

# Foraging decisions and behavioural flexibility in trap-building predators: a review

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## ABSTRACT

Foraging theory was first developed to predict the behaviour of widely-foraging animals that actively search for prey. Although the behaviour of sit-and-wait predators often follows predictions derived from foraging theory, the similarity between these two distinct groups of predators is not always obvious. In this review, we compare foraging activities of trap-building predators (mainly pit-building antlions and web-building spiders), a specific group of sit-and-wait predators that construct traps as a foraging device, with those of widely-foraging predators. We refer to modifications of the trap characteristics as analogous to changes in foraging intensity. Our review illustrates that the responses of trap-building and widely-foraging predators to different internal and external factors, such as hunger level, conspecific density and predation threat are quite similar, calling for additional studies of foraging theory using trap-building predators. In each chapter of this review, we summarize the response of trap-building predators to a different factor, while contrasting it with the equivalent response characterizing widely-foraging predators. We provide here evidence that the behaviour of trap-building predators is not stereotypic or fixed as was once commonly accepted, rather it can vary greatly, depending on the individual's internal state and its interactions with external environmental factors.

*Key words:* antlions, optimal foraging, searching behaviour, sit-and-wait predators, spiders, starvation.

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## I. INTRODUCTION

Trap-building (hereafter, TB) arthropod predators, such as pit-building antlions or web-building spiders, can be classified

as sit-and-wait predators, since they invest no energy or time in searching for prey, but need only a suitable place to construct a specific trap (Riechert & Luczak, 1982; Riechert, 1992; Eltz, 1997). The most obvious difference between

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sit-and-wait and actively foraging predators is the negligible cost associated with searching for prey. Other important distinctions are the capability of sit-and-wait predators to survive long periods of starvation by drastically reducing their metabolic and respiration rates, the capture of mostly actively searching prey, and the production of large clutch sizes compared to their more mobile relatives (Huey & Pianka, 1981; Simpson, 1995; Perry & Pianka, 1997). A notable difference between TB arthropod predators and other sit-and-wait predators is the trap constructed. The general goal of building a trap is to increase the predator's attack radius and the probability of capturing prey (Lucas, 1986; Heiling & Herberstein, 2000) and thus the trap can be considered as an "extended phenotype" of the TB arthropod predator (Dawkins, 1982, pp. 20, 198). The trap is not only a device to capture prey of suitable size (prey items that are too large may escape). It also enables the predator to expand the range of prey sizes captured and to attack fast-moving or relatively large prey that otherwise could not be easily caught (Heinrich & Heinrich, 1984; Mansell, 1988; Heiling & Herberstein, 2000), and to retain it until it can be immobilized (Lucas, 1989). Traps can also be used for purposes other than hunting, such as a mating platform in spiders (e.g. Elgar, 1991) or shelter from predation (Griffiths, 1980; Lucas, 1986).

Foraging behaviour has been studied extensively in widely-foraging predators. Classical foraging theory suggests that animals optimize the net rate of energy gain by attempting to gain maximum energy in minimum foraging time (e.g. Stephens & Krebs, 1986; Bell, 1991). More recent models have implemented several additional constraints to this optimization rule, such as avoiding predation and the cost of missed opportunities (e.g. Brown, 1988; Brown & Kotler, 2004). The exact investment in foraging is an integral part of foraging theory. For example, animals are expected to use different intensities of foraging according to internal and external factors which often contradict one another, such as hunger level and predation threat (Stephens & Krebs, 1986, ch. 7; Lima, 1998). Nevertheless, measuring foraging intensity is often difficult. For example, measuring search time may produce inaccurate results, because searching can be performed in various habitats that differ in their productivity and the risk they impose on the forager and because searching can be performed at different velocities and intensities (e.g. Fulton & Bellwood, 2002). An alternative method to estimate investment in foraging is by measuring giving-up densities (i.e. offering a known amount of food and measuring how much remains after the last animal stopped foraging; e.g. Brown, Kotler & Mitchell, 1994). This process can be exhausting for the experimental biologist and it produces an indirect measure of foraging intensity; unless the identities of the foraging animals are known, it does not allow the quantification of variation among individuals within the population (Ovadia & zu Dohna, 2003).

Compared to widely-foraging predators, significantly less attention has been devoted to the foraging behaviour of sit-and-wait predators and especially to TB arthropod

predators. The vast majority of TB arthropod predators belong to four distinct taxonomic groups: web-building spiders, pit-building antlion larvae, caddisfly larvae and wormlion larvae (Devetak, 2008; Ruxton & Hansell, 2009); the order of appearance here representing in decreasing order the intensity of research devoted to each group. Foraging effort among these predators is reflected mainly in the amount of energy invested in the process of trap construction and maintenance (Uetz, 1992; Eltz, 1997; Herberstein, Craig & Elgar, 2000b) which makes them interesting model organisms for studies of foraging behaviour. Owing to their restriction to a small area, it is possible to study large groups of TB arthropod predators in the laboratory, to estimate accurately the effects of different factors on investment in trap construction and to investigate inter-individual variability. For example, TB arthropod predators depend on their microhabitat in the process of trap construction and thus are especially useful for studying the effects of physical and microclimatological factors on foraging characteristics. In addition, studies of TB predators may be insightful because they do not always follow the classical predictions of foraging theory (Scharf & Ovadia, 2006). For example, not all antlion species relocate their pit in response to starvation, rather some of them simply starve to death (Matsura, 1987). In addition, antlion larvae do not always respond to changes in their prey location by moving their pits to richer prey areas (e.g. Heinrich & Heinrich, 1984; Matsura, 1987).

In this review, we focus mainly on antlions and spiders and comprehensively review different factors influencing their foraging behaviour. Arthropod behaviour was once considered to be instinctive and fixed (as noted in: Krink & Vollrath, 1997; Heiling & Herberstein, 1999), and the same attitude was common when comparing sit-and-wait predators to widely-foraging ones: the former were considered to rely more on instincts and less on learning and decision making (Huey & Pianka, 1981). One of our purposes here is to demonstrate that TB predators modify their foraging behaviour in response to internal and external factors. In other words, we hope to convince the readers that the view of limited behavioural flexibility in TB predators is superficial and that both spiders and antlions have different behavioural options when foraging and make decisions according to both external and internal factors, similar to widely-foraging predators (Bell, 1991). Another important goal is to test whether TB predators usually follow general predictions derived from foraging theory by comparing their context-specific behaviour with that of widely-foraging predators. In order to achieve these goals we first explain how investment in foraging can be quantified in TB arthropod predators. Second, we survey foraging decisions in antlions and spiders and compare them to widely-foraging arthropods. Third, we discuss evidence for learning in TB predators and compare it to other cases of arthropod learning. Finally, we conclude with suggestions for future directions of investigation.

### (1) How can the investment of trap-building predators in foraging be quantified?

Trap-building predators are similar to non-trap-building sit-and-wait predators in that they do not search for prey. However, TB predators invest energy in constructing an efficient trap, which might be costly. For instance, metabolic rates of antlions and spiders constructing traps are much higher than those at rest (Lucas, 1985; Tanaka, 1989), and specific proteins are required for web construction in the case of spiders. This investment in the trap is a proper point of comparison with searching activity and its associated costs in widely-foraging predators. Searching is not uniform, and it can be performed at different intensities. For example, many animals first search using directional movement, but after an encounter with a prey item, they switch to area-restricted search, using a more tortuous movement path in order to locate other prey nearby (e.g. Carter & Dixon, 1984; Bell, 1991, p. 89). We will later present an analogy to this behavioural flexibility in TB predators. Furthermore, widely-foraging predators move among patches, and they are expected to do so when the gain of a specific patch falls below that of the average expected gain from the habitat (Stephens & Krebs, 1986). Similarly, TB predators relocate their traps more often when prey are scarce (e.g. Riechert, 1992; Hauber, 1999; Nakata & Ushimaru, 1999). This point of comparison is discussed briefly here, since it is summarized elsewhere (Scharf & Ovadia, 2006). Finally, widely-foraging predators use different search tactics for different prey types or depending on the spatial distribution of the prey (e.g. Greeff & Whiting, 2000; Fulton & Bellwood, 2002). In other words, different prey types are better detected or encountered in different ways. As discussed later, this important behavioural flexibility exists also in TB predators, and is not trivial: like most sit-and-wait predators, TB predators are generalists, and as such they may not gain sufficient benefit from adapting their foraging behaviour to trap specific prey.

The three major ways in which TB predators can respond to changes in internal and external factors are by modifying trap size, modifying trap shape or architecture and relocating the trap. We focus here on modifications of trap size and shape because: (1) factors triggering trap relocations were summarized elsewhere (Riechert & Gillespie, 1986; Scharf & Ovadia, 2006); and (2) trap modifications are analogous to modifications in searching intensities in widely-foraging predators. A good question at this point would be to what extent can these traps be modified, and the answer is quite surprising. Spiders can modify their traps in various ways. They can obviously enlarge or reduce their trap size (e.g. Riechert, 1981; Sherman, 1994; Higgins, 1995) and can even avoid constructing a web altogether, at least in the short term (Pasquet, Ridwan & Leborgne, 1994; Salomon, 2007). Other possible modifications are changes in shape but not size (e.g. constructing asymmetric webs: Herberstein & Heiling, 1999), in the decorations added to the web, whose function is probably to attract prey (Craig, 2003 ch. 6; Bruce, 2006; Blamires, Hochuli & Thompson, 2008)

and in the chemical components of the web, which may affect web function (Tso, Chiang & Bleckledge, 2007). Since antlion larvae do not produce their trap as spiders, but dig a pit in loose soils, they may be slightly more restricted in potential modifications. They can increase the trap size (e.g. Lomascolo & Farji-Brener, 2001) or shape, by changing the pit diameter-to-depth ratio (e.g. Lucas, 1986). Analogously to web decorations in spiders, some species construct furrows radiating from the pit in order to extend further their attack radius (Mansell, 1988; Matura & Kitching, 1993).

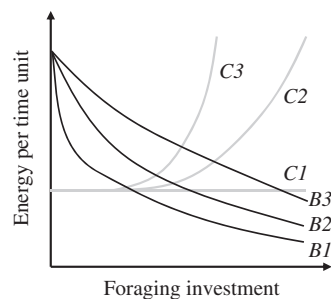
## II. FACTORS AFFECTING FORAGING BEHAVIOUR IN TRAP-BUILDING PREDATORS

### (1) Effect of hunger level and prey abundance on foraging behaviour

Although hunger level is one of the most obvious factors triggering a search for food, it was not explicitly incorporated in classical foraging models (Houston *et al.*, 1988). The most common way to consider hunger level in foraging theory is through dynamic optimization models, which refer to the current state of the foraging animal and optimize behaviour accordingly (Stephens & Krebs, 1986, ch. 7). Reference to hunger levels is usually combined with predator avoidance considerations (i.e. the energy gain—predation avoidance trade-off). In general, hungry animals should be more prone to take risks and increase their foraging effort (e.g. Houston *et al.*, 1988; Abrams, 1991). Increase in prey abundance may lead either to an increase, no change or a decrease in foraging intensity, depending on factors such as current energetic state, time constraints and mortality risk (Abrams, 1991; Ludwig & Rowe, 1990).

Our general expectations for the effect of hunger level and prey availability as well as other factors on foraging investment in traps by TB predators are summarized in Fig. 1. Foraging theory predicts that when additional energy always provides a fitness benefit (i.e. an energy maximizer *sensu* Schoener, 1971), the forager should invest in foraging until the marginal cost (MC) and marginal benefit (MB) of foraging are equal (e.g. Mitchell *et al.*, 1990). Hence, we expect the investment in the trap to be positively correlated with the relative difference between the MC and the MB of the optimal forager. Increased hunger level decreases the MC, because as hunger level increases, the forager's perceived cost of predation decreases (i.e. prey is ready to take larger risks; Brown, 1988). Hunger also increases the MB and thus it should result in increased foraging investment. Prey abundance is positively correlated with the forager's MB while having little or no effect on the MC. Thus, foraging investment should increase with increased prey abundance (Fig. 1).

Hungry widely-foraging predators search more intensively for food and are more ready to initiate an attack on their prey (e.g. Whitham & Mathis, 2000; Claver & Ambrose, 2001). They also shift to the local search mode, i.e. area-restricted search, much more readily (Bell, 1991, p. 231).



**Fig. 1.** Hypothesised changes in the marginal benefit (MB) and marginal cost (MC) of foraging among trap-building (TB) predators and the effect on foraging investments of factors such as hunger level, prey availability, predation risk, conspecific density and abiotic conditions. Three levels of MB (B1–B3) and of MC (C1–C3) are presented. Foragers should invest in foraging (reflected in trap size) as long as the MB is higher than the MC; the investment should increase with increasing difference between the MB and MC. Increased hunger level decreases the MC (e.g. from C3 or C2 to C1), while increasing the MB (e.g. from B1 or B2 to B3) and thus should result in increased foraging investment. Prey abundance is positively correlated with the MB (e.g. an increase from B1 or B2 to B3), while having no effect on the MC and thus will also result in increased foraging investment. Predation risk should be positively correlated with the MC (e.g. an increase from C1 or C2 to C3) while having little effect on the MB, meaning that foraging investment should decrease with increased predation risk. Exploitation competition reduces both MC and MB. If the reduction in the MC is greater than that of the MB, foraging intensity should increase, but otherwise foraging intensity should decrease. Interference competition can increase the MC of foraging while reducing the MB, consequently leading to decreased foraging investment. Foraging investment should be highest (minimal MC and maximal MB) within the range of favourable abiotic conditions. However, out of this range, foraging investment should decrease owing to the combined effect of increased MC and decreased MB.

Area-restricted search is a movement pattern, usually employed after finding a food item, characterized by more spatially restricted movements that increase the likelihood of encountering additional food items in the vicinity of the first (e.g. Carter & Dixon, 1984). For instance, starved ladybird beetles searching for their aphid prey were more ready to shift to local area-restricted search and this search pattern lasted longer compared to fed individuals (Nakamuta, 1985; Ferran & Dixon, 1993). In addition, the quality or size of the prey consumed is often positively correlated with the duration and intensity of the area-restricted search. For example, predatory bugs used much longer and intense area-restricted search when feeding on a 4<sup>th</sup> instar aphid rather than a 1<sup>st</sup> instar aphid (Bell, 1991, p. 216).

In TB predators, hunger level does not always play such an immediate and critical role in foraging decisions, such as the decision to relocate the trap (antlions: Matsura, 1987; Scharf & Ovadia, 2006; spiders, although to a lesser extent: e.g. Uetz, 1992). Several complementary reasons may explain this behaviour, such as the inability of antlions or spiders to

evaluate the quality of the current site when variability in prey arrival is high (Griffiths, 1986; Nakata & Ushimaru, 1999), the difficulty in distinguishing global from local shortage of prey (Caraco & Gillespie, 1986; Griffiths, 1986; Scharf, Golan & Ovadia, 2009b), and the risk involved with leaving the trap resulting from exposure to predation or cannibalism (Lubin, Ellner & Kotzman, 1993; Gatti & Farji-Brener, 2002). Owing to the uncertainty involved with relocation, an alternative strategy is often to enlarge trap size (Lomascolo & Farji-Brener, 2001). Indeed, hungry spiders and antlions were often documented to increase the investment in trap size (Riechert, 1981; Sherman, 1994; Lubin & Henschel, 1996; Herberstein *et al.*, 2000b; Arnett & Gotelli, 2001; Lomascolo & Farji-Brener, 2001). Nevertheless, following long-term starvation TB arthropod predators start neglecting traps (i.e. stop routine renewal/maintenance of the trap, as traps deteriorate with time) probably out of exhaustion (antlions: Heinrich & Heinrich, 1984; Eltz, 1997).

Scharf *et al.* (2009b) suggested a slightly more sophisticated explanation, namely, that trap size follows a hump-shaped pattern: maximal increase in pit size is achieved when providing antlion larvae with small prey. Larger prey, but also no prey, results in a smaller increase in trap size. The likely explanation is that when receiving small prey antlion larvae deduce that prey is available in their new position, in contrast to situations in which no prey arrives. Similarly, Higgins (1995) described the expected response of web-building spiders to a decrease in prey arrival, suggesting that the correlation between web size and prey availability should be negative at high food levels but positive at low food levels. When TB predators are satiated there is no longer a need to invest in the trap, at least temporarily. However, when receiving no prey at all, they have no evaluation of the current site and it is probably better to wait before reaching a decision whether to increase the trap size or to relocate. This behavioural response can be compared to the shift to area-restricted search in widely-foraging predators.

However, traps are not always reduced in size in response to prey consumption. For example, the traps of some TB arthropod predators were insensitive to prey abundance or were even increased in size when receiving more prey (Eltz, 1997; Blackledge & Wenzel, 2001; Segoli *et al.*, 2004; Blamires, Thompson & Hochuli, 2007). In our opinion, this inconsistency may reflect a similar situation to the decision between using the sit-and-wait rather than the actively searching strategy in widely-foraging predators. Some animals, such as geckos, beetles, dragonflies, centipedes and spiders (e.g. Huey & Pianka, 1981; Formanowicz & Bradley, 1987) can switch between these foraging modes, and often switch in accordance with prey abundance. Huey & Pianka (1981), for instance, describe a gecko species that ambushes prey when it appears at low densities but starts searching actively at high prey densities. An opposite trend is shown by species of beetles and centipedes (Formanowicz, 1982; Formanowicz & Bradley, 1987).

Hirvonen (1999) suggested a compromise similar to ours: at very low prey densities the sit-and-wait mode is adopted



to reduce the high costs of searching when little or no prey is captured (similar to reducing investment in traps in TB predators). As prey density increases a more active mode is adopted (similar to increased investment in traps), but as prey become very abundant the sit-and-wait mode is readopted (no need to invest in searching or enlarging the trap if prey reach the predator with little or no investment). The results obtained in an experiment are then dependent on which phase of this hump-shaped function is studied.

Spiders often exhibit web modifications other than changing web size in response to low prey abundance. For instance, they invest more in sticky threads and less in maintaining threads which support the structural stability of the web. This behavioural modification is adaptive because it increases capture success (Blackledge & Zevenbergen, 2007). Another well-studied example is silk decorations in three different families of spiders. We will not focus here on the function of web decorations since at least two comprehensive and detailed reviews already exist (Herberstein *et al.*, 2000a; Bruce, 2006). The decorations may serve several complementary purposes such as prey attraction, anti-predation and web protection, all of which remain controversial. However, it is generally accepted that prey abundance is correlated with investment in decorations (Craig *et al.*, 2001; Bruce, 2006) and that satiated spiders construct more decorations than hungry spiders (e.g. Tso, 1999; Herberstein *et al.*, 2000b; Seah & Li, 2002). The latter pattern contradicts the usual decrease in web size in satiated spiders, and is used as evidence against a function of web decorations as a foraging device (Bruce, 2006). Tso (2004) suggested that there is a threshold of silk reserves (or hunger level) below which decorations are not constructed. This solution is similar to that suggested by Hirvonen (1999), where below some energetic threshold the sit-and-wait foraging mode is preferred.

Other characteristics of prey abundance, such as prey variability and predictability, influence foraging in TB predators. For example, an abrupt cessation of prey supply triggers relocation while a gradual decrease does not (Vollrath, 1985; Jenkins, 1994). Because the consequences of prey predictability relate more to trap relocation than to trap size or shape, this topic, as well as risk-sensitive foraging in TB predators (e.g. Gillespie & Caraco, 1987) is beyond the scope of this review.

## (2) The interplay between behavioural flexibility, experience and prey characteristics

Predators often learn from experience as a means of coping with a changing environment (Krebs & Inman, 1992). Learning may be defined as the acquisition of memory or experience, allowing an individual to change its responses to specific stimuli or situations (Papaj, 1994; Dukas, 1998). Models incorporating learning from experience usually assume that different properties of foraging, such as recognition or handling time, improve with experience (e.g. Hughes, 1979; Stephens & Krebs, 1986, ch. 3). This gradual change is of great importance for prey-selection

models, since different handling/recognition times may lead to changes in prey preference (e.g. Kotler & Mitchell, 1995).

The wasp *Pepsis thisbe* serves as a simple though typical example of behavioural change through experience. An individual wasp attacks a spider, paralyzes it, and drags into its burrow. Although this behaviour may appear inflexible at first glance, wasps show some flexibility with experience gained. For instance, the time needed to approach and paralyze the spider is reduced with increasing number of spider prey encountered (Punzo, 2005). Evolutionary biologists often discount the ability of sit-and-wait predators to learn and to make complex decisions. Nevertheless, based on the above definition, some decisions of relocation and of trap modifications in response to prey arrivals may be an outcome of learning. The paradigm of limited learning ability of sit-and-wait predators was postulated in Huey & Pianka's (1981) pioneering work on lizard foraging modes, though it is rarely tested. There is no study summarizing learning in sit-and-wait predators of any taxon and attempts to compare learning and decision-making in sit-and-wait predators with their widely-foraging relatives are very rare (but see Day, Crews & Wilczynski, 1999).

TB predators change their behaviour in a context-dependent manner, based on experience. Whether this behavioural flexibility can be considered as "learning" is debatable. Nevertheless, the decision-making process of TB predators is sophisticated, regardless of whether or not it should be defined as learning. Antlions show clearly different responses to an abrupt halt *versus* a gradual decrease in prey arrival (Vollrath, 1985; Jenkins, 1994; Scharf & Ovadia, 2006): after a sudden complete cessation of prey arrival individuals often relocate their trap, while a gradual reduction does not necessarily trigger this behaviour. There is no threshold below which relocation occurs, and therefore it is not a fixed response but can be regarded as a sophisticated example of behavioural flexibility. Antlions experiencing unsuccessful feeding events (i.e. prey detection/capture without consumption) increase pit depth, compared to a successful capture treatment and a control group (Lomascolo & Farji-Brener, 2001; Scharf, Barkae & Ovadia, 2010). Similarly, spiders detecting prey without capturing it increased the total thread length and capture areas of their webs compared to a control group (Nakata, 2007). So why do these predators not always construct larger traps? The cost of trap maintenance may increase at an accelerating rate as trap size increases. Perhaps wind and other disturbances under natural conditions obscure differences that can be observed under more benign laboratory conditions. Finally, larger traps might be costly, or more prone to predation than smaller ones. Hauber (1999) observed that Florida scrub-jays, which occasionally dig antlion larvae out of their pits, preferred larger pits. This may also be the case for other visually-hunting predators.

TB predators modify trap dimensions and structure in response to different prey types encountered. The most common comparison is prey-size categories. The spider *Parawixia bistriata* constructs either smaller or larger webs,

adapted for the capture of smaller or larger prey. The decision which web to construct is correlated with the abundance of small *versus* large prey (Sandoval, 1994). Several studies in spiders showed that increased prey size resulted in increased web size, and especially in an increase of the web's capture area (Schneider & Vollrath, 1998) suggesting behavioural change with experience. Similarly, orb webs are often constructed with a narrow mesh when small prey are abundant probably improving the capture success of this size category (Murakami, 1983; Heiling & Herberstein, 2000; Watanabe, 2001; but see Eberhard, 1986, for evidence that large-mesh webs are designed to catch small, weakly flying prey). These two examples demonstrate the flexibility of web construction and suggest that TB predators respond to temporal patterns in their surroundings in a manner that could contribute to their foraging success.

Some spiders do not only increase web size in response to larger prey types but also vary web structure: *Nephila pilipes* spiders fed with crickets built a stiffer web than spiders fed with flies (Tso *et al.*, 2007). Other spiders enlarge the web in the direction of the prey arrivals: when fed above the hub, spiders constructed more symmetrical webs but when fed below the hub, spiders invested more in the lower region of the web, thus showing not only plasticity in size but also in shape (Herberstein & Heiling, 1999; note that different prey types also induced changes in web structure and shape; Schneider & Vollrath, 1998). Moreover, spiders exposed to light of different wavelengths constructed webs including different pigments, a behaviour which is adaptive in attracting prey to the web (Craig, Weber & Bernard, 1996). It is important to note that some of these behaviours may be innate and not necessarily related to learning. In any case, they indicate a high level of behavioural plasticity triggered by external and internal factors.

Several studies failed to show any change in trap characteristics following feeding with a particular prey type (Olive, 1982; Herberstein *et al.*, 2000c; Prokop, 2006). For example, there was no increase in web dimensions of *Argiope trifasciata* and *Araneus trifolium* when the diet was switched from flies to grasshoppers (Olive, 1982). Furthermore, in antlions and spiders there was no change in attack times or successful captures of prey with experience [Olive, 1982; Scharf *et al.*, 2010; but see Morse (2000) for contrasting evidence for such an improvement with experience]. A plausible suggestion is that behaviour in some species is canalized in order to achieve some optimum or average capture success across different situations (Olive, 1982).

### (3) Effect of predation risk on foraging behaviour

Predation risk has long been considered a fundamental part of foraging theory, usually leading to reduced foraging effort (e.g. Brown, 1988; Ludwig & Rowe, 1990; Bouskila & Blumstein, 1992). Notably, the effect of predators on the effort invested by the prey while foraging can vary substantially. For instance, foraging effort of foragers exposed to risk of predation should increase as their energetic state deteriorates (Abrams, 1991) or when they

are constrained by season length (Ludwig & Rowe, 1990). Recent models present a more sophisticated situation: encounters with predators may lead either to an increase or a decrease in foraging effort, depending on the information provided by such encounters. If an encounter indicates likely additional frequent encounters with predators (i.e. a positive autocorrelation of predator encounters in time), foraging should be decreased; however, if an encounter with a predator is followed by a quiet period (a negative autocorrelation of predator encounters in time), foraging should be increased (McNamara *et al.*, 2005). In short, predation risk is positively correlated with the forager's MC while having little or no effect on its MB. We can therefore predict that the foraging investment of TB predators should decrease with increased predation risk (Fig. 1).

Natural selection should favour behavioural changes in potential prey to make it more difficult to capture when exposed to predation risk (Lima, 1998). As a consequence, potential prey reduce foraging effort in various ways, such as reducing searching intensity, shifting activity period or hesitating more before initiating an attack on their own prey (e.g. Kotler, Ayal & Subach, 1994; Whitham & Mathis, 2000), since intensive foraging increases the probability of being caught by predators (Gotthard, 2000). This indirect behavioural effect (e.g. a reduction in foraging intensity in the presence of increased predation risk) imposed by predators might have a larger impact on population dynamics than the simple numerical direct response (i.e. the number of prey items actually captured by the predators; Lima, 1998; Schmitz, Krivan & Ovadia, 2004). Some studies criticize the frequently used procedure of confronting a single prey type with only one predator species, since under natural conditions most species face threats from more than one predator (e.g. Sih, Englund & Wooster, 1998; Schmitz, 2007). The response to multiple threats may be additive but often is not, and owing to conflicting demands may result in a completely different response than that given towards each predator separately (e.g. Van Son & Thiel, 2006; Schmitz, 2007). Response to predation risk is often context-dependent and is strongly influenced by individual state, such as hunger level (Lima, 1998), and by the perception of the common type of predation risk in the animal's natural habitat (i.e. animals might have been selected to respond more strongly to some predator cues while ignoring others; Botham *et al.*, 2008).

Few studies have focused on the effect of predators on the behaviour of TB arthropod predators, as reflected in trap construction or maintenance. Li & Lee (2004) reported that spiders exposed to an odour cue of their predators reduced the frequency of construction of web decorations as well as web size and total amount of silk compared to a control group. Similarly, web-building spiders exposed to the odour of ants (predators and kleptoparasites) delayed re-building the web (Y. Lubin, A. Pasquet & R. Leborgne, unpublished data). Loria *et al.* (2008) found that pit-building antlions reduced pit construction activity when exposed to two predators differing in foraging mode. The relatively sessile antlions were much more affected (i.e. a sharper decrease in activity) by the

more active predator, a predatory ground beetle than by a sit-and-pursue wolf spider. Furthermore, antlions change their behaviour depending on habitat structure: relocation and pit construction rates were lower in shallow sand than in deep sand. Shallow sand probably did not provide sufficient shelter from predation compared to deep sand. In our opinion, these studies indicate a shared response of TB and widely-foraging predators to predation risk: foraging activity as manifested in trap construction or size is reduced. Another study failed to show any effect of predation risk on spider web architecture or decorations (Bruce & Herberstein, 2006).

There is a great deal of opportunity for further studies on TB predators in relation to trap plasticity induced by predation risk. It would be interesting to incorporate hunger level in order to test for the conflicting demands of foraging and avoiding predation. It would also be interesting to investigate the effects of multiple predators. For example, antlions experience predation from several species of skinks that “swim” through the sand or from birds using aerial attacks. It is not known whether the behavioural consequences of predation risk in TB predators are translated into life-history parameters such as growth rate, development time or adult body mass. Life-history theory often assumes a trade-off between foraging and predation risk, i.e. that there are severe costs to growing fast (e.g. Gotthard, 2000; Scharf, Filin & Ovadia, 2009a), but this is rarely tested explicitly.

In some antlion species parasitism may pose a greater risk than predation. For example, in *Myrmeleon hyalinus* about 18% of 280 collected antlion larvae were parasitized by parasitoid flies (I. Scharf, unpublished data). It is possible that parasitoids are attracted more to larger pits. Both the risk of predation and of being parasitized may offset the benefits of maintaining large pits. Indeed, Ruxton & Hansell (2009) note that the conspicuous nature of the traps especially in antlions but also in spiders (e.g. Hieber & Uetz, 1990) probably exposes them to considerable predation and parasitism pressure, and they suggest that the easy detection of the pits limits their abundance in nature.

#### (4) Effect of conspecific density on foraging behaviour

The response of widely-foraging animals to changes in their density (i.e. intensity of conspecific competition) is not straightforward. It depends on how the MB and MC change with density and on the type of competition involved (exploitation or interference; Mitchell *et al.*, 1990; Davidson & Morris, 2001). In general, exploitation competition reduces both MC (e.g. by increasing hunger level) and MB (because less food is available). According to Mitchell *et al.* (1990), if the reduction in the MC is greater than the reduction in the MB, foraging intensity should increase, but if the MB decreases more strongly, foraging intensity should decrease. Interference competition, on the other hand, increases the MC due to aggressive interactions and a reduction in the encounter rate with resources. The latter also induces a decrease in the MB. Clearly, the combined effect of increased MC with decreased MB should be decreased

foraging investment (Fig. 1). Both an increase and a decrease in foraging effort with increased conspecific density are evident in nature. Several rodent species reduce their *per capita* activity at high densities, probably due to increased interference competition (e.g. Abramsky & Pinshow, 1989; Mitchell *et al.*, 1990; Davidson & Morris, 2001). By contrast, other species (e.g. fish) forage more when density increases, probably because safety in numbers (i.e. dilution effect) allows individuals to forage in more risky areas (e.g. Grand & Dill, 1999).

The most obvious costs to living in a group involve competition: indirect exploitation and direct interference, which both increase with conspecific density. A group of widely-foraging predators may experience interference in various ways, such as an increase in vigilance of their prey, making its capture more difficult (i.e. a reduction in the MB; Stillman, Goss-Custard & Alexander, 2000). Moreover, a group of foragers may be more easily detected by their own predators (i.e. an increase in the MC; Ioannou & Krause, 2008). Some of the possible benefits are a decrease in the variance of prey uptake rates (Ruxton, Hall & Gurney, 1995) and the dilution of risk (Hamilton, 1971). Spatial position inside the group is also relevant and involves a trade-off between foraging opportunities and safety: inner positions are perhaps safer but receive fewer prey arrivals, while outer positions are more prone to predation but experience better foraging opportunities. This pattern is similar for mobile groups of actively searching predators and also for sedentary clusters of sit-and-wait predators (e.g. Rayor & Uetz, 1990; Gotelli, 1997; Lubin, Henschel & Baker, 2001; Krause & Ruxton, 2002, p. 80; Scharf & Ovadia, 2006). The costs and benefits of living in groups are comprehensively summarized in Krause & Ruxton (2002), with some reference to stationary groups.

Most spiders and all antlion species are solitary predators. However, they often occur at high densities, owing to the uneven distribution of suitable microhabitats for trap construction (e.g. Matura, Yamaga & Itoh, 2005) and clumping of food resources (the latter is more evident in spiders, e.g. Uetz, Kane & Stratton, 1982). Interestingly, both taxa show a clumped pattern at a larger scale but a regular (or random) pattern at a finer scale (Matura & Takano, 1989; Matura *et al.*, 2005; Birkhofer, Henschel & Scheu, 2006). High densities increase aggressive interactions in both antlions (e.g. Matura & Takano, 1989; Day & Zalucki, 2000) and spiders (e.g. Wagner & Wise, 1997), which often end in cannibalism. Exploitation also increases with density in its special form of “shadow competition” (one TB predator catches the moving prey before it encounters other predators; e.g. Wilson, 1974; Lubin *et al.*, 2001; Rao, 2009). Interference may be dominant over exploitation in most TB predator systems, because crowding usually results in reduced trap size and foraging effort. We suggest that here the MB and MC of investment in traps is related to the relative strength of exploitation *versus* interference competition.

Surprisingly, crowding may sometimes contribute to capture success, when a prey is slowed down and becomes



more vulnerable as it crosses several traps in succession (known as the “ricochet effect”; Rypstra, 1989; Uetz, 1989; Rao, 2009). It is still unclear how common the “ricochet effect” is and how much it contributes to capture success [but see Rao (2009) for how it can considerably moderate the effect of “shadow competition”]. There is no documentation of this phenomenon outside spiders. The benefits of aggregation regarding diluting of predation risk have rarely been tested in spiders or antlions. One study found a decrease in the success of a predatory wasp with an increase in spider group size, possibly owing to ‘early warning’ through vibrations in the colony web (Uetz *et al.*, 2002). *Stegodyphus dumicola* spiders living in groups protected against predatory ants by constructing large structures of sticky silk, which could only be supported by groups. However, group-living spiders were more likely to be infested with a fungal parasite, suggesting a trade-off between predator avoidance and parasitism (Henschel, 1998).

The benefits of aggregation are likely to depend on predator type. The risk may be diluted when the predator is relatively small (such as another arthropod) and takes only one or two prey items per attack, however, if the predator is large (such as birds or lizards) it may consume all individuals within a group, and aggregation in this case will increase the cue attracting the predator (Tinbergen, Impeken & Franck, 1967; Taylor, 1976; Scharf *et al.*, 2008a). Therefore, the advantages and costs of aggregation in TB predators may differ among species and systems.

We previously noted that some antlions may be affected to a larger extent by parasites than by predators. If each parasite attacks only a single antlion, aggregation might dilute the risk. Furthermore, the pits of antlions are probably detected visually by relatively large predators such as birds. However, when nearest neighbour distances (NNDs) are small, each attack on a pit may result in the destruction of surrounding pits, making the neighbouring antlions more difficult to capture. This untested suggestion could conceivably trigger aggregation in antlion larvae, in contrast to Ruxton & Hansell’s (2009) suggestion that the conspicuousness of antlion pits can be a major factor limiting their abundance.

Increased density affects the spatial pattern of TB predators. In clusters of antlions or spiders, at low densities TB predators are usually randomly distributed inside the cluster, but at higher densities their dispersion is regular (Matsura & Takano, 1989; Day & Zalucki, 2000). Such changes in spatial pattern may minimize the decrease in the NND as density increases (i.e. maximizes NND). Indeed, Matsura & Takano (1989) used a null model neatly showing that at high densities the NND is greater than that expected under random distribution, indicating the existence of a regular pattern. It is not known whether the spatial pattern is affected also by other factors such as hunger level or body size. For example, do hungry TB predators increase NND, resulting in a more regular pattern at low density compared with satiated predators?

When density is increased smaller antlions are affected to a greater extent and decrease their pit size to a greater

extent than larger individuals (Griffiths, 1991, 1992). In spiders, several studies showed that NNDs are larger and the spatial pattern resembles more a regular one in poorer *versus* richer habitats (Burgess & Uetz, 1982), and similarly to antlions, NND is positively correlated with web size (Leborgne & Pasquet, 1987). This increase in NND with body size (positively correlated with trap size in TB predators) is a well-established rule (e.g. Blackburn & Gaston, 1997). Several studies showed that more competitive or larger individuals choose preferred locations while subordinate individuals occupied the inferior locations (e.g. Jakob, Porter & Uetz, 2001; Miyashita, 2001). Smaller individuals were also reported to construct webs later, after larger spiders have already completed theirs (Jakob, Uetz & Porter, 1998). This suggests the presence of interference competition during trap construction; smaller individuals are likely to be more affected, and thus avoid it by delaying construction. The presence of conspecifics also may be a cue for future competition either for space or prey; spiders in general construct webs faster in the presence of conspecifics compared to construction in isolation (Salomon, 2007). Ward & Lubin (1992) provide another example of inter- and intra-specific niche partitioning between smaller and larger web-building spiders based on prey size and predation risk. At high densities, small spiders built webs at dusk, taking advantage of numerous small insects, and were displaced by larger spiders building later in the evening when predation risk (from predatory insects and birds) was lower.

Trap size usually decreases with increasing density (e.g. Yothed & Moran, 1969; Gillespie, 1987; Griffiths, 1991; Devetak, 2000; Scharf *et al.*, 2009b) due to interference competition, but in some cases trap size was unchanged when density increased (Matsura & Takano, 1989). It is possible that the experimental densities used in the latter study were not high enough. An important measure unreported in such studies is the likely correlation between trap size and NND. Finally, there is a prominent interaction between prey availability and tolerance of conspecifics: spiders show greater tolerance of their neighbours at high levels of prey abundance (e.g. Riechert, 1981; Gillespie, 1987) and some spiders increase their tendency to hunt in groups and to increase group size when hunting larger prey items compared to smaller ones (Fernandez Campón, 2007).

### (5) Effects of temperature, light and substratum on foraging behaviour

Abiotic factors can be incorporated in foraging models as a part of the associated foraging costs, i.e. energetic, predation and missed opportunity costs (Brown, 1988). For instance, non-optimal temperatures can substantially increase the MC (e.g. Pereboom & Biesmeijer, 2003) while foraging on nights with a full moon increases the exposure of the forager to predators, leading to increased predation cost (e.g. Kotler, Ayal & Subach 1994). Such increases in energetic or predation cost may make foraging uneconomical. Additionally, lower temperatures may induce another type of cost—the cost of missed opportunities—as more time is



required to reach the preferred body temperature (Angilletta, 2009, ch. 4). Finally, habitat selection theory shows that selecting a sub-optimal habitat may result in increased metabolic costs or reduced prey abundance, but is often compensated by reduced conspecific density and competition (Rosenzweig, 1991).

Temperature is perhaps the most important (or at least the best-studied) abiotic factor affecting animal behaviour. Animals usually exhibit a hump-shaped response towards temperature as reflected in activity, foraging and physiological performance (Huey & Kingsolver, 1989; Angilletta, 2009). The optimal temperature is usually closer to the right side of the thermal range; increases are often followed by a sharp decrease in performance. Another important environmental factor affecting animal activity is the light level, which may be positively correlated with predation risk (e.g. Kotler *et al.*, 1994). Desert-dwelling gerbils searching for hidden seeds under bright light conditions search more randomly and use less area-restricted searching, indicating a lower foraging effort (Dall, Kotler & Bouskila, 2001). A burst of predator activity is often observed after the disappearance of a bright moon (Bell, 1991, p. 195). Other characteristics of the habitat may influence foraging behaviour as well as predator avoidance in widely-foraging animals: vegetation cover often reduces predation risk, as prey is less easily detected by predators (Brown & Kotler, 2004).

We expect that TB predators will show a hump-shaped activity pattern and investment in traps, as a function of temperature (and other abiotic factors). The MC will be minimal under favourable conditions and it is reasonable to assume that predators have the same thermal activity range as their prey (e.g. Marsh, 1987), and therefore that their MB under this thermal activity range will increase in line with increased prey activity (Fig. 1). Either below or above the range of favourable conditions, foraging investment should decrease due to the combined effect of increased MC with decreased MB. TB predators are heavily dependent on the physical properties of their immediate surroundings, as well as microclimatological conditions. Mean web mass in spiders follows a hump-shaped pattern in response to temperature, in a similar way to the activity patterns of widely-foraging ectotherms (Barghusen *et al.*, 1997). The strand density of the web's silk varied in the same way (Barghusen *et al.*, 1997), as did web capture area, which had a positive relationship with air temperature in another study (Blamires *et al.*, 2007). Since capture success is usually correlated with web dimensions (e.g. Blackledge & Eliason, 2007), optimal temperature could have significant consequences on fitness. By contrast, Herberstein & Fleisch (2003) failed to show any effect of temperature on web size, although they did show a negative correlation between higher temperatures and web decorations. They suggest that the temperature range tested was too narrow to show a response in the species studied. Finally, Vollrath, Downes & Krackow (1997) did not find any change in web size as a function of decreasing temperature, but observed an increase in spiral spacing, suggesting that it might help

in capturing larger prey, which are more active at low temperatures. Note that Vollrath *et al.* (1997) and Herberstein & Fleisch (2003) used two distinct temperatures rather than a temperature range as used by Barghusen *et al.* (1997).

Antlions probably exhibit the same hump-shaped pattern in pit sizes in relation to temperature. However, the existing literature shows only a positive correlation between these variables (Youthed & Moran, 1969). Additionally, Arnett & Gotelli (2001) reported that pit-building activity was reduced at a colder temperature, and was probably associated with a decrease in pit dimensions (they also used only two representative temperatures). We suggest that the temperature range tested was not sufficient to detect the likely decrease in pit volume or that the lack of a clear result arose from their experimental procedures: Youthed & Moran (1969) exposed antlions to a specific temperature for a certain period, then moved all antlions to one common temperature, where they were allowed to construct pits (rather than actually building pits at different temperatures).

The size of spider webs is negatively correlated with light levels (Adams, 2000; Herberstein & Fleisch, 2003), either due to predation risk (e.g. by birds), or because prey abundance in lit habitats is higher; spiders are easily satiated, and a reduction in the web size due to satiation may occur. Adams (2000), using light bulbs as a light source, supported the latter explanation. He noted that prey were more abundant close to the light source and foraging activity of spiders was reduced there (i.e. spiders built smaller webs). An opposite trend was shown by pit-building antlions, which increase pit dimensions under light conditions (Scharf, Subach & Ovadia, 2008b). This may be to adjust the timing of the hunting activity to that of the prey, which is mainly diurnal. In other words, pits may be repaired and enlarged just before the peak in activity of their diurnal prey, resulting in documentation of larger pits in daylight. This is in apparent contradiction to Adams (2000), but an important difference between those two studies was the absence of prey in the Scharf *et al.* (2008b) experiment. In other words, antlions in this case, could not satiate and consequently were not exhibiting satiation-related behaviour.

As an extreme example of the dependency on the immediate surroundings, many antlion species require a particular combination of loose soil and shelter from rain and often sun (Scharf & Ovadia, 2006). Antlion pits are affected by sand particle size, with maximal pit size in many species occurring in an intermediate particle size substratum (Devetak, Spornjak & Janzekovic, 2005). Others (e.g. Lucas, 1986) prefer small particle sizes, and this preference might be related to the type of sand in their natural habitat. Pit size is also positively correlated with sand depth (Scharf *et al.*, 2009b), although this might result from physical constraints rather than behavioural flexibility of the pit-builder. Spiders reduce web size in response to a decrease in available space, but they try to minimize the decrease in the size of the capture area (Krink & Vollrath, 2000). This evidence indicates that some regions of the web are more important for hunting.

Table 1. Comparison of foraging intensities and trap characteristics between widely-foraging and trap-building predators

| Response to...                        | Widely-foraging predators  | Trap-building predators   |
|---------------------------------------|--|---|
| Hunger level <sup>†</sup>             | Increase foraging intensity  | Increase trap size  |
| Prey type                             | Modify searching behaviour to improve capture success <sup>‡</sup> | Modify trap characteristics to improve capture success <sup>‡</sup> |
| Conspecific density                   | May increase or decrease foraging intensity                        | Usually decrease trap size  |
| Predation threat                      | Usually decrease foraging intensity                                | Decrease trap size or the tendency to construct trap                |
| Unfavourable environmental conditions | Decrease foraging intensity  | Decrease trap size or the tendency to construct trap                |

<sup>†</sup>Mild hunger level, prior to exhaustion.

<sup>‡</sup>See text for examples.

### III. THE ADAPTIVE VALUE OF TRAP MODIFICATIONS—A CRITIQUE

From Section II it is clear that TB predators modify their traps in response to various extrinsic and innate factors, such as hunger level and prey type, similarly to foraging behaviour modifications in widely-foraging predators (Table 1). Yet it is insufficient simply to show the presence of behavioural flexibility; it is also necessary to show that this behavioural flexibility improves foraging success in the short or long term. There is little evidence that these modifications improve the probability of prey capture. It is commonly accepted that larger prey types are caught in larger traps (e.g. Wilson, 1974; Heinrich & Heinrich, 1984; Lucas, 1986; Sandoval, 1994). However, the comparison has been made between different developmental stages (i.e. smaller and larger individuals), whereas it should be made between TB predators differing only in the one factor to be examined (e.g. hunger level). Variation in trap size and structure should take into consideration body size as the most prominent factor affecting trap size. Providing different prey sizes is known to affect pit sizes in antlions (Scharf *et al.*, 2009b). However, most variation in pit size could be attributable to size differences among antlions rather than to the different treatments. This example suggests that the additive effects of factors other than body size on trap size may be significant but of lesser importance.

### IV. CLOSING REMARKS

TB predators, unlike widely-foraging predators, were considered to have limited capacity to modify their foraging

strategy. We have shown here that TB predators exhibit impressive behavioural plasticity in relation to foraging decisions (see also Table 1). It is probable that some of these responses result from constraints (e.g. decreased pit or web size in response to limited space available for construction; Krink & Vollrath, 2000; Scharf *et al.*, 2009b), but other responses, particularly responses to biotic factors, are probably adaptive, and may be the result of natural selection owing to their positive effect on hunting success. A previous review on antlion foraging behaviour focused on the decision to relocate the trap (Scharf & Ovadia, 2006). Both trap relocation and trap modification are costly activities (e.g. Lucas, 1985; Tanaka, 1989) and it is interesting to consider the conditions that favour relocation *versus* trap modification. We suggest a hierarchical decision mode: (1) the predator has to decide which trap modifications to employ, because this is likely to be less costly than relocating the trap; (2) whether to stay or to relocate the trap. These decisions are often related to prey availability.

In addition, TB predators usually follow general predictions derived from classical foraging theory, such as response to starvation and predation risk. Trap modifications or trap relocation (Scharf & Ovadia, 2006) will reflect foraging decisions. Measuring such behavioural responses in TB predators is relatively straightforward, making them suitable animal models for testing foraging theory. Nevertheless, there are several obvious limitations to this approach. For instance, with their slower metabolic rate, TB predators may require longer periods to respond to hunger level (e.g. antlions responded to a starvation treatment only after 15–20 days; Heinrich & Heinrich, 1984; Eltz, 1997). Moreover, some TB predators, especially antlions, are highly dependent on the physical properties of the microhabitat, preferring a site more physically suitable for trap construction to a prey-rich site (e.g. Gotelli, 1993; Gatti & Farji-Brener, 2002). Spiders are usually less dependent on the microhabitat, because they are not dependent on the substratum (e.g. sand) for trap construction. Possible future studies could investigate how spiders trade-off prey abundance with physical limitations, such as space. Another significant constraint is the ability to evaluate the environment when stochastic variation in prey arrival is large (Edwards *et al.*, 2009). In such cases frequent relocations may be observed to reduce the probability of remaining too long in an inferior site (Nakata & Ushimaru, 1999). Other limitations, which are more system-specific, are also likely to exist; it is important to understand the system fully in order to explain the deviations of TB predators from expected foraging behaviour.

We suggest that future studies of foraging behaviour in TB predators should focus on four areas of unfulfilled potential. First, exploring the relationship between behaviour and environment, or more specifically, understanding why some TB predator species respond more readily to some biotic or abiotic conditions than others (e.g. Matura & Murao, 1994; Miyashita, 2005), and explaining such differences in the context of adaptation to the natural habitat. Foraging experiments are often conducted out of the natural context,

and integrating the natural history and environmental characteristics should improve our understanding and ability to explain differences among systems. Pit-building antlions and web-building spiders have developed independently similar foraging strategies, making them interesting subjects for the study of convergent evolution. A set of correlated traits used by TB predators (i.e. a syndrome) probably represents a local optimum in evolution. Characterizing these optima would also help to show how evolution is often biased in recurring ways, in a similar way to the establishment of ecomorphs where the occupants of different structural habitats have consistent and characteristic morphologies.

Second, deviations from the predictions of foraging theory are often of high value (e.g. the antlion *Myrmeleon bore* rarely relocates, even in response to starvation; Matsura, 1987). Moreover, optimal foraging theory makes many assumptions, such as the animal's ability to estimate reasonably habitat quality. A recent study suggests that owing to the stochastic nature of prey arrival, TB predators might be unable to make this estimation, questioning their ability to forage optimally (Edwards *et al.*, 2009), and suggesting that differentiating among sites is beyond their perceptual abilities (Bouskila & Blumstein, 1992). If this suggestion is valid for most TB predators (and it should depend on the stochasticity level of their prey arrivals), an alternative unifying theory of how TB predators forage should be developed. However, foraging theory has progressed considerably since the marginal value theorem, and TB predators may conform well to other predictions of foraging theory.

Third, there is still little evidence that predators affect the foraging behaviour of TB predators. Sih *et al.* (1998) noted that exposure to a single predator in an experiment is simplistic; in nature multiple predators are present, and net effects may not be additive (i.e. exposure to multiple predators may not necessarily result in further decreases in activity). There are no such experiments with TB predators. Furthermore, combining the effect of predators and parasites may enrich our understanding of trade-offs involved and of the different defence mechanisms employed by TB predators. The combined effect is not straightforward. On the one hand, the value of foraging activity may rise because foragers should aim at compensating for the extra nutritional requirements caused by the parasites. On the other hand, foraging with a parasite load may be more risky if parasitized foragers are weaker and hence more prone to predation (Lozano, 1991).

Finally, longer term experiments studying the consequences of foraging decisions on life-history variables are required. A common criticism of behavioural ecology is that the documented behavioural responses have little long-term impact on fitness. Thus, future experiments should connect the presence of short-term behavioural flexibility with lifetime fitness expressed as offspring production or at least with life-history traits such as body size and development time. Such experiments in the laboratory and under field conditions would throw light on the relevance of trap modifications and foraging decisions to the TB predator's life.

## V. CONCLUSIONS

(1) Sit-and-wait and TB predators were previously considered to show stereotypic or automatic behaviour. We have argued that TB predators can exhibit substantial flexibility in trap construction, maintenance and structure, in response to various innate and extrinsic factors.

(2) We describe in brief the classical predictions of foraging theory, as developed for widely-foraging animals. We then argue and demonstrate that TB predators are suitable subjects for testing foraging theory, while their investment in foraging can be quantified according to trap construction and relocation.

(3) Hungry widely-foraging animals usually search more intensively for prey. Similarly, TB predators increase their trap size as their hunger level increases, until limited by exhaustion. In both widely foraging and TB predators, the relationship between foraging intensity and prey abundance follows a hump-shaped pattern. Increased investment in traps (or in searching for prey) occurs only at intermediate levels of prey abundance. Predation risk triggers a decrease in trap size or reduces the incidence of trap construction. It is possible that these activities expose the TB predators themselves to predation.

(4) Conspecific density has a complex effect on foraging intensity. In widely foraging predators it can result in either an increase or a decrease in searching effort. However, in TB predators, conspecific density usually reduces the investment in traps, suggesting that in most systems interference is dominant over exploitation competition.

(5) TB predators are in general heavily dependent on the physical characteristics of their environment. We illustrate that TB predators (mainly web-building spiders) are likely to exhibit a hump-shaped investment in traps as a function of temperature.

(6) We recommend four future directions for research: (a) exploring differences among different systems/species of TB predators; (b) explaining deviations from the predictions of foraging theory; (c) combining the effect of predators with other stressors, such as parasites; (d) conducting long-term experiments and testing the consequences of different foraging strategies on life-history variables.

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