



Convergent evolution of antlions and wormlions: similarities and differences in the behavioural ecology of unrelated trap-building predators

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Abstract

Antlions and wormlions are unrelated insect taxa, but both construct pit traps in loose soil and hunt similar prey. Owing to the likeness of their hunting strategies, and since no other animals construct similar traps, they demonstrate an intriguing case study of convergent evolution. We reviewed the literature of the last 16 years and compared the existing knowledge on trap-building antlions and wormlions. Whereas the knowledge on antlions has been accumulating, studies on wormlions are lacking, in particular studies on how wormlions sense prey and their cognitive abilities. Shared characteristics of the taxa include responses to increasing conspecific density, such as populating suboptimal microhabitats and altering their spatial pattern. The taxa differ, however, in other aspects, such as response to disturbance, prey size range, diversity in habitat selection and behavioural plasticity. We provide recommendations for future research on several levels of biological organization. If such research is conducted on co-occurring antlions and wormlions, the findings will contribute to a greater understanding of this convergent evolution, the extent to which it exists, and its limitations. This in turn will contribute to understanding how natural selection in specific environments has shaped similar phenotypes and which constraints limit the phenotypic outcome.

Keywords Behavioural plasticity · Cognitive ecology · Habitat selection · Soil-dwelling · Myrmeleontidae · Temperature · Vermileonidae · Vibrations

Introduction

Predatory trap-building arthropods present an extreme case of sit-and-wait predators because they not only ambush prey but also construct a trap for this purpose (Scharf et al. 2011). On the one hand, they invest little energy and time in searching for prey; on the other hand, they invest energy in constructing and maintaining the trap. Measuring the benefits and costs of trap building provides an exciting model for studying the evolutionary drivers and constraints of this

hunting strategy. The three most familiar taxa of trap-building predators are spiders, antlions and wormlions (Blamires 2020). Among the trap-building insects, antlions (Neuroptera: Myrmeleontidae) are the most well-studied ones, utilizing trap construction as part of their larval foraging strategy (Ruxton and Hansell 2009). A very similar trap construction has evolved separately in wormlion larvae (Diptera: Vermileonidae), demonstrating an interesting case of convergent evolution (Dor et al. 2014), which can be defined as “the independent evolution of similar features in different evolutionary lineages” (Losos 2011, see Stayton 2015 for other definitions).

Although antlions and wormlions differ strikingly in their morphology, they both construct conical pitfall traps in the surrounding substrate (Wheeler 1930), which are hard to discern without digging the predator out (Fig. 1). They are the only animals known to construct pitfall traps in sand. Their trapping method has many similarities to web construction by spiders and to the evolution of traps in carnivorous plants—an interesting case of convergent evolution in its own right (Ellison and Gotelli 2009). Remarkably, other

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Fig. 1 An aggregation of pitfall traps (Tel Aviv University, Tel Aviv, Israel) and the two predators, an antlion (a *Myrmeleon* sp. left) and a wormlion (a *Vermileo* sp. right) larva, dug out of their traps. Each square stands for 1 mm. The largest trap in the photo centre was dug by an antlion, whereas all others by wormlions. Photos were taken by the authors

fly families might be predators or live in sand, but never hunt prey using pits (Skevington and Dang 2002). Regarding antlions, the vast majority (~90%) of the ~2,000 described species in the Myrmeleontidae family do not dig traps and simply ambush prey while being buried in sand (Badano et al. 2016). Thus, by sharing the same hunting method, which has evolved separately, probably no more than twice in the animal kingdom, and by evolving in similar habitats, it is expected that many other phenotypic traits of pit-building antlions and wormlions will converge too. For instance, both have a long larval period of a year or more and short-lived weak-flying adults (Wheeler 1930). Both are opportunistic predators consuming mostly ants (Simon 1988; Skevington and Dang 2002). Furthermore, if we assume there is only a limited number of ways to be a successful “pit-building predator”, then natural selection is expected to draw similarities between the phenotypes of antlions and wormlions (Speed and Arbuckle 2017).

There is still an important difference in how the antlion and the wormlion traps are dug, as antlions use spiral digging while wormlions use central digging, with the former considered to be more efficient (Franks et al. 2019). Whatever the case, the purpose of constructing a trap is identical

in both taxa: enlarging the attack range of the predator, facilitating the attack of large and/or fast-moving prey and increasing the probability of capture success by channeling the prey to the predator (Mansell 1988; Scharf et al. 2011). Little is known about non-trap-building species of antlions, as the scientific focus has been almost solely on species producing facultative or obligatory trap-building larvae. Non-trap-building species often use a strategy termed sit-and-pursue, meaning that they ambush prey without a trap and change their ambush position much more frequently than trap-building species (Loria et al. 2008). Little is also known about adult antlions and wormlions (but see Matura et al. 2005; Adar and Dor 2018).

The research on the behavioural ecology of trap-building insects has almost exclusively focused on the foraging context, with two main research trends: the study of microhabitat preferences and behavioural plasticity, both presumably selected to increase the successful capture of prey. Antlion and wormlion larvae live for a year or even longer (three- and six-instar stages, respectively, Wheeler 1930), which is quite unusual for insect larvae. They inhabit areas with suitable loose soil, such as sand or loess, and use their traps to hunt co-occurring arthropods, mostly ants (estimated to be over 70% of the diet of several trap-building antlion species, Simon 1988). Supporting this finding, artificial traps placed next to antlion and wormlion traps indicate that ants comprise the vast majority of arthropods caught in the traps (Glenn and Holway 2008, Bar-Ziv et al. 2018, Jingu and Hayashi 2018, Turza et al. 2020). Similar to many other predator–prey interactions, it is possible that their relationship with ants is an “arms race”, in which there is selective pressure on antlions (possibly also on wormlions) to hunt ants more efficiently and on ants to avoid predation (Hollis et al. 2015; Hollis 2017). This may also be reflected in the thermal range within which both players are active (Marsh 1987). Although antlion larvae remain motionless at the bottom of their traps most of the time, due to the abundant mechanoreceptor setae all over their body (Acevedo Ramos et al. 2020), they can react to potential nearby prey, primarily by means of sand tossing. This illustrates that they are sensitive to their surroundings, rather than limited in their cognitive abilities, which antlions were long suspected of being. In wormlion larvae, there is no comparable abundance of mechanoreceptors, and how they detect prey and react to it is less understood.

Here, we focus on the behavioural ecology of trap-building antlions and wormlions. There are several previous reviews on antlions (Scharf and Ovadia 2006; Scharf et al. 2011), describing the factors that trigger trap relocation and the factors that affect trap size. More specialized reviews have focused on the exploitation of prey-induced vibrations on the sand by antlions, the biomechanical costs and benefits of traps or on a single antlion species (Devetak 2014;

Blamires 2020; Farji-Brener and Amador-Vargas 2020). We believe that a new review is timely, focusing on the following topics: (1) There is currently no review comparing antlion and wormlion behaviour. This is important in order to evaluate to what extent the convergent evolution between the two insect taxa has led to similar behaviours. Studying both together will help to achieve one of the main goals of behavioural ecology, namely understanding how evolution has shaped behaviour. Furthermore, wormlion research is lagging behind antlion research. We would like to encourage researchers to study wormlions too and most desirably in direct comparison with antlions under the same experimental framework. (2) The last broad review on the microhabitat selection of antlions (Scharf and Ovadia 2006) is nearly outdated, and novel information has accumulated on further aspects of habitat choice. This especially holds true regarding the effects of abiotic factors and the more recent work on wormlions. (3) Over the last few years, new research on learning in antlions has also accumulated. As cognition is increasingly appreciated as an important component of animal behaviour, we also wish here to highlight this aspect. (4) Recent studies on trap-building predators have considered their behaviour in the context of “animal personality” and examined their behavioural consistency. Reviewing this theme is also of interest, in light of its current popularity in behavioural ecology and the relatively weak support it has received to date in trap-building insects.

We searched the Scopus database (agricultural and biological sciences subject area) for documents that included the terms “antlion or ant-lion or ‘ant and lion’” in either the title, abstract or keywords. We limited the search to the period after the first-noted review was written (2005–2021). We also searched by the term “wormlion” (in the same subject area and period) in order to find documents relating to wormlions. Among the found documents, we selected most non-taxonomic papers concerning the two taxa ([Supplementary Material](#)).

Foraging and microhabitat selection

A review by Scharf and Ovadia (2006) summarized the literature in terms of the factors affecting microhabitat selection in antlions. These factors were mostly biotic, such as prey abundance, competition and cannibalism, together with some abiotic factors, such as microclimate and disturbance to the traps. Despite the numerous cited works, the review authors could not always reach decisive conclusions, due to the diversity of habitats from which antlions originate, and the use of different methodologies in the different studies. For instance, there was variability among the species and studies in regard to the antlions’ sensitivity to starvation and to their preferred microhabitat (lit or shaded). We

found 26 papers written between 2005 and 2021, relating to microhabitat selection in antlions and wormlions. The new findings can hardly be considered conclusive for antlions but do lead to a deeper understanding of wormlions (Table 1).

As described earlier (Scharf and Ovadia 2006), high density in antlions is unfavourable, as it leads to a lower proportion of individuals able to construct traps, more frequent relocation and the construction of smaller traps. This holds true also for wormlions (Dor et al. 2014; Katz et al. 2017b). Furthermore, in both taxa, the spatial distribution pattern undergoes change from random to regular with increasing density, indicating an increase in interference, e.g. by sand tossing (Matsura and Takano 1989; Dor et al. 2014). Antlions display a range of responses to a low abundance of prey—from starvation to death after not moving for weeks, to relocation to another site within days (reviewed in Scharf and Ovadia 2006). There has been only a single additional study since 2005 on trap relocation by antlions in response to starvation: when starved, the majority of *Myrmeleon persimilis* larvae relocated in search of a more suitable area within 2 weeks (Tsao and Okuyama 2013). In wormlions, however, the effects of starvation seem to be on the other end of the continuum, with little response in terms of relocation (Scharf and Dor 2015; Katz et al. 2017b). Disturbance to the antlion larvae traps, which leads to partial or full trap destruction, seems to have a lower effect in terms of relocation but does lead to a reduction in trap size (Scharf and Ovadia 2006). This has been partially corroborated by some newer findings, in which disturbance resulted in no increase or even a decrease in relocation tendency (Barkae et al. 2010; Tsao and Okuyama 2013). Wormlion larvae, when disturbed, also rebuilt smaller traps (Scharf and Dor 2015). Although they hardly responded to starvation, they did relocate more frequently following disturbance (e.g. when sprayed with water simulating rain, Scharf et al. 2018).

The preferred light conditions would seem to be one factor that best divides trap-building antlion species into two types, those inhabiting lit areas and those inhabiting shaded sites (Scharf and Ovadia 2006, for newer works, see Lima and Faria 2007, Scharf et al. 2008a, 2008b). There is also evidence of different species sharing the same habitat, but with a distinct preference for shaded and sheltered vs. lit and open areas (Barkae et al. 2012; Klokočovník et al. 2020). Wormlions, in contrast, strictly prefer shade (Adar et al. 2016a; Katz et al. 2016, 2017a), and their preference for positions next to walls in urban habitats might be explained by the shade casted by such walls (Scharf et al. 2020a, 2021a). Recently, additional studies have been devoted to determine the traits of the preferred substrate. Here too, it seems that antlions diversify more in their preferred substrate than wormlions: for example, *M. hyalinus* and *M. immaculatus* prefer finer and coarser sand, respectively (Devetak and Arnett 2015, see also Devetak et al. 2005,

Table 1 List of works on microhabitat selection in antlions and wormlions. Symbols “+” indicate the type of factor(s) studied in each work

Taxon	Species	Reference	Sand traits	Light conditions	Disturbance to the traps	Prey availability	Conspecific density
Antlions	<i>Euroleon nostras</i>	Devetak et al. (2005)	+				
	<i>Myrmeleon bore</i>	Matsura et al. (2005)	+				
	<i>Myrmeleon brasiliensis</i>	Lima and Faria (2007)		+			
	<i>Myrmeleon hyalinus</i>	Loria et al. (2008)	+				
	<i>Myrmeleon hyalinus</i>	Scharf et al. (2008a)		+			
	<i>Myrmeleon hyalinus</i>	Scharf et al. (2008b)		+			
	<i>Myrmeleon hyalinus</i>	Scharf et al. (2009a)	+				
	<i>Myrmeleon hyalinus</i>	Barkae et al. (2010)			+		
	<i>Myrmeleon hyalinus</i>	Barkae et al. (2012)	+				
	<i>Cueta lineosa</i>						
	<i>Euroleon nostras</i>	Devetak et al. (2012)	+				
	<i>Myrmeleon persimilis</i>	Tsao and Okuyama (2013)			+		+
	<i>Myrmeleon hyalinus</i>	Devetak and Arnett (2015)	+				
	<i>Myrmeleon immaculatus</i>						
	<i>Euroleon nostras</i>						
	<i>Neuroleon microstenus</i>						
	<i>Myrmeleon formicarius</i>	Klokočovník et al. (2020)	+				
<i>Euroleon nostras</i>							
<i>Baliga micans</i>	Fukada and Nisimura (2021)	+					
Wormlions	<i>Vermileo vermileo</i>	Devetak (2008)	+				
	<i>Vermileo</i>	Dor et al. (2014)					+
	<i>Vermileo</i>	Scharf and Dor (2015)			+		+
	<i>Vermileo</i>	Adar et al. (2016a)	+	+			
	<i>Vermileo</i>	Katz et al. (2016)		+			
	<i>Vermileo</i>	Katz et al. (2017a)		+			
	<i>Vermileo</i>	Katz et al. (2017b)	+			+	+
	<i>Vermileo</i>	Scharf et al. (2018)	+				
	<i>Vermileo</i>	Bar-Ziv et al. (2019)	+				
	<i>Vermitigris</i>	Miler et al. (2019)	+				
<i>Vermileo</i>	Scharf et al. (2020a)	+	+				
<i>Vermileo</i>	Scharf et al. (2021a)		+				

When only the genus name is given, the species is either not known or not yet undescribed

Matsura et al. 2005, Devetak et al. 2012 for other reports of preferred sand particle sizes). In comparison, three wormlion species from three distinct geographical regions all prefer very fine sand (Devetak 2008; Bar-Ziv et al. 2019; Miler et al. 2019).

Fine sand and coarse sand present different advantages. For instance, potential prey can more easily escape a trap built in coarser sand (Botz et al. 2003), and such a trap requires more investment in maintenance, as large sand particles tend to fall back into the trap (Lucas 1982). It is also possible that the construction of traps in coarse sand requires more energy than in fine sand, especially for large individuals. Indeed, the preference for fine sand is stronger in small wormlions than in large ones (Bar-Ziv et al. 2019). However, as we describe later in the text, coarse sand enables a

better transmission than finer sand of the vibrations caused by potential prey, probably facilitating their capture by trap-builders (Devetak et al. 2007; Podlesnik et al. 2019).

Both antlions and wormlions prefer deep sand over shallow sand (Loria et al. 2008; Scharf et al. 2009a, 2020a; Adar et al. 2016a). The preference for deep sand is more critical for large individuals than for small ones, which are more limited by their body size when constructing traps (Bar-Ziv et al. 2019). Both antlions and wormlions prefer dry sand, because wet sand impairs trap construction and aids the escape of prey from the trap (Scharf et al. 2018; Miler et al. 2019). Comparison of a pair of co-occurring antlion and wormlion species revealed that the antlion preference for dry sand was greater than that of the wormlion (Miler et al. 2019), possibly because the latter is more vulnerable

to desiccation. That said and although antlions prefer dry sand, they avoid extremely dry sand (i.e. up to 30% relative humidity is preferred over 0%), perhaps owing to the cost of water loss (Fukada and Nisimura 2021). Very few studies have focused on adult antlions and wormlions, and we are aware of only two studies on the microhabitat selection of adult ovipositing females. While the preference for medium size sand particles in the antlion *M. bore* is similar for both the larval and the adult females (Matsura et al. 2005), the preference for deep sand in wormlion larvae is not supported by the adult females, which showed no preference (cf. Bar-Ziv et al. 2019; Adar and Dor 2018).

This brief overview of the newest antlion and wormlion literature regarding microhabitat selection already indicates some differences between the two taxa: namely, more typically passive starvation tolerance, a possibly higher disturbance sensitivity and more highly preferred shade and a fine, powder-like substrate, in wormlions than in antlions.

Plasticity in foraging behaviour

The behavioural plasticity of antlions has been receiving increased attention, as evidenced of a more recent review focused solely on this aspect (Scharf et al. 2011). Studies on plasticity focus on how antlions modify their foraging behaviour in response to biotic and abiotic factors. Such modifications are presumed to be adaptive, such as enabling the more efficient capture of prey. Other behavioural modifications, such as the construction of smaller traps under starvation, are either intended to save energy or are a by-product of exhaustion. It is important to experimentally examine the contribution of any such behaviour to foraging performance before determining whether it is indeed adaptive. We found 54 papers published between 2005 and 2021, relating to the behavioural plasticity of antlions and wormlions. These works primarily focused on the foraging strategy of larvae and how it changes, depending on various types of environmental input (Table 2). We refer to behavioural plasticity in response to starvation, temperature and substrate characteristics, competition and cannibalism and vibrations on the sand. We discuss those studies and the issues below.

Starvation

Antlions and wormlions are both quite tolerant of starvation (Arnett and Gotelli 2003; Scharf and Dor 2015) but can respond quickly to the movement of prey even after a long period at rest. The general prediction regarding the effect of starvation is that investment in foraging should increase with an increase in hunger up to the point of exhaustion and then gradually decrease (a hump-shaped pattern of an increase followed by a decrease, Scharf 2016). In antlion species with

facultative trap-building larvae, this should be reflected in ambushing without the trap during either extreme starvation or full satiation, but in establishing a trap in-between (supported by recent literature: Elimelech and Pinshow 2008; Tsao and Okuyama 2012). This effect should be similarly found in species characterized by an obligatory trap-building strategy, by building smaller traps during extreme starvation or full satiation and larger traps in-between. Such responses, however, are not always displayed (Liang et al. 2010; Scharf et al. 2010; Farji-Brener and Amador-Vargas 2020), as fed antlion larvae often do not reduce their trap size. Because those studies were conducted in the laboratory, without disturbance, it is therefore still possible that satiated individuals whose traps are destroyed are less likely to reconstruct the traps than somewhat hungrier ones. Similarly, such a hump-shaped pattern might still be discovered when examined in the field. This expectation is also not always realized in wormlions, in which starvation leads to a gradual decrease in trap size but not to an increase (Scharf and Dor 2015).

The “physiological history” prior to starvation is relevant to predicting how the trap-builder will respond to starvation. For example, in antlions, intense feeding immediately prior to starvation leads to faster mass loss and a higher likelihood of trap relocation, while a more moderate feeding or a gradual decline in prey encounter leads to better starvation tolerance (Jenkins 1994; Scharf et al. 2009b). In a comparison between two antlion populations, it was found that those that decreased their activity to a larger extent under starvation lost less mass, but also benefited less in terms of growth rate upon the renewal of feeding, compared to those that decreased their activity more moderately (Rotkopf et al. 2013). This somewhat resembles the finding from a comparison between wormlion populations in urban and in more natural sites, in which the former constructed larger traps and responded faster to prey than the latter (Samocho and Scharf 2020). It is possible that urban wormlion populations might be less tolerant to starvation than wormlions in natural areas.

Temperature and substrate characteristics

Despite undeniable preferences for certain soil traits by both antlions and wormlions, the larvae must sometimes settle for unfavourable conditions. Certain abiotic factors may similarly lead to a hump-shaped pattern of investment in foraging, as described above for starvation. For example, temperatures that are below or above the optimum should affect foraging negatively and limit physiological capacities and reactions in comparison to an optimal, moderate temperature. However, most of the experimental evidence indicates a more positive linear relationship between temperature and foraging performance in antlions, such as trap construction and hunting (Klokočovnik et al. 2016, Antoř et al. 2018,

Table 2 List of works on behavioural plasticity in antlions and wormlions. Symbols (“+”) indicate the type of factor(s) studied in each work

Taxon	Species	Reference	Starvation	Temperature and substrate characteristics	Competition and cannibalism	Vibrations on the sand	Operant learning
Antlions	<i>Euroleon nostras</i>	Fertin and Casas (2006)		+			
	<i>Euroleon nostras</i>	Devetak et al. (2007)		+		+	
	<i>Euroleon nostras</i>	Fertin and Casas (2007)				+	
	<i>Myrmeleon</i>	Swenson et al. (2007)			+		
	<i>Myrmecaelurus</i>	Elimelech and Pinshow (2008)	+				
	<i>Myrmeleon crudelis</i>	Farji-Brener et al. (2008)		+			
	<i>Euroleon nostras</i>	Mencinger-Vračko and Devetak (2008)				+	
	<i>Myrmeleon hyalinus</i>	Scharf et al. (2008c)		+			
	<i>Myrmeleon</i>	Burgess (2009)		+			
	<i>Myrmeleon crudelis</i>	Guillette et al. (2009)				+	
	<i>Myrmeleon hyalinus</i>	Scharf et al. (2009b)	+				
	<i>Cueta sauteri</i>	Liang et al. (2010)	+				
	<i>Myrmeleon hyalinus</i>	Scharf et al. (2010)					+
	<i>Myrmeleon</i>	Hollis et al. (2011)					+
	<i>Myrmeleon hyalinus</i>	Barkae et al. (2012)				+	
	<i>Cueta lineosa</i>						
	<i>Euroleon nostras</i>	Klokočovnik et al. (2012)			+		
	<i>Myrmeleon persimilis</i>	Tsao and Okuyama (2012)	+				
	<i>Myrmeleon hyalinus</i>	Rotkopf et al. (2012)			+	+	
	<i>Cueta lineosa</i>						
	<i>Myrmeleon hyalinus</i>	Rotkopf et al. (2013)	+				
	<i>Myrmeleon hyalinus</i>	Barkae et al. (2014)				+	
	<i>Myrmeleon acer</i>	Beponis et al. (2014)			+		
	<i>Myrmeleon hyalinus</i>	Rotkopf and Ovidia (2014)	+		+		
	<i>Euroleon nostras</i>	Klokočovnik et al. (2016)			+		
	<i>Myrmeleon bore</i>	Kuszevska et al. (2016)					+
	<i>Myrmeleon hyalinus</i>	Barkae et al. (2017)				+	
	<i>Cueta lineosa</i>						
	<i>Myrmeleon bore</i>	Miler et al. (2017)					+
	<i>Myrmeleon bore</i>	Antoľ et al. (2018)			+		
	<i>Myrmeleon</i>	Miler et al. (2018a)				+	
	<i>Myrmeleon bore</i>	Miler et al. (2018b)					+
	<i>Euroleon nostras</i>	Podlesnik et al (2019)			+		+
	<i>Myrmeleon hyalinus</i>	Devetak et al. (2020)			+		
	<i>Cueta lineosa</i>						
	<i>Myrmeleon crudelis</i>	Farji-Brener and Amador-Vargas (2020)	+				
	<i>Myrmeleon crudelis</i>	Farji-Brener et al. (2020)				+	
	<i>Myrmeleon formicarius</i>	Klokočovnik et al. (2020)				+	
	<i>Euroleon nostras</i>						
	<i>Myrmeleon inconspicuus</i>	Martinez et al. (2020)					+
<i>Myrmeleon bore</i>	Miler et al. (2020)			+			
<i>Euroleon nostras</i>							
<i>Myrmeleon hyalinus</i>	Ovidia et al. (2020)				+		
<i>Cueta lineosa</i>							
<i>Myrmeleon brasiliensis</i>	Abot et al. (2021)			+			

Table 2 (continued)

Taxon	Species	Reference	Starvation	Temperature and substrate characteristics	Competition and cannibalism	Vibrations on the sand	Operant learning
	<i>Euroleon nostras</i>	Miler and Czarnoleski (2021)		+			
	<i>Myrmeleon hyalinus</i>	Miler and Scharf (in press)					+
Wormlions	<i>Vermileo</i>	Dor et al. (2014)		+	+		
	<i>Vermileo</i>	Scharf and Dor (2015)	+				
	<i>Vermileo</i>	Adar et al. (2016a)		+			
	<i>Vermileo</i>	Adar et al. (2016b)		+			
	<i>Vermileo</i>	Katz et al. (2017a)		+			
	<i>Vermileo</i>	Katz et al. (2017b)			+		
	<i>Vermileo</i>	Bar-Ziv and Scharf (2018)		+			
	<i>Vermileo</i>	Bar-Ziv et al. (2018)			+		
	<i>Vermileo</i>	Katz and Scharf (2018)				+	
	<i>Vermilitigris</i>	Miler et al. (2018a)			+		
	<i>Vermileo</i>	Samocha and Scharf (2020)	+				
	<i>Vermileo</i>	Scharf et al. (2020b)			+	+	
	<i>Vermileo</i>	Scharf et al. (2021a)		+			
	<i>Vermileo</i>	Scharf et al. (2021b)			+		

When only the genus name is given, the species is either not known or not yet undescribed

see also earlier works, such as Youthed and Moran 1969, Arnett and Gotelli 2001). This probably stems from insufficient temperature ranges tested so far (i.e. performance under higher temperatures needs to be tested). Although antlions occurring in lit (hotter) and shaded (cooler) sites differ strongly in temperature tolerance (Rotkopf et al. 2012; Miler et al. 2020), both groups display a surprisingly high tolerance. Some species, especially those from open, sun-exposed areas, thrive under ground temperatures as high as 50 °C, well above the physiological limits for many ectotherms (Marsh 1987), although trap temperatures are probably a few degrees lower (Green 1955). Consequently, studies might fail to reach test temperatures above the optimal ones for antlions.

It is easier to reach stressfully high temperatures for shade-preferring species, such as *Euroleon nostras*, than for those occupying open areas, such as *M. bore*, with the former showing more pronounced effects of short-term exposure to a temperature of 40 °C (Miler et al. 2020). The negative effect of high temperature is also clear in *E. nostras*: the antlions constructed smaller pits after being kept for a month at 31 °C compared to a control kept at a more benign 25 °C (Miler and Czarnoleski 2021). The reason for the high thermal tolerance of most antlion species might be a consequence of their arms race with ants: ants seek to be active in higher temperatures than antlions, to avoid

predation, while antlions follow the ants and remain vigilant in high temperatures rather than entering “heat torpor” (Marsh 1987).

In wormlions, which strictly prefer shade and also seem less resistant to desiccation, appropriate test conditions might be more easily reached. Indeed, the average trap area of wormlion larvae placed under optimal, below-optimal and above-optimal temperatures, shows a hump-shaped pattern, as expected (Katz et al. 2017a). Importantly, wormlions show no or weak thermal acclimation to stable temperatures (Bar-Ziv and Scharf 2018). Acclimation to unfavourable low or high temperatures has not been examined to date in any antlion species. Furthermore, the results and conclusions of thermal experiments conducted in the laboratory need to be verified in the field, where larger masses of ground may serve as a buffer against thermal fluctuations.

Several studies have investigated how antlions from populations of *M. hyalinus* or *M. immaculatus* across a climatic gradient differ in morphology, life-history traits, starvation tolerance and behaviour (Arnett and Gotelli 1999, 2003; Scharf et al. 2008c; Rotkopf and Ovidia 2014; Alcalay et al. 2015). While individuals of both species are larger in colder habitats than in warmer ones, the two species differ across populations in several other important traits (Arnett and Gotelli 1999; Scharf et al. 2008c). For example, *M. immaculatus* from colder habitats tolerate starvation

better, while there is no difference between colder or warmer habitat populations in *M. hyalinus* (cf. Arnett and Gotelli 2003; Rotkopf and Ovadia 2014). Furthermore, development takes longer in the southern and warmer population in *M. immaculatus*, while the opposite holds true for the southern and warmer population of *M. hyalinus* (cf. Arnett and Gotelli 1999; Scharf et al. 2008c). This difference may be explained by the differences in the length of the season suitable for growth, which is shorter in the southern and northern habitats of *M. hyalinus* and *M. immaculatus*, respectively (harsh summer vs. harsh winter). It would also be of interest to understand whether such differences originate from phenotypic plasticity or are genetic adaptations to specific environments. Common-garden experiments offer a powerful method by which to distinguish between the two (e.g. Purcell et al. 2016).

Other abiotic factors, such as sand particle size, might constrain foraging behaviour, by limiting trap construction and maintenance or prey detection (Fertin and Casas 2006; Devetak et al. 2007, 2020; Burgess 2009; Klokočovník et al. 2012; Podlesnik et al. 2019). It is yet to be determined whether trap-builders can compensate for such constraints by being more responsive to vibrations on the sand (i.e. increased sensitivity to vibrations in suboptimally constructed traps as a compensation mechanism). There are several other sources of interference with trap construction and maintenance. For instance, prey corpses may deter live ants from approaching the trap, and it is unclear to what extent trap-builders can effectively dispose of such corpses (Beponis et al. 2014), although wind may help to blow them away. In addition, as many antlions prefer shaded microhabitats below trees, they must also cope with the plant litter that trees produce and which fall onto the traps (Farji-Brener et al. 2008; Abot et al. 2021). Trap-builders in urban habitats might also encounter human litter, potentially negatively affecting trap size (Dor et al. 2014; Adar et al. 2016a, 2016b). Field experiments on the effects of such potential disturbances are missing. To date, little is known regarding the impaired performance of trap-building insects under suboptimal abiotic conditions and even less on the coping mechanisms under these conditions.

Competition and cannibalism

Although antlions are solitary predators, they often aggregate and form uncooperative groups, probably due to the limited suitable areas for trap establishment and low dispersal ability following female oviposition. The same holds true for wormlions. There is currently no in-depth study on the relocation distances and the ability of antlions and wormlions to move from one suitable microhabitat to another. The foraging behaviour of antlions and wormlions undergoes

change in response to competition, which naturally escalates with the increasing density of conspecifics (Scharf et al. 2011). The more recent literature confirms earlier reports of trap size being restricted in antlion aggregations at high densities (Swenson et al. 2007). It also contributes to the knowledge in describing how the reduction in density that follows results in a compensatory trap size increase (Farji-Brener et al. 2020).

Wormlions create aggregations at a generally higher density than antlions (Dor et al. 2014; Bar-Ziv et al. 2018), and it seems that the competition among neighbouring antlions is stronger than that among wormlions. In the laboratory, on the one hand, high density alters the spatial pattern of traps from random to regular, reduces the probability of constructing a trap, triggers relocation and decreases the attractiveness of sites (Dor et al. 2014; Katz et al. 2017b; Scharf et al. 2020b). On the other hand, there is a positive correlation between the sizes of the traps of neighbouring wormlion larvae (Dor et al. 2014). Furthermore, when placing a pair of wormlions differing in size in a limited area, both wormlions reduce their trap area, indicating that both pay a price in competition (Scharf et al. 2021b). In contrast, a pair of large and small antlions of the species *Macroleon quinquemaculatus* constructed larger and smaller traps than expected, respectively, paying a size-dependent price for competition (Griffiths 1992).

Interspecific competition between potentially co-occurring species and the possible processes of habitat partitioning has also received some recent interest. In antlions, this has been studied with *M. hyalinus* and *Cueta lineosa*, as well as with *E. nostras* and *M. formicarius* larvae. The former species in each pair outcompetes the other in common conditions, as evidenced by the direction of intra-guild predation, rate of trap construction, response time to prey and prey capture success (Barkae et al. 2012; Klokočovník et al. 2020; Ovadia et al. 2020). A similar asymmetry, but in prey size range, was found between the co-occurring *Myrmeleon* antlions and *Vermigitris* wormlions (Miler et al. 2018a). However, as also found, under harsher conditions (i.e. characterized by higher temperature), *C. lineosa* is superior to *M. hyalinus* in terms of survival rate, starvation tolerance and foraging success (Rotkopf et al. 2012; Barkae et al. 2017). In mixed populations of antlions and wormlions, the latter plausibly possess an advantage which ultimately allows them not to be driven out of the shared microhabitat. The advantage that each species has in direct competition is yet to be explored. Except for the studies by Miler et al. (2018a, 2019), no other studies have examined together co-occurring populations of antlions and wormlions and particularly the mechanisms that enable their coexistence.

As noted previously (Scharf et al. 2011), although a high density of larvae leads to an increase in cannibalism in antlions, certain abiotic factors (e.g. deep sand) were found

to provide an escape from such a fate (Barkae et al. 2014). This might plausibly also apply to intra-guild predation in mixed populations. While wormlions have been considered non-cannibalistic to date, a recent study has demonstrated a low rate of cannibalism also in wormlions, albeit much lower than that reported for antlions (Scharf et al. 2021b).

Vibrations on the sand

Many soil-dwelling predators use vibrations on the sand to locate prey, while prey species use vibrations mostly to avoid and deter predators (reviewed in Hill 2009). Antlions are no different, and they use vibrations to aid their hunting efforts (Devetak et al. 2007; Fertin and Casas 2007). Antlions with functional traps, exposed to recordings of ants moving on the sand, toss sand in the direction of the incoming recorded vibrations. Recordings of antlion behaviour in arenas with different species of approaching prey confirmed the high accuracy of the direction of sand tossing and showed that antlions can react to potential prey even from a distance of 10 cm (Mencinger-Vračko and Devetak 2008). This high sensitivity to vibrations was later confirmed, with buried antlions being shown to move towards the surface in response to the vibratory signals of prey (Podlesnik et al. 2019). It was also found that substrates differ in their conductivity of vibrations, with smaller particles conducting vibrations less well. In another experiment (Martinez et al. 2020), antlions reacted faster to artificial signals mimicking the approach of the prey towards the trap (first weaker then stronger vibrations) than to similar consecutive vibrations (strong vibrations, one after another). Overall, antlion sensitivity to vibrations seems very high. Specifically, heat-stressed larvae showed decreased vibration sensitivity (Miler and Czarnoleski n.d., in review), indicating that this behavioural feature is not fixed. While it is logical to assume that wormlions too are able to sense vibrations on the sand, how they do so has never been studied, nor from what distance they are able to locate and respond to prey. Here too, comparative experiments between the taxa will be of interest, adding new layers to the research on the convergent evolution.

The antlions' sensitivity to vibrations has been used in a series of works on the cognitive abilities of larvae. Cognition can be defined as processes connected to the acquisition, retention and use of information—all three of which are integral to fitness (Shettleworth 2001; Dukas 2004). The examination of antlion cognition began with observations of the behavioural reactions of larvae to vibrational signals delivered near the edge of the traps and either associated with prey or not (Guillette et al. 2009). In each case, signals were delivered by means of dropping a small amount of sand near the antlion trap, simulating the movement of prey on the sand. The signals were delivered either immediately before the prey was dropped into the trap (the trained group

of larvae) or at a different time than the feeding time (the control group), over several days (the training phase). A test was then performed, comprising signal delivery and documentation of behaviour. In order to capture an approaching prey, the trained larvae moved their heads and mandibles and tossed sand more frequently than the control group. This was interpreted as the first evidence of learning in antlions. Learning had consequences for both development and body mass: antlions in the trained group developed faster and increased faster in mass (Guillette et al. 2009, Hollis et al. 2011).

Antlion learning is even more complex (Kuszevska et al. 2016): Firstly, larvae can be trained to differentiate weak/strong signals associated with small/large ants, respectively, and subsequently react to strong signals but not to weak ones. This makes sense, as it pays to ignore a small, energetically low-value ant, but not a large one. Secondly, when a vibratory signal was either associated or not with the loss of an already captured prey, the trained group responded by burying themselves together with the prey following the signal, to prevent prey loss. These results were later built on, to understand the factors affecting the efficiency of the learning process, which was highly variable among individuals (Miler et al. 2017, 2018b). The most recent study on antlion cognition has demonstrated that antlions can be trained in a T-maze to turn to a specific side, where sand was available, and to avoid a side making them fall on a hard surface (Miler and Scharf in press). This is the first evidence of operant conditioning in antlions, on top of the already known associative learning.

Regarding wormlions, nothing is known about their vibratory responsiveness or their cognitive plasticity and learning skills. Notably, however, wormlion larvae demonstrate a low perceptual range, only of a few cm, in regard to their favoured environmental conditions (Katz and Scharf 2018; Scharf et al. 2020b). These findings could indicate that wormlions are more limited in their ability to gather information. However, it is also possible that they are indeed highly responsive to vibrations, similarly to antlions, because a limited visual perception is likely to drive the evolution of other, compensatory, sensory modalities.

Behavioural consistency and personality

The advantage of studying behaviour under a “personality framework” lies in a better understanding of which behaviours correlate with each other and have probably undergone selection as a unit (Dingemanse and Réale 2005). Behavioural consistency is also important as a necessary step, for example, before determining “personality” (Bell et al. 2009). We found six papers written between 2005 and 2021, relating to this subject in antlions and wormlions. In

an ethological study (Klokočovník and Devetak 2014), the stereotypic behavioural sequence of hunting behaviour in *E. nostras* antlion larvae was described, elaborating upon earlier research. Occasional deviations from the typical sequence were noted, such as prey beating during prey capture and head roll during trap maintenance. Another study (Alcalay et al. 2014a) described how second and third instar antlion larvae differ in some specifics in their foraging behaviour: namely, trap size, response time to prey and prey exploitation efficiency. All these metrics were higher in third than in second instars, which underline the importance of differentiating between instar stages in experimental studies, in addition to differences in body mass. Furthermore, a positive correlation was found between trap size and prey exploitation efficiency, and the response time to prey and relocation distance, suggesting that individuals either focus on foraging or intend to relocate. Third instars also demonstrated consistency in their trap size and response time to prey when measured twice over several days. As a side note, antlion instars do not only differ in size but also in allometry. Whereas *Myrmeleon hyalinus* third instar larvae possess larger heads relative to the rest of the body than second instar larvae, the opposite holds true for *M. crudelis* (cf. Scharf et al. 2008c with Farji-Brener et al. 2021).

Alcalay et al. (2014b) further reported consistency in movement distances over several days and examined under several conditions. Antlion larvae from different populations display generally similar foraging syndromes, in which trap size is highly correlated to response time to prey and prey exploitation efficiency (i.e. core “foraging performance syndrome”, Alcalay et al. 2015). It may therefore be beneficial to study more than a single behavioural response, in order to more fully describe the behavioural state of trap-builders. Wormlions, in comparison, seem to be less consistent in certain behaviours over time than antlions, with some behaviours being less consistent than others. For example, while the preference for shade and the tendency to construct a trap were consistent over a few days, other behaviours, such as relocation distance, were not (Katz et al. 2016). In general, examining behavioural consistency over longer periods is important, because it is questionable whether the behavioural consistency of trap-builders lasts more than a few days. If it does not, and considering antlions’ and wormlions’ long lifespan of a year or more, the relevance of “personality” to trap-builders is questionable as they might demonstrate “episodic personality” at the most. This is similar, for example, to bumblebees and their response to novelty, which is consistent only over a few hours, which makes sense as plasticity in this regard is more desirable and probably selected for (Muller et al. 2010). Similarly, the responses of the gloomy octopus to a conspecific, a food item and a novel item were correlated for a single day, but

the responses to each stimulus were shown to be uncorrelated over a few days (Pronk et al. 2010).

More research is needed as it is possible that trap-builders indeed possess profound personalities, just not in all behavioural traits, not at all developmental stages and/or more in the field than in the laboratory, as in other taxa (reviewed in Bell et al. 2009). Importantly, in both antlions and wormlions, consistency was higher under favourable than unfavourable conditions (moderate vs. harsh temperatures, Alcalay et al. 2014b; Katz et al. 2017a). This is perhaps similar to the increase in phenotypic divergence of a species under suboptimal conditions (Köhler et al. 2009).

Research directions

We have focused so far on various aspects of microhabitat selection, behavioural plasticity and personality in trap-building antlions and wormlions. We now turn to research gaps and recommended directions for further research. Experimental studies presenting direct comparisons of antlion and wormlion larvae are scarce (Scharf et al. 2017; Miler et al. 2018a, 2019) and thus need to be continued and expanded in order to acquire a better understanding of their similarities and differences (Table 3). The gaps in knowledge are significant and relate to different biological levels of organization of the two taxa, from the genetic level to community ecology.

Regarding the genetic level, it would be interesting to determine the differential gene expression among antlions that do not build traps, switch between trap construction and sit-and-pursue foraging mode and obligatory trap-builders. Obtaining a clue regarding the possible genes involved in trap construction, one could then examine whether wormlions express the same genes and compare them to related Dipterans, which clearly do not. Such a comparison could reveal convergence at the genetic level, although such genetic convergence is not essential. On the physiological level, there is limited evidence that antlions use toxins, produced by bacteria, to paralyze their prey (Matsuda et al. 1995; Yoshida et al. 1999). It is unknown whether such toxins are the rule in most trap-building antlions and, if so, whether wormlions possess similar or other toxins. If the answer to the last question is negative, it might explain why antlions of a similar size to wormlions can, for example, capture larger prey (Miler et al. 2018a, b). On the behavioural level, while there is accumulating evidence of antlion ability to sense vibrations and associate them with prey arrival, nothing is known in this respect in regard to wormlions. Priority should also be given to determine how wormlions perceive their environment and their response to vibrations in particular. It is probable that wormlion larvae are indeed responsive to vibrations, considering their lifestyle, general

Table 3 Patterns of similarities and differences between antlion and wormlion larvae in two research areas, microhabitat selection and behavioural plasticity, emerging from the literature. Reactions to the

listed factors, at this point, should still be treated as hypotheses to be tested more rigorously

Research area	Factor	Antlions	Wormlions
Habitat selection	Density	Similar avoidance of high density	
	Sand depth	Similar preference for deep sand	
	Starvation	Diverse avoidance	Weak avoidance
	High disturbance	Weaker avoidance	Stronger avoidance
	Shade	Diverse preference	Strict preference
	Sand particle size	Diverse preference	Strict preference
	Sand dryness	Stronger preference	Weaker preference
Behavioural plasticity	Starvation	No general pattern in both taxa	
	Temperature and soil characteristics	No general pattern	Preference for fine sand and lower temperature
	Competition and cannibalism	Stronger reactions	Weaker reactions
	Associative learning	Possible	Unknown
	Vibrations on sand	High responsiveness	Unknown

similarity to antlions and the high prevalence of this ability in insects (Cocroft and Rodríguez 2005).

Although antlions use spiral digging and wormlions use central digging, it is unknown to what extent pit structure differs between the taxa. For instance, two antlion species (*M. hyalinus* and *Cueta lineosa*) differ greatly in pit structure (Devetak et al. 2020), but the pit structure of any wormlion species has not been studied. The same holds for pit slope, which has been studied only in antlions (Lucas 1982; Büsse et al. 2021). Another interesting direction lies in determining the level of environmental specialization of antlion or wormlion species (e.g. their occurrence in different habitats, the prey they are able to catch and foraging modes) and comparing this to their cognitive abilities. There might be a link between specialization and cognition (e.g. generalists sometimes outperform specialists; Henke-von der Malsburg et al. 2020).

Many basic questions on the life history of both taxa are still unanswered, especially regarding the adult stage, such as how many eggs does each female lay, how long do they live and how far do they disperse. Answers to such questions would be meaningful for understanding the population genetic structure and level of isolation. Regarding their ecology, it is not yet clear why wormlions are much more successful than antlions in urban habitats. This might be related to a greater similarity of some urban microhabitats, such as thin layers of sand below covers providing shade, to their natural habitat, such as caves; the availability of small ants, which might be sufficient for wormlions, but not for antlions; or the favourable conditions provided by positions next to walls (Bar-Ziv et al. 2018; Scharf et al. 2020a, 2021a). This remains to

be uncovered. In general, questions related to behavioural plasticity and how well animals cope with environmental changes are urgent, owing to the intensity of global changes (Tuomainen and Candolin 2011; Gunderson and Stillman 2015). Wormlions, common in Mediterranean cities, may represent well other soil-dwelling insects in cities and serve as a bio-indicator of pollution in urban soils (McGeoch 1998). While there are known phenotypic differences among antlion populations across climatic gradients (e.g. Arnett and Gotelli 1999; Scharf et al. 2008c), there are no parallel studies on wormlions. Similar phenotypic differences among wormlion populations would strengthen the evidence that climate is indeed responsible for such differences.

The interactions of trap-builders with other co-occurring species, and the exact identity and interaction with their prey, competitors, parasites and predators, are also mostly unknown. Regarding predation, for instance, there are anecdotal reports on birds, scorpions and ants preying on antlions, but no thorough examination of predation (or parasitism) risk has been carried out in any of the trap-building insects (Hauber 1999; Gatti and Farji-Brener 2002; Segev et al. 2020). Understanding the predation risks in trap-builders, and whether antlions and wormlions experience similar risks, will enable determination of whether they employ similar mechanisms for coping with such risks (e.g. death-feigning, Sendova-Franks et al. 2020). Ruxton and Hansell (2009) have suggested that one reason why traps are uncommon as a foraging strategy in nature is due to their conspicuousness and possible attraction of predators. This suggestion has never been experimentally examined. Another unusual ecological

interaction is suggested to exist between gazelles and antlions in the desert, in which the former break the soil crust, increasing the habitat available for the latter (Shanas et al. 2018). Placing trap-builders within larger biological networks will help to understand the role they play in their community.

Concluding remarks

Research on trap-building insects has to date only scratched the surface of possible research directions. We believe there is a great advantage to studying antlions and wormlions together, in order to better understand the extent and limitations of their evolutionary convergence. This advantage lies in the fact that their general convergence is doubtless, as they are only distantly related taxa. In the orb-weaving spiders, for example, there is an ongoing discussion on whether different lineages evolved similar predatory strategies independently (i.e. converged, Kullmann 1972) or whether orb-weaving is homologous, originating from a common ancestor, as suggested by some of the newest phylogenetic analyses (Coddington et al. 2019, see Dimitrov and Hormiga 2021 for a review). This highlights the uniqueness of the antlion-wormlion convergent evolution, triggered by the similar microhabitats and hunting strategy shared by the two taxa.

Antlions and wormlions possess a highly similar hunting strategy, unique in the animal kingdom. A closer inspection, however, demonstrates many behavioural differences between the taxa, plausibly owing to the different constraints imposed on each taxon, and the fine dissimilarities in their habitat. The question why pit building evolved so few times remains open, and we cannot rule out the possibility that chance alone is responsible for it (Stayton 2015). We speculate that the reason for many of the differences between pit-building antlions and wormlions lies at the distinct morphology of the two taxa. For instance, the lack of obvious weaponry in wormlions compared to antlions, which have strong mandibles, might limit the wormlion ability to handle large prey, but also might limit cannibalism, enabling them to occur in much higher densities than antlions. To date, the knowledge on antlion habitat selection and foraging behaviour is relatively good, with an improved understanding of antlion cognitive skills. However, the ratio of studies on antlions vs. wormlions is greater than 10:1, and more studies on wormlions are needed. An additional weakness of wormlion studies is that of the focus on a much lower number of species, questioning the ability to truly reach generalizations.

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Declarations

Conflict of interest The authors declare no competing interests.

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