetle larva. B: Pit-trapping strategy defined as having a cone-shaped pit. A pit-trapping individual in the picture is located at the apex of the pit.

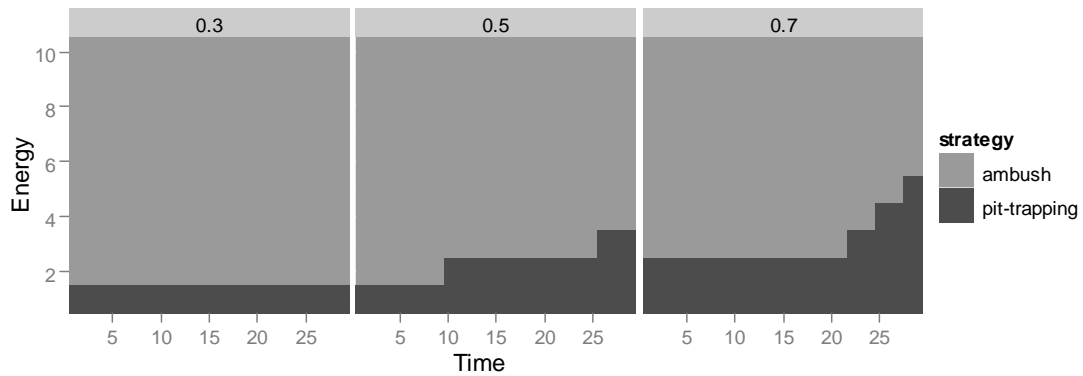


Fig. 2-2. Optimal behavioral strategy solutions obtained by the dynamic optimization model. The panel values (i.e., 0.3, 0.5, and 0.7) are the values of  $f_p$ . The other parameters are:  $d_P = 0.2$ ,  $d_A = 0.1$ ,  $f_A = 0.1$ ,  $c_P = 0.1$ ,  $c_A = 0.1$ . Although not shown in the figure, when  $f_p = 0.2$ , the ambush strategy is better than the pit-trapping strategy in the entire state variable space.



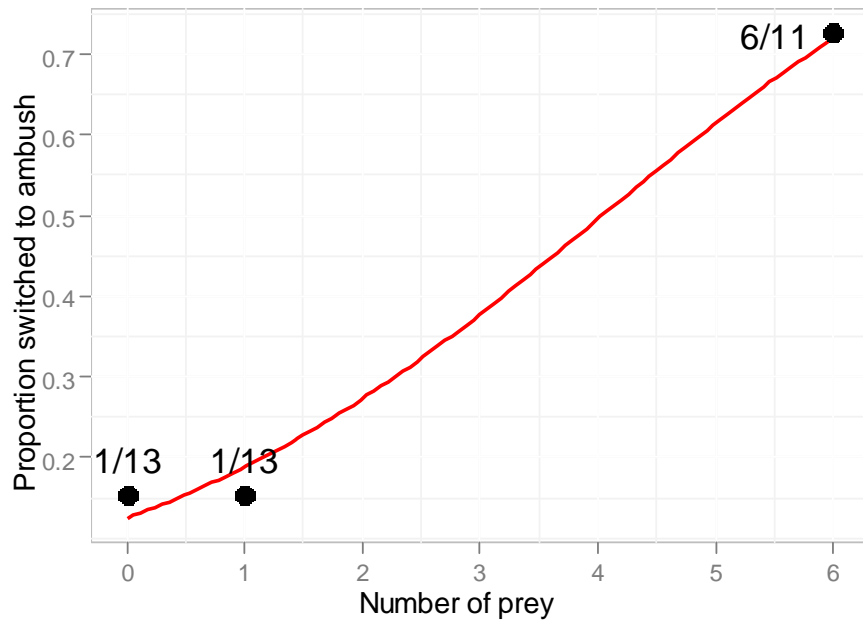
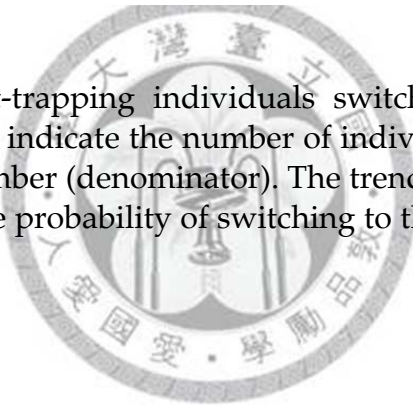


Fig. 2-3. Proportion of pit-trapping individuals switched to exhibit the ambush strategy. The ratio numbers indicate the number of individuals switched the strategy (numerator) to the total number (denominator). The trend line is based on  $\text{logit}(p) = -1.944 + 0.482x$  where  $p$  is the probability of switching to the ambush strategy, and  $x$  is the number of prey given.



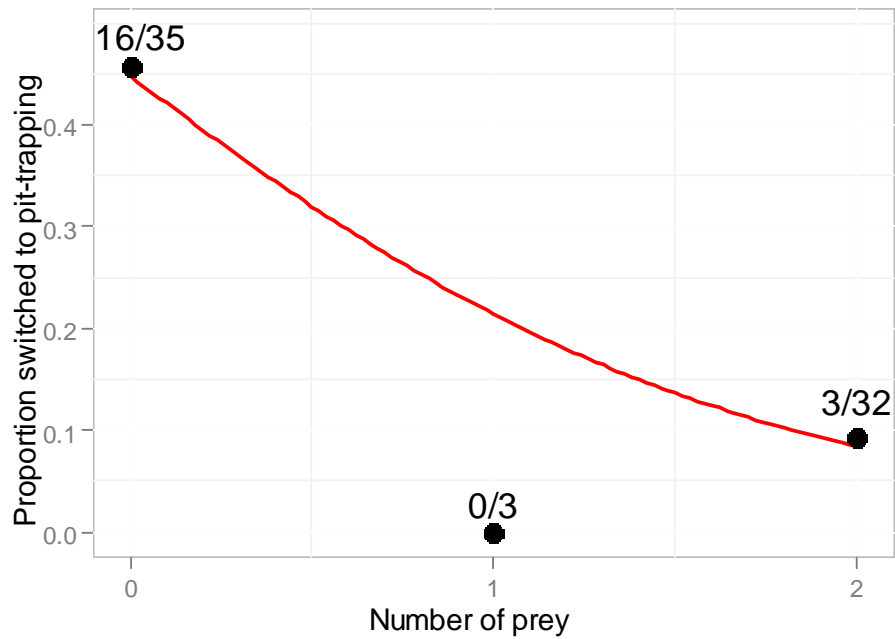
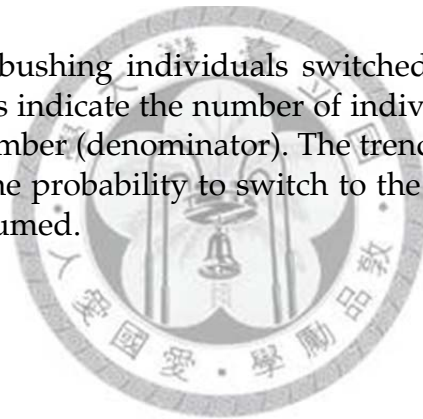


Fig. 2-4. Proportion of ambushing individuals switched to exhibit the pit-trapping strategy. The ratio numbers indicate the number of individuals switched the strategy (numerator) to the total number (denominator). The trend line is based on  $\text{logit}(p) = -0.208 - 1.092x$  where  $p$  is the probability to switch to the pit-trapping strategy, and  $x$  is the number of prey consumed.





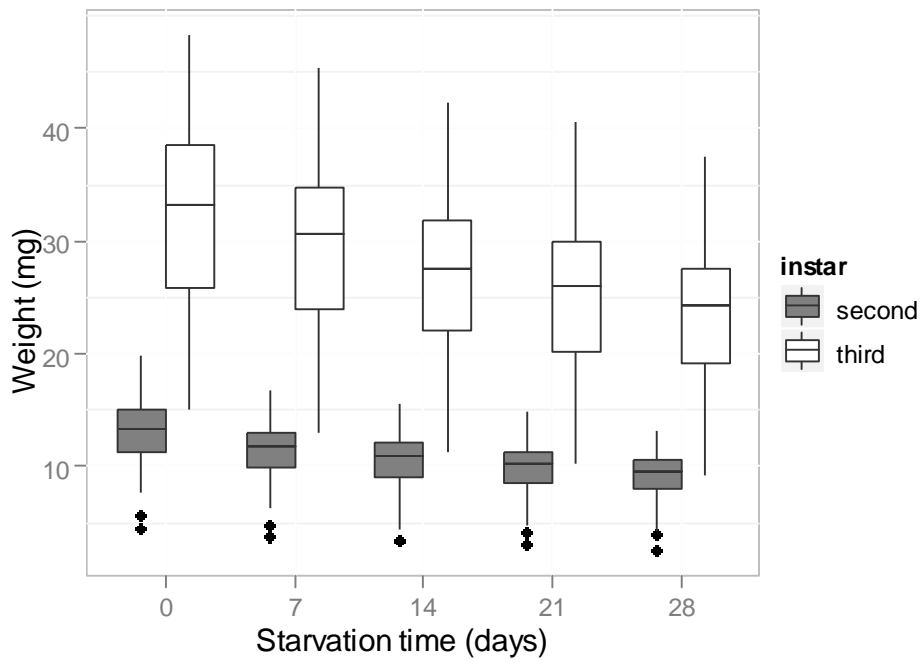


Fig. 2-5. Box plots showing weight loss during starvation in *Myrmeleon persimilis*. Starvation time = 0 corresponds with satiation.





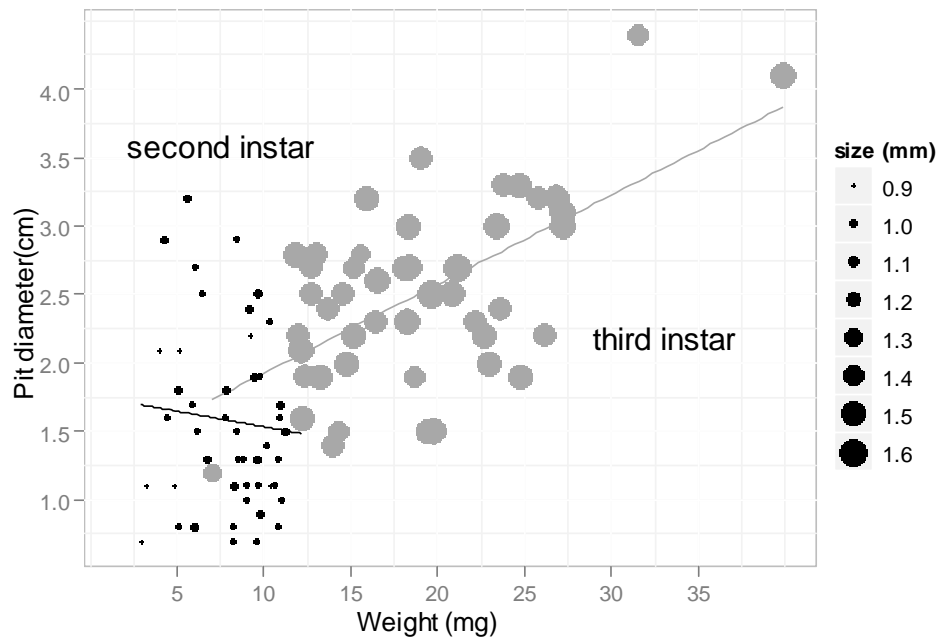


Fig. 2-6. Relationship between the weights and pit diameters of antlions. Black and grey points show second instar individuals and third instar individuals, respectively. The lines are the best fit straight lines to the data: second instar ( $y = 1.74 - 0.02x$ ) and third instar ( $y = 1.32 + 0.06x$ ). Size (represented by the point size indexed in the legend) is the head width of the antlion. The second instar and the third instar larvae are distinct in their sizes (the largest second instar larva is 1.03 mm and the smallest third instar larva is 1.32 mm in the samples).



## Chapter 3

# Use of social information in relocation decisions of the antlion larva, *Myrmeleon persimilis* (Neuroptera: Myrmeleontidae)

### 3.1. Introduction

Antlion larvae (Neuroptera: Myrmeleontidae) are typical sit-and-wait predators. Many species of antlions build conical pit traps in fine-particulate substrates to capture mobile invertebrates (Wilson 1974; Heinrich and Heinrich 1984; Crowley and Linton 1999). The success of this trap-foraging strategy depends on the quality (e.g., prey abundance) of the location in which the traps are situated; it is important for antlions to select profitable locations for constructing their pits (Wilson 1974; Riechert 1976; Hart 1987).

A number of factors affect pit relocation decisions in antlion larvae (Scharf and Ovadia 2006). For example, abiotic factors such as temperature (Arnett and Gotelli 2001) and light intensity (Scharf et al. 2008b) influence the pit relocation behavior in *Myrmeleon immaculatus*. Farji-Brener (2003) found that *M. crudelis* actively selected microhabitats with fine-grained particles. As far as biotic factors are concerned, Wilson (1974) first suggested the importance of shadow competition in pit site selection in antlions. In shadow competition, stationary foragers influence the prey availability of each other due to their spatial proximity to the prey. In antlions, individuals in the “upstream” (prey move from upstream to downstream) can intercept prey paths, thus ones located “downstream” will experience reduced prey intake (Linton et al. 1991).

Antlions are commonly found in aggregation in the field (Fig. 3-1). Besides shadow competition, aggregation may also intensify intraguild predation and cannibalism (see Chapter 2). Visual predators may more easily detect aggregates of pits than isolated pits (e.g., Hauber 1999). Furthermore, because pit-foraging individuals are at their larval stages, mate finding is also not likely to be a factor (but

see Scharf and Ovadia 2006). All these arguments make it difficult to explain the aggregation behavior.

One factor that has not been examined in the pit aggregation in antlions is social information. Facing variable environments, animals should gather available information to reduce the uncertainty; in particular, social information is cues generated by other individuals which engage in the same activity (Dall and Johnstone 2002). Social information helps an individual to exploit resources more efficiently than solely relying on its personal information. For example, group-living birds choose their foraging strategies depending not only on personal patch-sampling experience but also on other individuals' successful foraging activities (Templeton and Giraldeau 1995). Likewise, it is possible that antlion larvae gather information from their neighbors to determine the quality of the habitats. For example, antlions toss sands outside their pits, e.g., for the maintenance of the pits (Youthed and Moran 1969; Lucas 1982; Griffiths 1986). The sand particles often enter the pits of neighboring antlions (Heinrich and Heinrich 1984). Thus antlions are likely to be able to detect the presence of neighboring antlions and their activities without directly encountering each other. If the presence of neighbors presents the information about the location, it would influence the relocation decision. However, the role of social information in the decision making of antlions has not been studied.

In this study, we examined the potential role of social information in the relocation decision making of the antlion larva, *M. persimilis*. In particular, we examined whether a strategy that leads to aggregations (i.e., *decreasing relocation tendency when neighbors exist*) can be an adaptive strategy. More specifically, an individual based computer model was built to test whether the strategy can be a unique evolutionarily stable strategy. In addition, an experiment was conducted to examine how the social information (i.e., sand particles from neighboring antlions) influences the relocation decision of the antlion.

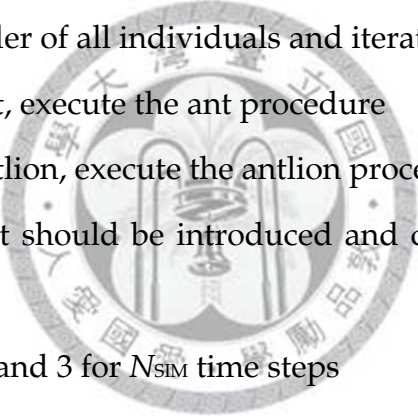
## 3.2. Materials and methods

### 3.2.1. Individual based model

#### 3.2.1.1. General flow

An individual based model (IBM) that simulates a scenario where multiple antlions forage in a common environment was created. The model runs in discrete time. After the initialization (Step 1, described below), the simulation repeats the same procedures in each discrete time step (Steps 2 and 3) for  $N_{SIM}$  time steps ( $N_{SIM}$  can be set arbitrary).

#### Simulation steps

1. Create the environment and locate individuals in the environment
  2. Randomize the order of all individuals and iterate them
    - a. If it is an ant, execute the ant procedure
    - b. If it is an antlion, execute the antlion procedure
  3. Check if a new ant should be introduced and create an ant if it should be created
  4. Repeat the steps 2 and 3 for  $N_{SIM}$  time steps
- 

In the following sections, the detailed procedures of the simulation steps are described. The section *Environment* (3.2.1.2) describes the initial setup (Step 1) and the introduction of new ants (Step 3). The sections *Ants* (3.1.2.3) and *Antlions* (3.1.2.4) describe the procedures for ants and antlions (Step 2), respectively.

#### 3.2.1.2. Environment

This is a two-dimensional spatially explicit model. The environment is a square ( $101 \times 101$  units). The model is point-process based in which organisms (ants and antlions) can be located at any points in the space (e.g., two dimensional coordinates described by two floating points). The center of the environment is (0,0) (the first

number is the  $x$ -coordinate, and the second number is the  $y$ -coordinate). The four corners of the environment are  $(-50.5, 50.5)$  [top-right],  $(50.5, 50.5)$  [top-left],  $(-50.5, -50.5)$  [bottom-right], and  $(50.5, -50.5)$  [bottom-left]; thus, the length of one side is 101 units as described. New ants enter the environment at a given time interval  $\tau$ . For example, when  $\tau = 500$ , a new ant is introduced every 500 time steps. Ants come into the environment from one of the four corners of the environment with a small margin; the four entering corner points are  $(-50, 50)$ ,  $(50, 50)$ ,  $(-50, -50)$ , and  $(50, -50)$ . From which one of the four corners ants enter the environment is randomly chosen at the specified time intervals  $\lambda$ . For example, suppose  $\lambda = 1000$ , then at least for 1000 time steps, ants enter the environment from the same corner. Thus,  $\lambda$  indicates the environmental predictability. The higher the value of  $\lambda$ , the more predictable the environment (i.e., prey entrance location) is. Every individual (both ants and antlions) has its heading direction (discussed in details below). When a new ant enters from the corner, its initial heading direction is randomly chosen from a uniform distribution whose domain in the angles of the two adjacent corners (90 degrees).

Although the environment is a square, antlions in the environment are restricted within a circular area whose radius is 50 units centering at  $(0,0)$ . Antlions cannot move outside the circular area. Thus the four ant entering points are outside the environment of antlions; this prevents the entering points to be within a pit of an antlion (although it still depends on the size of a pit, further discussed below). The location of each antlion at the beginning of the simulation is randomly chosen in the circular environment.

### 3.2.1.3. *Ants*

Each ant has its own heading direction that is randomly changed at each time step. Suppose that the current heading angle is  $\theta_c$ , at each time step (Step 2a in the simulation step described above), the new heading direction becomes  $\theta_{NEW} = \theta_c + U_1 + U_2$  where  $U_1$  and  $U_2$  are random numbers generated from the uniform distributions

whose domains are  $(0, \theta_A)$  and  $(-\theta_A, 0)$ , respectively.  $\theta_A$  is a parameter of the model that determines the tendency for an ant to move straight. For example, when  $\theta_A = 0$ , ants do not change the heading directions at all. At each time step, ants move forward (i.e., heading direction) for a specified distance determined by a parameter,  $d_A$ . When an ant moves outside the environment, the ant does not re-enter the environment.

#### 3.2.1.4. Antlions

Although the number of antlions can be set arbitrarily in the simulation, we considered an environment with two antlion larvae to simplify the scenario. Each antlion can be in one of the two states: stay state or relocation state. When an antlion is in the stay state, the antlion stays at the current location with a pit whose diameter is  $\pi$ . If an antlion is in the relocate state, it moves in the environment for  $T_R$  time steps. The movement detail follows that of the ant discussed above, but instead of the parameters for the ant (i.e.,  $\theta_A$  and  $d_A$ ), the antlion has its own parameters, i.e.,  $\theta_L$  and  $d_L$ , whose values may be different from those of the ant. However, when an antlion that is in the middle of relocation enters the pit of the other antlion, it will change the heading angle to escape from the pit (no cannibalism is possible). Suppose an antlion steps into a pit and the direction (i.e., angle) of the pit owner is  $\theta_o$ , then the new heading angle will be  $\theta_o + W$  where  $W$  is a random number generated by a uniform distribution whose domain is  $(90, 100)$  with the probability 0.5 or  $(-100, -90)$  with the probability 0.5. This prevents two antlion to be too closely located. When an antlion steps outside the environment, it changes its heading direction towards the center  $(0, 0)$ . Lastly, it was assumed that the pits of two antlions do not overlap. Thus, at the end of the relocation state, if the antlion is at unfavorable place (i.e., too close to the other antlion), the relocation state extends (the antlion keeps moving after  $T_R$  steps) until it reaches a favorable point. As soon as it reaches the point, a new stay state begins.

The transition from the relocation state to the stay state is deterministic as



described above. However, the transition from the stay state to the relocation state depends on an antlion's experience at the current location and is stochastic. Suppose that an antlion just entered the stay state, then the antlion remains in the stay state for the duration of  $T_s$  time steps. After  $T_s$  time steps, the antlion continues to remain in the stay state or switch to the relocate state is determined by the prey capturing success during the previous  $T_s$  time steps.

At the beginning of  $T_s$  interval, two internal perception variables ( $h$  and  $m$ ) relating the prey capture success are set to 0 (i.e.,  $h = m = 0$ ). Both variables change based on the antlion's experience. When the antlion captures an ant,  $h$  and  $m$  change according to Eq. (3.1), and when the antlion fails to capture a prey, the variables change according to Eq. (3.2),

$$h_{t+1} = \rho h_t + 1 \quad \text{and} \quad m_{t+1} = \rho m_t, \quad (3.1)$$

$$h_{t+1} = \rho h_t \quad \text{and} \quad m_{t+1} = \rho m_t + \exp\{\kappa x\}, \quad (3.2)$$

where  $\rho$  describes memory retention and the subscript represent the discrete time step. When  $\rho = 1$ , the antlion does not forget the previous experience.  $\kappa$  describes the effect of neighboring antlions, and  $x$  is the number of the neighbors (antlions are considered neighbors if their distance is less than  $\delta$ ). In this study, because there are only two antlions,  $x$  is either 0 (i.e., no antlion in the neighborhood) or 1 (i.e., the other antlion is in the neighborhood). When the perception antlion is independent of the neighbors (i.e.,  $\kappa = 0$ ), a missed capture results in the increment of 1 in  $m$  [Eq. (3.2)]. Because  $m$  relates to unsuccessful capture experience, when  $\kappa$  is negative, biologically it is interpretable that the presence of the neighbor makes the antlion to discount the unfavorable experience (i.e., missed prey capture) whereas when  $\kappa$  is positive, the presence of the neighbor has the opposite effect.

Although the experience affects the perception towards the environment, antlions also have prior perceptions (e.g., innate perception) about the probability of capturing a prey for each time step. We can use a beta distribution to describe the internal perception,  $\text{Beta}(\alpha, \beta)$ . The beta distribution is defined between 0 and 1, and

thus is an appropriate distribution for the probability of perception. The parameters of the beta distribution (i.e.,  $\alpha$  and  $\beta$ ) define the distribution, e.g., mean  $\mu = \alpha / (\alpha + \beta)$  and variance  $\sigma^2 = \alpha\beta / ((\alpha + \beta)^2(\alpha + \beta + 1))$ . For example, high values of  $\mu$  indicate that antlions perceive the local environment (e.g., pit location) is good. We assumed the prior perception is the uniform distribution (i.e.,  $\alpha = \beta = 1$ ) to represent an unbiased perception.

This internal perception is updated by the experience (i.e., actual successes and misses of prey captures). If we consider  $h$  and  $m$  (described above) are binomial experience (i.e.,  $h$  successes in total  $h + m$  trials), we can integrate the experience and the prior perception to derive the posterior perception (e.g., perception towards the environment given the experience and the prior perception). Because the beta distribution is the conjugate prior of the binomial distribution, the posterior distribution is also a beta distribution,  $\text{Beta}(\alpha + h, \beta + m)$  (Gelman et al. 2004). At the end of the stay state (i.e., when it decides to continue to stay or relocate), a random variable is generated from  $\text{Beta}(\alpha + h, \beta + m)$ , and if it is less than a threshold value  $\phi$ , it relocates; if it is greater than  $\phi$ , it continues to stay at the current location. Thus, if an individual captures many prey (i.e.,  $h$  is high), the antlion is more likely to continue to stay at the current location. Relating the parameter  $\kappa$  discussed above, when  $\kappa$  is negative, antlions are less likely to relocate when there is a neighbor whereas when  $\kappa$  is positive, antlions are more likely to relocate when there is a neighbor. When  $\kappa$  is 0, the presence of neighbor does not directly influence the decision, but shadow competition can still operate. In other words, even when  $\kappa = 0$ ,  $h$  and  $m$  can be still influenced by the presence of neighbors indirectly.

### 3.2.1.5. Analysis

The role of social information (i.e., presence of neighbor) in the relocation decision making was examined. We considered the parameter  $\kappa$  to be the strategy of an antlion, and which value of  $\kappa$  can be an evolutionarily stable strategy (ESS) was

examined. An ESS is a strategy, when adopted by every individual in the population, cannot be invaded by any other strategies (Maynard Smith 1972). The game theoretical consideration was necessary because the prey capturing success of an antlion depends on the decision of the other antlion in the same environment. For simplicity, we assumed that  $\kappa$  can be one of the three values:  $-1$ ,  $0$ , or  $1$  (for the biological interpretations, see the previous section). Many outcomes are possible (e.g., no ESS, every strategy is an ESS). In this study, we focused on finding the situation whether  $\kappa = -1$  is the only unique ESS because this result most closely ties to the ubiquitous aggregations in the field. One simulation run consisted of 500 000 time steps ( $N_{\text{SIM}}$ ). Because each antlion can have one of the three strategies, there are nine possible combinations between the two antlions. The number of prey captured in one simulation run was used as a surrogate for the fitness of the individual.

To examine the effects of the memory  $\rho$  and the environmental variability  $\lambda$ , the values of these parameters were also varied. The values of the all parameters used in the simulation are shown in Table 3-1. All possible factorial combinations of the parameters were examined, and for every parameter combination, 300 replications were conducted.  $\lambda = 100\ 000$  represents a relatively predictable environment whereas the environment with  $\lambda = 100$  is highly unpredictable. In particular, because  $\lambda = \tau$ , each ant enters the environment from a random corner.

### 3.2.2. Laboratory experiment

#### 3.2.2.1. Study animals

The antlion species used in this study is *Myrmeleon persimilis* (Neuroptera: Myrmeleontidae), an endemic and the most widespread coastal species of genus *Myrmeleon* in Taiwan (Stange et al. 2002). *M. persimilis* larva, like other antlion species, has three instar stages and usually undergoes eclosion during February to May (unpublished data).

*M. persimilis* larvae were collected from coastal habitats in Shimen District, New

Taipei City (25°18'N, 121°32'E). It is a sandy region with abundant rainfall. When it rains, *M. persimilis* larvae burrow few centimeters under the sand surface (directly beneath the original pit site) and come out when the sand is dried. The common plant species in the habitat include wormwoods (*Artemisia capillaries*), tree heliotropes (*Tournefortia argentea*), Hosobawadan (*Crepidiastrum lanceolatum*), and Indian Blankets (*Gaillardia pulchella*) (personal observations). *M. persimilis* larvae usually make pitfall traps under bushes but sometimes in open field to capture small invertebrates such as ants (*Pheidole megacephala*) and larvae of darkling beetles. The potential predators of larval *M. persimilis* in this habitat include dipteran larvae (Therevidae), ground beetles, and larvae of other antlion species (e.g., *Distoleon littoralis*).

#### 3.2.2.2. Effects of prey supply and sand tossing on relocation

Effects of food supply and social information on pit relocation behavior in antlions were studied. Relocation behavior can be defined as moving to a new location and constructing a new pit. There were four treatment combinations formed by two factors (with or without prey supply, and with or without sand tossing), and each combination included 15 hunger controlled third instar *M. persimilis* larvae. Antlions used in the experiment were individually housed in containers filled with sands (44.5 cm by 34.7 cm, sand depth 4 cm) maintained in a controlled environment: temperature ( $25 \pm 2^\circ\text{C}$ ), humidity ( $40 \pm 5\%$ ), and L:D 14:10 cycle. In the groups with food supply, each larva was fed with one flour beetle larva (*Tribolium confusum*) a day. In the treatment groups with sand tossing, 0.25 mL of sand was introduced to a pit four times (2 sec interval between each introduction). A plastic tube was used to make the sand slid down into a pit. These details were decided based on preliminary observations on the actual sand tossing behavior of the species. In the treatment group with both food supply and sand tossing, larvae received prey first. After the prey were consumed, the sand tossing manipulation was applied. The treatments were applied daily for one month. Whether the antlions relocated or not was

examined daily.

### 3.2.2.3. Statistical analysis

The effect of the treatments on the propensity to stay at the same location was examined using the Cox's proportional hazard analysis. Some individuals did not relocate at all during the experiment (i.e., 30 days). Those data were included as censored data. Three models were considered: model explained by (1) sand tossing treatment only, (2) prey treatment only, and (3) both treatments. The best model was selected based on Akaike Information Criterion (AIC) (Akaike 1973).

How the treatments affected the probability of relocation (i.e., number of relocations during the experiment) was examined using Binomial Generalized Linear Mixed Model (GLMM). Because whether the antlions relocated or not was recorded daily, the number of relocations in 30 days was modeled as a binomial process. Because each individual was repeatedly measured for 30 days, the random intercept and the random time effect (grouped by individual) were also included in the model. The best model was also chosen based on AIC based on maximum likelihood. The parameter estimates of the best model are presented based on the restricted maximum likelihood (Zuur et al. 2009).

## 3.3. Results

### 3.3.1. Individual based model

When antlions have sufficient memory (i.e.,  $\rho \geq 0.7$ ), and the environment is not highly variable (i.e.,  $\lambda = 100\ 000$ ), the unique best strategy was always  $s_1 = -1$  (Fig. 3-2). That is, regardless of the opponent's strategy ( $s_2$ ), the best strategy (i.e., evolutionarily stable strategy) is to decrease the relocation probability when there is a neighbor. In any other parameter combinations, no one strategy outperformed the other strategies regardless of the opponent's strategy.

However, the trends do not confirm that there is no unique ESS in the other

parameter combinations nor  $s_1 = -1$  is the ESS when  $\rho \geq 0.7$  and  $\lambda = 100\,000$  because these are the results of the stochastic simulations. Although a large number of replications were performed (i.e., 300 runs), when there is high variability, the current trends may change and stabilize as the replication is increased. To gain some confidence on the monotonic trends (i.e., the unique ESS exists when  $\lambda = 100\,000$ ), the statistical significance of the monotonic trend was examined. Because the significance has to be confirmed at all the three opponent strategies simultaneously, the significance level  $\alpha = 0.05/3 \approx 0.017$  should be used for each independent test. When  $\rho = 0.9$ , the highest  $p$ -value with Kendall's tau correlation test was 0.002, but when  $\rho = 0.7$ , the highest  $p$ -value was 0.026. Thus at the conventional significance level (i.e., allowing 5% type I error), the ESS is statistically supported when  $\rho = 0.9$ , but when  $\rho = 0.7$ , the significance level was not attained (only marginally significant). However, as discussed above, this does not mean  $s_1 = -1$  is not an ESS when  $\rho = 0.7$ . In particular, because this is a computer simulation, the sample size can be increased arbitrarily, and thus  $p$ -value of statistical tests can be made small arbitrarily. However, the analysis based on the limited number of simulations informs the strength of the selection (i.e., effect size).

### 3.3.2. Effects of prey supply and sand tossing on relocation

Time to relocation was highly variable among the treatments. When neither prey nor sand tossing was given, 14 out of 15 individuals relocated within 30 days, and fewer individuals relocated in the other treatments (Fig. 3-3). Based on AIC, the best model is the model that includes only the sand tossing treatment (Cox's proportional hazard model, sand tossing treatment coefficient =  $-0.66$ ). Thus, the analysis suggests that the prey supply treatment did not affect the relocation pattern. The negative coefficient of the sand tossing treatment indicates that the treatment decreased the likelihood of relocation.

Some individuals relocated multiple times during the experiment. The number



of relocations is shown in Figure 3-4. According to the best model, both the sand treatment and the prey treatment had negative effects on the relocation number (Binomial GLMM, [fixed effects] intercept = -1.428, prey = -0.722, sand = -0.482, time = -0.069; [random effects in terms of variance] intercept = 0.051, time = 0.002); these effects of the treatments are also visually apparent in Figure 3-4. Both treatments had the negative effect on the number of relocations. The negative time coefficient indicates that the probability of relocation also decreased with time.

### 3.4. Discussion

The simulation results of the individual based model enlighten us on the conditions where the neighbor-dependent movement is an evolutionarily stable strategy (ESS). When the environment is relatively predictable and antlions can learn from their experience, a better pit site location can be found with the social information rather than independently searching for sites. The laboratory experiment also showed the consistent results in which simulated sand tossing decreased the relocation frequency. These results suggest that social information may be a key factor to explain the commonly found aggregations in the field.

Both the environmental predictability  $\lambda$  and the learning ability  $\rho$  are important parameters for the evolutionarily stable strategy to exist. In particular, the ESS exists only when the environment is relatively predictable (high  $\lambda$ ) and the learning ability is high (high  $\rho$ ) (but see *Results* for the interpretation caveats) (Fig. 3-2). This result is consistent with an existing theory on learning behavior (Stephens 1993). Suppose if individuals cannot learn about the environment (low  $\rho$ ), they cannot rely on other individuals for assessing the quality of the location because none of them are reliable. Similarly, if the environment is completely random (e.g.,  $\lambda = 100$ ), no matter how high the learning ability  $\rho$  is, the environment presents no information to be learned. Thus, in these situations, no clear patterns were observed and the average energy gains are equivalent for all  $\rho$  (Fig. 3-2). However, when the environment is not



completely random and the animals can learn, each individual is likely to stay where they have the successful capture experience. This result implies that the presence of other individuals also gives information about the quality of the location. Therefore, the evolutionarily stable strategy is to decrease the relocation probability when neighbors exist.

In the experiment, prey supply offered antlions direct information about the pit site quality. On the other hand, sand tossing may have provided indirect information about the environment as discussed above. These statements were consistent with the results of the experiment; antlions decreased the number of relocations with respect to both the prey supply and sand tossing simulations (Fig. 3-4), and the effect of prey supply was stronger (see the estimated model parameters in *Results*). Similarly, as far as the duration to stay at the initial location is concerned (Fig. 3-3), only sand tossing had an effect on the duration to stay at the initial location although prey supply did not have an effect. These results suggest that antlions use their own experience as the primary factor to decide their own foraging decisions but still uses the social information in a lesser degree to reduce uncertainty about the environment, consistent with how the decision making process was modeled in the individual based model.

There are a few important caveats in the experiment. It has been suggested that antlions can perceive cues from sand tossing events as social information (Simberloff et al. 1978). However, this detail must be confirmed with further experiments. For example, the sand tossing manipulations used in the experiment may be perceived as cues from prey although they were intended as cues from conspecifics (Guillette et al. 2009). Detailed responses of larvae to sand tossing in different amount, intensities, or frequencies, should all be examined experimentally. Field observations on interactions between neighboring individuals are also worthwhile. Furthermore, although the larvae used in our experiments were all third instars, relocation tendency among antlions may vary between instar stages (Griffiths 1993). In fact,

Gotelli (1997) found that third instar larvae seldom relocate. The movement decisions between individuals across different instar stages should be further examined.

Our study suggests that antlions decrease relocation tendency when neighbors exist, and this strategy is an evolutionarily stable strategy. Although antlions do not form an aggregation cooperatively, the ESS leads to an aggregation because each individual is less likely to relocate when it is close to other individuals. However, because antlions still use their own experience as the primary information, they would not be trapped at poor pit site locations simply because of (potentially misleading) social information. Given the results, it is important to validate some details of the model in future studies. For example, although Bayesian information updating was used in the model (Dall et al. 2005), little is understood how insects update their perceptions towards the environments as they gain experience. As decision making processes are the key in the aggregation phenomenon, detailed examinations of them would provide useful insights in the social interactions.



Table 3-1. Parameters of the individual based model, their definitions and default values. When multiple values are shown, all the possible factorial combinations of the values of the different parameters were examined. For details, see Analysis (section 3.2.1.5).

definition	symbol	value
Environmental predictability	$\lambda$	100, 100000
Ant abundance	$\tau$	100
Stay interval	$T_S$	250
Relocation interval	$T_R$	250
Internal perception	$\alpha$	1
Internal perception	$\beta$	1
Memory	$\rho$	0.1, 0.3, 0.5, 0.7, 0.9
Relocation threshold	$\phi$	0.1
Neighbor effect	$\kappa$	-1, 0, 1
Predator movement	$d_L$	20
Prey movement	$d_A$	10
Predator movement angle	$\theta_L$	10
Predator movement angle	$\theta_A$	10
Pit diameter	$\pi$	16
Neighbor distance	$\delta$	20



Fig. 3-1. Aggregations formed by *Myrmeleon persimilis* larvae. A: Several individuals built pits close to each other in the field. B: Movement traces (arrow) left by individuals can be found near pits.

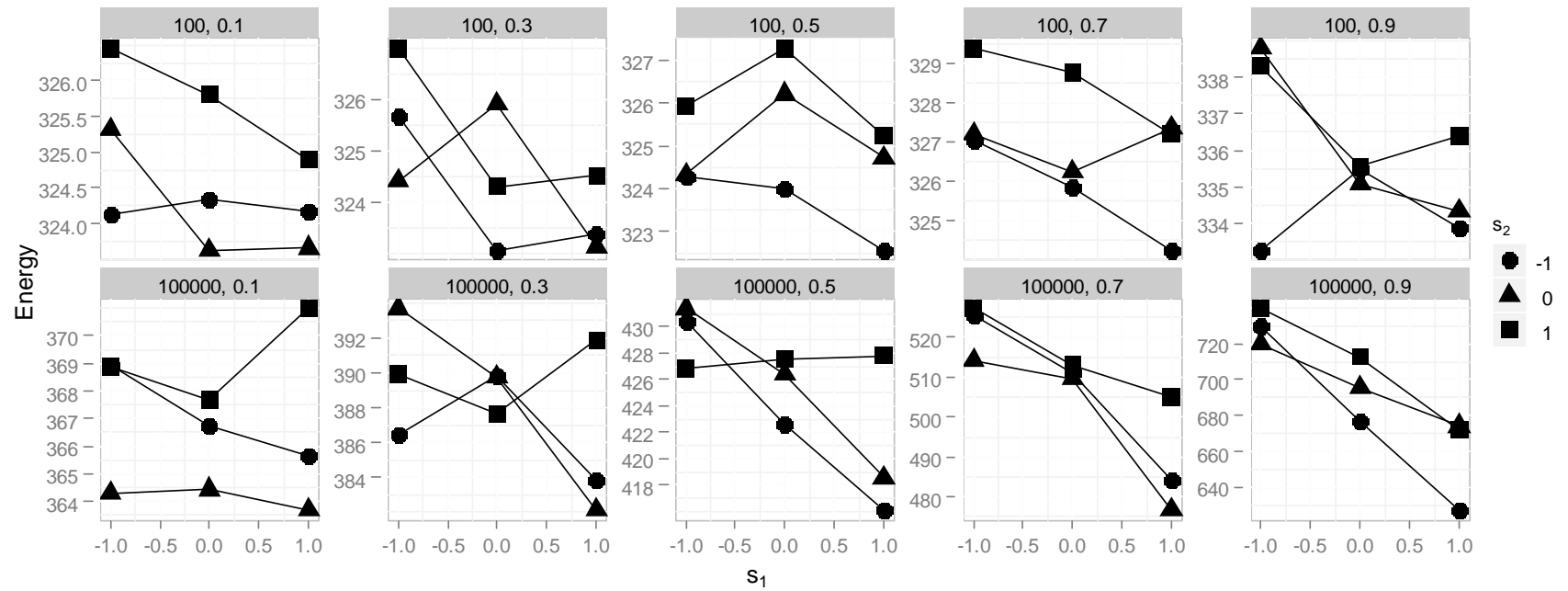


Fig. 3-2. Average energy attained by antlions at the end of a simulation run. The strategy of the focal individual is  $s_1$ , and the opponent's strategy is  $s_2$ . The two numbers in the panels indicate the  $\lambda$  (100 or 100000) and  $\rho$  (0.1, 0.3, 0.5, 0.7, 0.9).

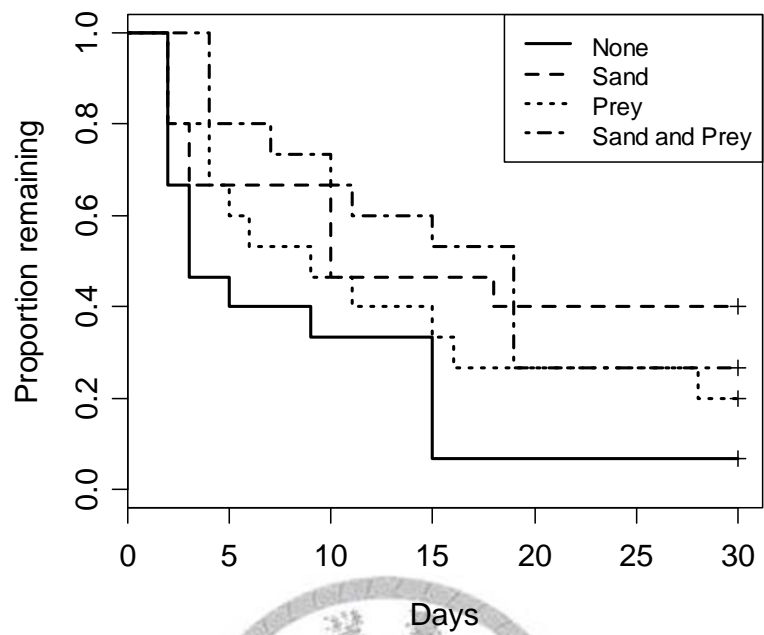


Fig. 3-3. Proportion of larvae remaining at the initial locations. Sample size is 15 for each treatment combination.





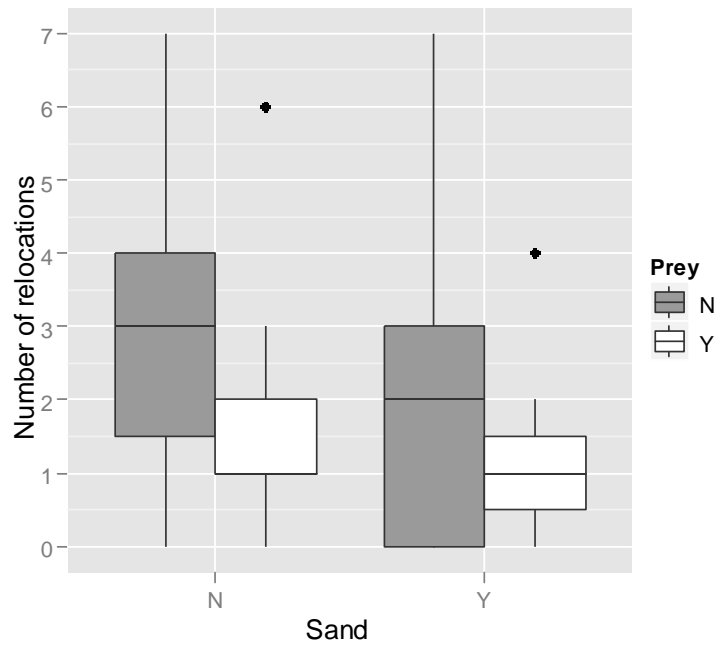


Fig. 3-4. Boxplots of the number of relocations in 30 days. Each treatment combination contains 15 replications. Y(es) and N(o) indicate the presence and the absence of the treatments, respectively.







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