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Effects of hunger on prey capture and ingestion in *Dugesiella echina* Chamberlin (Orthognatha, Theraphosidae)

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Summary

The effect of varying levels of food deprivation on prey capture and ingestion in *Dugesiella echina* was investigated. The strike response, capture success, awareness field, tendency to capture consecutive prey and ingestion time improved significantly as a function of increasing hunger levels. The position of the spider relative to that of its prey as well as the running speed of the prey had pronounced effects on capture success. The significance of hunger and its relationship to the feeding behaviour of this spider is discussed.

Introduction

Recent behavioural and neuroethological investigations of predatory behaviour in arthropods have identified numerous parameters which affect its occurrence (see reviews by Curio, 1976; Feder & Lauder, 1986) in addition to characterising the integrative role of the central nervous system in the control of hunting behaviours (Camhi, 1984; Punzo, 1985, 1988; Punzo & Malatesta, 1989). There has been a great deal of interest in identifying those factors which determine when and to what extent a potential predator will initiate the search for prey (Krebs, 1978). Among internal physiological factors, the degree of hunger (food deprivation) often determines when foraging and prey search tactics are initiated (Dixon, 1959), the duration of search and pursuit behaviours (Krebs, 1978), the capture rate (Holling, 1966), the range of prey species acceptable as food (Beukema, 1968; Anderson, 1974), and the distance over which a predator can detect its prey (Drees, 1952; Holling, 1966; Dethier, 1982; Bleckmann & Lotz, 1987). Thus, hunger is a

primary factor in determining the degree of readiness of a predator to respond to the presence of a potential prey organism. This is particularly applicable to spiders in that the amount of food ingested can remain within the digestive system for long periods of time (Anderson, 1974; Foelix, 1982) resulting in a broad spectrum of hunger levels (Nakamura, 1987) even though food deprivation can be tolerated for prolonged periods (Baerg, 1958; Anderson, 1974).

Most of the previous research on predation in spiders has focused on factors influencing the types of prey captured (Morse, 1979; Roach, 1987), primary sensory cues utilised in prey capture (Den Otter, 1974; Forster, 1982; Bleckmann & Lotz, 1987), the sequential analysis of the units of predatory behaviour (Drees, 1952; Robinson, 1969; Lubin, 1980), sites chosen for prey capture (Morse, 1987; Roach, 1987), and ecomorphological factors associated with hunting behaviour (Rovner, 1980; McReynolds & Polis, 1987). Relatively few studies have addressed the relationship between hunger and predation. In an early study on the hunting behaviour of the salticid spider, *Epiblemum scenicum* (Clerck), Drees (1952) showed that the size of acceptable prey increased as a function of increasing food deprivation. Gardner (1964) demonstrated that all behavioural components of the hunting sequence are enhanced by increasing levels of hunger in the salticid, *Phidippus clarus* Keyserling. More recently, Nakamura (1972, 1987) has shown that the amount of food ingested by the wolf spider, *Pardosa laura* Karsch, is largely determined by the degree of distension of the gut.

The purpose of the present study was to investigate the relationship between hunger and prey capture in the tarantula spider, *Dugesiella echina* Chamberlin. North American theraphosid spiders, such as *D. echina*, are excellent examples of sit-and-wait predators (Schoener, 1969). Long-lived females that occupy a single burrow for several years may be periodically exposed to prolonged periods of fasting when prey availability is low (Baerg, 1958; Minch, 1977, 1978). Although little information is available on the feeding

activities of these spiders in nature, it seems likely that gorging under conditions of high prey density is adaptive. Gorging has been shown to be adaptive in other ambush predators (Beukema, 1968; Curio, 1976) and may represent an evolutionary stable strategy (ESS) in theraphosid spiders. Thus, hunger levels (degree of satiation) should directly affect the readiness to respond to potential prey. Tarantulas typically wait motionless at the burrow entrance and strike when a prey organism moves within a certain minimal distance (Baerg, 1958; pers. obs.). The distance from prey to predator has been referred to as the awareness or attack field (Holling, 1966; Curio, 1976) and represents an important parameter for experimental analysis. In addition to hunger, the awareness field is itself influenced by a number of factors which include the rate of movement of prey (Beukema, 1968; Bleckmann & Lotz, 1987), and the position of the predator with respect to the prey (Holling, 1966; Forster, 1982).

In view of these considerations, the present study was undertaken in order to determine the effects of various levels of food deprivation on the following parameters of prey capture in *D. echina*: (1) per cent strikes elicited by moving prey; (2) per cent capture success as a function of prey running speed and position of the predator; (3) distance over which moving prey elicited a strike response (awareness field); (4) per cent of spiders capturing consecutive prey; (5) ingestion time as a function of predator size.

Methods

Adult *Dugesia echina* females were collected from shrub desert and sotol-grassland associations in the Black Gap Wildlife Area, Brewster County, Texas, during June and July, from 1981 to 1987. A detailed description of the vegetational zones and geology of this area is available in Maxwell *et al.* (1967). Spiders were collected at night from burrow entrances as described by Punzo (1988) and transported back to the laboratory. Spiders were housed separately in well-ventilated plexiglass cages provided with water and fed weekly on a varied diet of local insects including cockroaches, grasshoppers and beetles. All spiders used in this study were in their first year of captivity. During experiments, crickets (*Acheta domestica*) in the size range of 0.4 ± 0.1 g were used as prey organisms. A different spider was used for each parameter in all experiments in order to minimise the effects of previous experience on prey capture. These experiments were conducted over a six-year period reflecting the availability of spiders. Voucher specimens have been deposited in the Invertebrate Collection at the University of Tampa. Statistical methods throughout this study follow those described by Sokal & Rohlf (1981).

The test chamber used to determine the effects of various levels of food deprivation on the per cent strike (attack) response elicited by moving prey and the mean distance over which moving prey elicited an attack (awareness field) is shown in Fig. 1. The chamber was constructed of clear plexiglass. Since pilot studies had

shown no significant effect of light intensity on the prey capture behaviour of this spider, all observations were conducted under standard fluorescent lighting. A different female spider (7.0 ± 1.0 g) was used for each level of food deprivation and prey running speed tested. Since preliminary observations showed no significant differences between male and female tarantulas, females were chosen for analysis owing to their longer life span (Baerg, 1958) and sedentary habits (Minch, 1978). Individual spiders were allowed to habituate to the test chamber for 30 minutes before the initiation of all test trials. The degree of food deprivation was defined as the time (hours) elapsed since the last feeding, as previously described by Dethier (1982). All spiders were maintained on a feeding regime consisting of 2.0 ± 0.2 g of live insect prey/week (excluding crickets) for 4 weeks before testing.

To determine the effects of hunger on the per cent SR (strike response) of *D. echina*, 20 different spiders were tested individually at each level of food deprivation (6, 12, 24, 36, 48, 60 and 72 hours). Before the start of a test trial, a cricket was placed in the prey-holding section of the test chamber (Fig. 1, P). A movable restraining door (d) prevented the cricket from entering the main runway. The spider was placed in the predator section (S) in a forward-facing position to the entrance of the runway and the prey. The floor of the apparatus immediately in front of the predator section was marked with a mm-grid (Fig. 1, dashed lines). At the start of each trial, the restraining door was lifted manually and a gentle stream of compressed air was introduced through an intake tube as shown in the diagram. In response to the air flow, the cricket would immediately move directly through the runway to the entrance of the predator section. The presence or absence of a strike was recorded for each observation. All observations were photographed with a Nikon FE 2 35 mm camera using a 75-150 mm zoom lens and with a Cine-8 high speed camera (Visual Instrumentation Corp.) at 100 frames/s. A Lafayette Super 8 Analyser (Model 1026) was used for frame-by-frame analyses.

The same protocol was used to determine per cent capture success as a function of food deprivation level and position of the predator relative to that of the prey. Numerous personal observations on captive tarantulas have indicated that they are capable of detecting a moving insect regardless of whether it is in front of (forward-facing, FF) or behind (rear-facing, RF) the

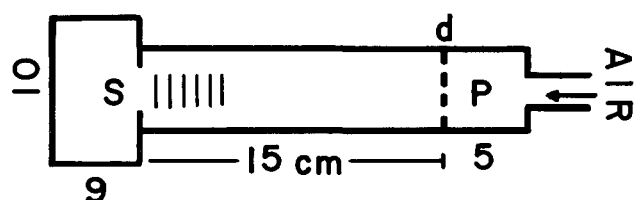


Fig. 1: Test chamber used to determine the effects of food deprivation on prey capture behaviour of *Dugesia echina*. Not drawn to scale. S = location of spider, P = location of prey at start of a test trial, d = movable restraining door. Arrow shows direction of air flow. Dashed lines represent mm grid.

spider. However, no previous attempt has been made to quantify the difference, if any, in the ability of these spiders to detect prey as a function of the position of the predator. In these experiments, the spider and cricket were placed in the chamber as described above. Using a glass rod, the spider was gently manoeuvred into a FF or RF-position relative to the oncoming prey. The per cent capture success was recorded for further groups of 12 different spiders in either the FF or RF-position at four food deprivation levels (6, 24, 48 and 72 hours). A capture attempt was considered to be successful if a spider firmly grasped a cricket using its pedipalps. A capture attempt was considered a failure if a spider missed the prey entirely or if it grasped the prey only momentarily before it escaped.

Another series of experiments was conducted using the same apparatus and protocol in order to determine the mean distance over which moving prey elicited a strike response as a function of hunger level. Further groups of 10 different spiders were tested in the FF-position under food deprivation levels of 6, 24, 48 and 72 hours. The distance (cm) at which a strike was elicited from the spider was recorded using the mm grid on the floor of the runway at the entrance to the predator chamber (Fig. 1, S, dashed lines). An analysis of variance was used to test for the overall effect of hunger on the awareness field and Scheffe *F*-tests were used for intergroup comparisons (Sokal & Rohlf, 1981).

The effect of prey running speed on per cent capture success by *D. echina* was tested using the apparatus shown in Fig. 2. This apparatus was constructed of clear plexiglass. The spider was positioned in a chamber at the centre of the runway (Fig. 2, S). At the start of each trial, the restraining door to the prey chamber (d) was lifted manually and a stream of compressed air was used as described previously to initiate running behaviour of the cricket (P). Two photoelectric cells (Thornton Co., Chicago, Model 50L) were placed 3 cm apart (Fig. 2, pp) immediately adjacent to the entrance of the predator chamber (S). These photoelectric cells were connected to a Simpson Model HK electronic timer. As soon as the cricket passed the proximal photoelectric cell the timer was automatically started. When the cricket passed the second (distal) photoelectric cell immediately adjacent to the entrance of the predator chamber, the timer was automatically stopped. This procedure allowed the exact determination of prey running speed (cm/s) and its effect on the

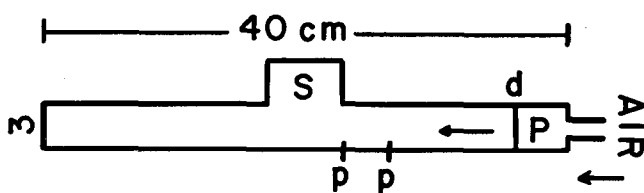


Fig. 2: Apparatus used to determine the effects of prey running speed on the capture success of *Dugesiella echina*. S = location of spider, P = location of prey at start of a test trial, d = movable restraining door, p = photoelectric cells.

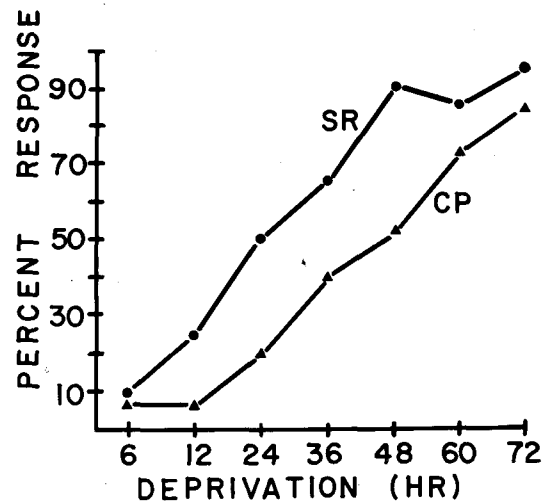


Fig. 3: The effect of food deprivation (hours) on the per cent strike response (SR) of *Dugesiella echina* to a moving cricket and the frequency of occurrence of capturing two consecutive prey (CP) in immediate succession.

per cent capture success of these spiders. For analysis, prey running speeds were categorised within five classes: 0.5, 1.0, 1.5, 2 and 2.5 cm/s. The data for 10 different spiders under three food deprivation levels (6, 24 and 72 hours) for each of the prey running speed intervals listed above were used for analysis.

One of the objectives of this study was to identify behavioural acts that might serve as reliable indices of hunger level. Experiments were conducted using 15 different spiders at each of seven levels of food deprivation (6, 12, 24, 36, 48, 60 and 72 hr) in order to establish the reliability of repeated prey capture as a behavioural index of hunger. Each spider was placed in a plastic cage (30 × 15 × 15 cm) provided with a sand substrate and allowed to habituate to the test chamber for 30 minutes. Using a pair of long forceps, a single cricket was dropped immediately in front of the spider (touching the pedipalps) and the presence or absence of a strike and capture sequence was recorded. If the first cricket was captured, a second was offered immediately in similar fashion and the response of the predator recorded. In this way it was possible to assess the relationship, if any, between various levels of food deprivation and the tendency to accept consecutive prey (CP).

Experiments were also conducted to assess the effects of hunger and predator size on the amount of time required to ingest a single cricket weighing 0.4 ± 0.1 g. Three predator size classes (4.0, 7.0 and 10.0 ± 0.2 g), each comprising 15 different spiders, were tested under four deprivation levels (6, 24, 48 and 72 hours) in the plastic container previously described. In each test, a single cricket was placed in the chamber. The amount of time required for each spider to ingest the prey was recorded. Ingestion time was defined as the amount of time that elapsed between the grasping of the prey and the discarding of undigested cuticular fragments. Each spider was tested only once in order to minimise the effects of experience. An analysis of variance (Sokal & Rohlf, 1981) was used to test for overall effects of hunger level and predator size on ingestion time.

Results

The tendency of *D. echina* to attack and capture crickets increased with duration of food deprivation (Fig. 3). The overall effects of hunger on the SR ($\chi^2 = 39.37$, $df = 6$, $p < 0.001$) and CP ($\chi^2 = 15.98$, $p < 0.001$) of these spiders were highly significant. At 6 and 12 hours, the SR rate was only 10 and 24%, respectively. At 24 hours, a SR rate of 50% was observed. Deprivation periods of 36 to 72 hours resulted in a SR rate of 65-97%. Clearly, after 36 hours these spiders show a significantly enhanced tendency to respond to moving prey. This is confirmed by the results observed for the CP rate at 48-72 hours. Thus, the frequency of occurrence of consecutive prey capture may be used as a reliable behavioural index of hunger level.

The ability of *D. echina* to capture prey as a function of hunger level and bodily position is shown in Fig. 4. There was a significant effect of hunger on capture success ($\chi^2 = 11.21$, $df = 3$, $p < 0.01$) regardless of predator position, with a significantly higher capture rate at 48 and 72 hours of food deprivation. The results also show that FF spiders exhibit a significantly higher capture rate ($G = 16.14$, $df = 3$, $p < 0.001$) than RF spiders. This is not surprising since this is the ambush position most often observed in the field (Baerg, 1958; Hjelle, 1972; Minch, 1977; pers. obs.). Spiders in the FF position were observed to strike directly at the moving cricket. Spiders in the RF position, however, were required to make a 180° turn in order to grasp the prey. The difference in per cent capture success between RF and FF spiders was greatest at 6 hr and progressively decreased to 72 hr.

The effect of food deprivation on the distance over which prey elicited a strike response (Fig. 5) was highly significant (ANOVA: $F_{3,56} = 175.27$, $p < 0.001$). Spiders experiencing higher hunger levels were capable of detecting and responding to moving prey at a significantly greater distance than those tested under reduced

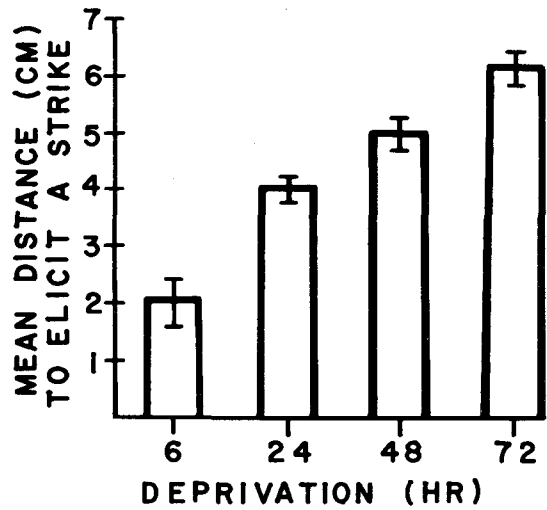


Fig. 5: The effect of food deprivation on the distance (cm) over which moving prey elicited a strike (awareness field) from *Dugesia echina*. Vertical lines represent ± 1.0 S.E.

hunger conditions. Spiders deprived of food for 48 and 72 hours exhibited a strike response at a mean distance of 5.1 and 6.2 cm, respectively. However, this awareness field was reduced to 2.1 cm at a deprivation level of 6 hr. These data clearly show that the tendency of *D. echina* to respond to prey of this size is significantly increased after 48 hours of food deprivation. In addition, Scheffe *F*-tests (Sokal & Rohlf, 1981) showed significant differences in the awareness fields exhibited by this spider between 6 and 24 ($F = 51.18$, $p < 0.01$), 24 and 48 ($F = 17.31$, $p < 0.05$) and 48 and 72 hours ($F = 7.34$, $p < 0.05$) of deprivation.

The effects of food deprivation and prey running speed on the capture rate of *D. echina* are shown in Fig. 6. The overall effects of hunger ($\chi^2 = 131.09$, $df = 2$, $p < 0.01$) were found to be highly significant. Capture rates were higher at 72 hours of food deprivation regardless of prey running speed. At low hunger

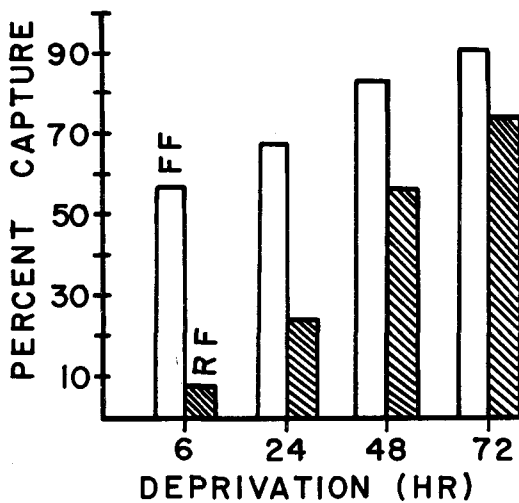


Fig. 4: Per cent capture success of *Dugesia echina* as a function of food deprivation (hours) and position of the predator relative to that of the prey. FF = forward-facing, RF = rear-facing.

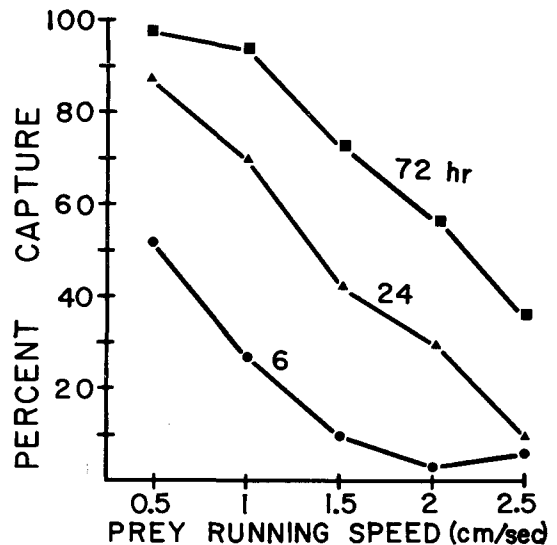


Fig. 6: The effect of food deprivation (hours) and prey running speed (cm/s) on the per cent capture success of *Dugesia echina*.

levels (6 hr), the per cent capture rate was only 3-8% for relatively fast moving prey (2-2.5 cm/s) and 28-52% for slower moving prey (0.5-1.0 cm/s). At 72 hours deprivation, however, capture rates were considerably higher (38-98%, respectively). Thus, although prey running speed does affect the ability of *D. echina* to perform a successful capture over a range of food deprivation levels, the relationship is much more pronounced when these spiders are deprived of food for 24 or more hours.

Fig. 7 shows the effects of food deprivation on the ingestion times for three predator size classes: 4, 7 and 10 ± 0.2g. There was a highly significant overall effect of deprivation level (ANOVA: $F_{3,44} = 893.75$, $p < 0.0001$) and predator size ($F_{2,33} = 62.34$, $p < 0.001$) on ingestion times. Larger spiders exhibited more rapid ingestion rates at all levels of deprivation. The data also show that ingestion time can vary widely as a function of hunger. For example, at 6 hours of deprivation, the mean ingestion time for all predator size classes ranged from 16.4-22.2 hours. At increased hunger levels (72 hours), the mean ingestion time was significantly reduced. A series of Scheffe *F*-tests (Sokal & Rohlf, 1981) were computed to test for between-group differences. The results of these comparisons are shown in Table 1. Significant differences were found between all predator size classes except 7 and 10g spiders at 72 hr of deprivation. This suggests that larger tarantulas process food at similar rates under higher levels of hunger.

Discussion

This study shows that the length of food deprivation affects several parameters associated with prey capture by *D. echina*. Although the term hunger is generally

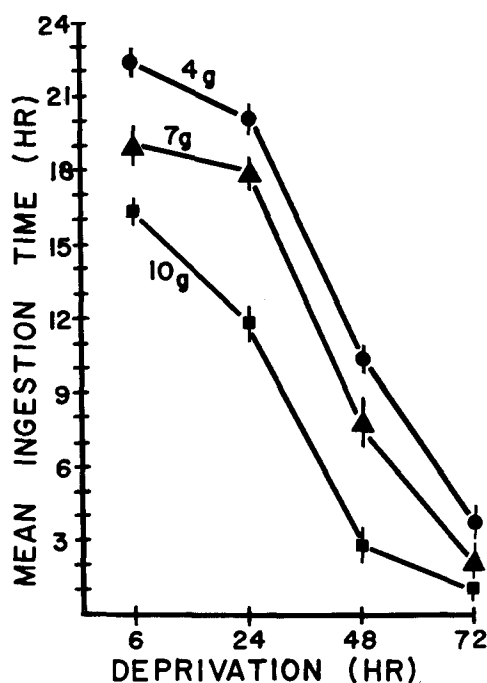


Fig. 7: The effect of food deprivation (hours) and predator size (g) on the amount of time required for *Dugesiella echina* to ingest a single cricket weighing 0.4 ± 0.1 g. Data points represent means ± 1.0 S.E. for 15 spiders.

associated with a collective series of internal messages related to a caloric deficit (Dethier, 1982), it has proved difficult to observe and quantify (Curio, 1976). The degree of hunger is influenced by the interval of fasting (deprivation) imposed upon the subject (Beukema, 1968; Cook & Cockrell, 1978) and has been shown to influence the degree of responsiveness of a predator toward potential prey (Curio, 1976; Punzo, 1980, 1985, 1988; Wigglesworth, 1966). Although the entire concept of motivation as a proximate cause of behaviour has been recently challenged (Kennedy, 1987), the notion of hunger as a drive state leading to goal-directed behaviours such as searching for food and prey capture has been used to explain the feeding behaviour of animals (Dethier, 1982; Tinbergen, 1951). This concept has also been extended to analyses of feeding behaviour in spiders (Anderson, 1974; Gardner, 1964; Nakamura, 1987). The results of this study showed that increasing food deprivation levels resulted in an increased tendency to attack and ingest prey as measured by per cent strike response and consecutive prey capture (Fig. 3), per cent capture success (Fig. 4) and the awareness field (Fig. 5). This is in general agreement with results reported for jumping spiders (Drees, 1952), fishing spiders (Bleckmann & Lotz, 1987), wolf spiders (Nakamura, 1972), coccinellid beetle larvae (Dixon, 1959) and praying mantids (Holling, 1966), although none of these studies dealt with the range of behavioural parameters addressed in the present study.

As mentioned previously, *D. echina* is an ambush predator that typically waits motionless and concealed at its burrow entrance (Baerg, 1958; Punzo, 1988). Thus, it is important to determine the awareness field for an ambush predator, and there is relatively little information available on this parameter for spiders. For *D. echina*, the reactive field of awareness ranges from 2.1 to 6.2 cm at lower and higher hunger levels, respectively (Fig. 5). Bleckmann & Lotz (1987) reported a 96% attack response for the fishing spider, *Dolomedes triton* (Walck.) towards moving prey at a distance of 2-13 cm. However, their study did not assess the effects of varying food deprivation levels on the attack response. An awareness field of 5-10 cm was reported by Drees (1952) for the salticid, *E. scenicum*, depending upon degree of satiation. The results of the present study indicate that the awareness field may be

Food deprivation (hr)	Comparisons between predator size classes (g)		
	4 and 7	7 and 10	4 and 10
6	7.85**	5.49*	26.48***
24	5.13*	30.24***	66.51***
48	7.04**	28.64***	62.42***
72	5.07*	NS	6.15*

Table 1: Scheffe *F*-test values (Sokal & Rohlf, 1981) for differences in ingestion rates of *Dugesiella echina* as a function of predator size (g) and level of food deprivation (hr). Levels of significance are < 0.05 (*), < 0.01 (**) and < 0.001 (***). NS = not significant.

used as a reliable behavioural index of hunger for *D. echina*. Thus, at higher hunger levels, *D. echina* is capable of detecting and reacting towards moving prey at a mean distance of 6.1 cm from the burrow. North American theraphosid tarantulas feed primarily on ground beetles, grasshoppers, caterpillars and crickets as well as other arthropods and to a lesser extent, small reptiles and rodents (Baerg, 1958; Hjelle, 1972; Minch, 1977; pers. obs.). These spiders detect their prey with several types of mechanosensitive sensilla distributed over the legs and pedipalps (Den Otter, 1974). Especially important are the trichobothria which are sensitive to air-borne vibrations and club-shaped tarsal sensilla responsive to substrate vibrations. In his neurobiological study of prey detection in the theraphosid spider *Sericopelma rubronitens* Ausserer, Den Otter (1974) showed that the trichobothria are capable of responding to moving air caused by the movement of a single cricket leg at a distance of 2 cm. Prey detection is, however, the result not only of the action of trichobothria but also of additional types of mechanoreceptive sensilla including slit sensilla, tactile hairs and joint receptors (Foelix, 1982). This explains the ability of *D. echina* to respond to prey at a distance of 6-7 cm. Visual and olfactory cues do not play an important role in the detection of prey (Den Otter, 1974). Although tarsal olfactory receptors have been identified on theraphosids (Den Otter, 1974; Foelix, 1982), they appear to function in assessing the palatability of the prey as food following capture rather than in the capture itself.

Once the prey moves within the awareness field and is detected, the tarantula orients to face the prey (FF), elevates the pedipalps and first pair of legs, grasps the prey with the front legs, pulls the prey towards the chelicerae and then exhibits the biting and ingestion sequence (Foelix, 1982; pers. obs.). Although a tarantula is capable of detecting a prey organism that is in front of (FF) as well as behind (RF) it, the per cent capture success is significantly higher in the FF position (Fig. 4). However, if the spider is in a RF position, as is commonly the case when engaging in burrow cleaning and excavation (Gabel, 1972; Hjelle, 1972; Minch, 1977), it is still capable of detecting and capturing moving prey. Regardless of position, the per cent capture success is significantly greater at higher levels of hunger (Fig. 4). It should be noted that theraphosids often lay down a network of silk threads around the burrow entrance which could effectively increase the awareness field (Minch, 1977). The ability of RF spiders to detect and respond to moving prey has also been reported for salticid (Forster, 1982) and ctenizid (Buchli, 1969) spiders, and vaejovid scorpions (Bub & Bowerman, 1979).

In the present study, hunger level was shown to affect the tendency of *D. echina* to capture consecutive prey (Fig. 3, CP). At higher levels of food deprivation, this tendency significantly increased. Although this opportunity is not likely to occur frequently under natural conditions, it provides a reliable behavioural index for the assessment of hunger level under laboratory conditions, not only for *D. echina* but also for other predators. Reliable behavioural correlates of

hunger are extremely important to any experimental analysis of parameters affecting feeding behaviour (Holling, 1966; Dethier, 1982; Kennedy, 1987). Hopefully, the tendency to capture consecutive prey can be used by future investigators interested in determining the relationships between degree of satiation and predation in the same way that the number of prey consumed in a given period of time has been used in the past.

Previous studies indicate that the level of food deprivation can affect the speed at which predators respond to prey as well as decisions to move to new foraging sites (Krebs, 1978). However, no comparable information is available on the relationship between predator capture success and prey movement speed. The combined effects of deprivation and prey running speed on capture success (Fig. 6) indicate that faster moving crickets are more difficult to capture regardless of hunger level. Tarantulas are commonly exposed to relatively fast-moving arthropods (e.g. crickets and ground beetles) which comprise a large part of their natural diet (Minch, 1977; Punzo, 1988). These theraphosids possess a number of adaptations which facilitate the capture of highly mobile prey including rapid strike response, extremely sensitive mechanoreceptors, densely arranged tarsal and metatarsal pile hairs bearing numerous barb-like projections at their distal end, dense tufts of scopula hairs covering the ventral regions of the tarsus and metatarsus which effectively increase the number of contact points that can be used to restrain a struggling prey, a hydraulic mechanism for rapid extension of the legs and a flexor-type leg musculature which increases grasping strength (Den Otter, 1974; Foelix, 1982). At higher hunger levels (Fig. 6, 72 hours), *D. echina* was able to capture even the fastest moving crickets (2.5 cm/s) at a relatively high success rate (38%). Slower-moving prey are captured with a greater frequency of success at all hunger levels. Some examples of slower-moving prey found in the natural habitat of these spiders include grasshoppers, cicada nymphs and caterpillars (pers. obs.). It is interesting to note that several rather slow-moving arthropods commonly encountered by these spiders such as blister beetles, some caterpillars and millipedes, are characterised by well-developed chemical defence mechanisms (Eisner, 1970).

The length of the deprivation period has also been shown to affect the rate of ingestion in a number of vertebrate and invertebrate predators (see reviews by Holling, 1966; Curio, 1976; Dethier, 1982). However, it was found to have no effect on the ingestion rates of mantids (Holling, 1966) and stickleback fish (Beukema, 1968). The results of this study indicate that deprivation period has a pronounced effect on ingestion time in *D. echina* (Fig. 7). This suggests that feeding rate is not solely determined by mechanical limitations imposed by morphological characteristics associated with the mouthparts and accessory feeding structures. When a predator attacks a prey organism, a certain period of time must be allocated to capture and ingestion (i.e. handling time). This, in turn, determines the number of prey which can be consumed and con-

tributes in a significant way to the overall energy budget of the predator (Krebs, 1978). Ingestion rate is one component of overall handling time and is directly affected by hunger level as well as the size of the predator (Fig. 7). At greater periods of food deprivation (72 hours), smaller individuals require 3.8 hr for ingestion of a single cricket weighing 0.4g whereas larger spiders reduce this to 1.1 hours. At 24 hours of deprivation, 11.8-20.3 hours are required for ingestion. These values represent relatively long ingestion times when compared with other predators, even when one considers the weight of prey ingested as a function of predator weight (Holling, 1966; Cook & Cockrell, 1978). There is little information available on ingestion time for spiders. Previous studies focused primarily on the amount of prey captured per unit time (Gardner, 1964; Morse, 1979) or the amount of time allocated to feeding over a daily period (Minch, 1978; Morse, 1984, 1987; Higgins, 1987). At 72 hours of deprivation (Fig. 7), spiders weighing 4g ingested an amount of food equivalent to 10% of their body weight in 3.8 hours. At 24 hours, *D. echina* required 20.3 hours to ingest the same amount of food. These tarantulas are capable of consuming prey as large or larger than themselves (Baerg, 1958) and may require more than 36 hours to do so (pers. obs.). They appear to be opportunistic feeders that will accept arthropods and small vertebrates as prey. There is no information available which would suggest that these tarantulas exhibit a preference for certain size classes of prey. However, desert floodplains and sotol-grassland habitats are commonly characterised by periodic fluctuations in prey density depending upon annual precipitation levels (Barbault & Halfter, 1981). Thus, *D. echina* is periodically exposed to conditions of low prey density and may have to survive prolonged periods of fasting. These sedentary spiders apparently do not move to different locations during periods of prolonged drought (Minch, 1977; pers. obs.) and are capable of withstanding long periods (months) without food (Baerg, 1958). There would seem to be a selective advantage for a foraging strategy that favours gorging when prey densities are high. Such gorging tactics have been shown to be adaptive in other ambush predators (Curio, 1976).

Conclusions

The results of the present study clearly indicate that the length of food deprivation has a pronounced effect on several important parameters of prey capture and feeding behaviour in *D. echina* including the readiness to respond to prey (strike response), capture success, awareness field, tendency to capture consecutive prey and ingestion time. In addition, the position of the spider relative to that of its prey as well as the running speed of the prey were also found to have a significant effect on prey capture success. Parameters such as strike response, awareness field and tendency to capture consecutive prey represent reliable behavioural indices of hunger in *D. echina* and hopefully will provide a useful framework for future studies on predation and feeding behaviour in other arachnids.

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