Size differences in predatory responses of *Nephila clavipes* (L.) spiderlings

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Summary

Juvenile predatory behaviour of the Golden-web spider *Nephila clavipes* (L.) was observed in the field. Spiderlings in four immature sizes were observed capturing *Drosophila melanogaster* Emigen. Predatory patterns were composed of distinct behaviours in consistent temporal relationships. Differences between sizes occurred that probably reflect changes in the predator-to-prey size ratio. Small spiderlings held the cheliceral capture bite longer and were more likely to wrap prey; they also were less effective in immobilising *Drosophila*. Some responses of larger juveniles, such as long approach latencies and plucking, may have resulted from difficulty locating small prey in webs of larger mesh size.

Introduction

Mature orb weaving spiders capture prey with a predictable series of behaviours: the prey is located, attacked, immobilised, removed from the viscid spiral, and transported to the feeding site (Robinson, 1975). Different prey types and sizes consistently elicit predatory patterns that vary in the approach and the subsequent treatment of prey (Robinson, 1969; Robinson & Mirick, 1971; Robinson *et al.*, 1969; Robinson & Robinson, 1976). The development of these relatively stereotyped sequences, however, has not been investigated in detail.

Predatory behaviour of early instar spiderlings has been described in a jumping spider (Forster, 1977)

and an orb weaver (Hill & Christenson, 1981), and deficiencies in prey capture have been noted in inexperienced spiders (Hill & Christenson, 1981; Reed *et al.*, 1970; Robinson & Robinson, 1976). Although spiderlings frequently executed orientation and approach responses, initial capture attempts were often unsuccessful (Forster, 1977; Hill & Christenson, 1981). On their first capture opportunity as adults, *Araneus diadematus* Cl. reared to maturity without the experience of preying on a web failed to orient to or approach prey in the viscid spiral (Reed *et al.*, 1970). Mature *Argiope* reared on dead prey did capture the first live prey encountered, but they exhibited prolonged approach latencies and immobilisation bite durations compared with those reared on live prey (Robinson & Robinson, 1976).

In this study we examined predatory responses of juvenile *Nephila clavipes* (L.) in order to describe developmental changes in (1) behaviours employed in predatory sequences and (2) speed or facility in capturing prey. For this field study, we recorded predatory responses to a single prey type, *Drosophila melanogaster* Emigen, wild variants of which are found in the study area. Immature *Nephila* tested included sizes ranging from post-dispersal to sexual differentiation.

Natural history of *Nephila clavipes*

Life cycle

The life span of *N. clavipes* in the temperate United States is one year. In fall, females lay several hundred eggs under a leaf canopy and cover them with nonviscid silk (Christenson & Wenzl, 1980). The eggs hatch approximately one month later, and the first moult occurs after about a week (Moore, 1977). The second instars overwinter inside the egg sac, emerging in March (Moore, 1977). Spiderlings then form a tangled communal web just above the egg sac (Hill & Christenson, 1981). Several webs may be constructed as the group ascends along tree branches. The second moult occurs in the communal web about a week after eclosion.

Nephila juveniles disperse from the communal group in the third instar (Moore, 1977), when cephalothorax-abdomen length is about 2-3 mm. In Louisiana, dispersal generally occurs in April. Spiderlings then build small solitary orbs consisting of a

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three-dimensional superstructure supporting a viscid spiral that is repaired daily. Spiderlings of different sizes show progressive changes in body morphology (Moore, 1977) accompanied by changes in web geometry (Brown, 1981). As body size increases, spiderlings build larger webs with an increasingly open silk mesh owing to a decreased number of radial and concentric strands (Brown, 1981).

Sexual differentiation becomes evident in May and June as males develop visible pedipalpal emboli. Differentiation, occurring in the fifth instar according to Moore (1977), is sometimes distinguishable in 5 mm males but generally occurs when they have reached 7-9 mm. After males moult to the final instar they cease building and repairing their own orbs, moving to those of females. Females mature when about 20-24 mm (Wenzl, 1980).

Adult predatory behaviours

Typically, the spider assumes a head-down predatory posture at the orb hub. Prey impact is signalled by vibrations of the web radii. Predatory responses of adult *N. clavipes*, as detailed by Robinson & Mirick (1971), usually begin with an orientation followed by a rapid approach or plucking, which involves jerking the web strands by flexing the first pair of legs. *Nephila* use a biting attack to immobilise prey. If the prey is heavy and large, the spider may maintain a cheliceral bite at the capture site. Alternatively, it may rapidly lunge forward, execute a short-duration bite, then withdraw before biting again. In order to free prey that are entangled in the viscid strands, the spider extends its legs, pushing on the web while pulling on the prey. Prey are cut out and wrapped at the capture site if not easily lifted. In contrast, very light prey are immediately seized in the chelicerae and carried to the hub.

Nephila usually wrap prey at the hub before feeding. To wrap, the spider holds the web with its first and second pairs of legs and the prey with the third pair, tilting its abdomen towards the prey. Silk is cast forwards from the spinnerets with the tarsi of the fourth pair of legs, while the prey is rotated with the third pair. When the spider has finished wrapping, it may groom, cleaning its legs with the chelicerae or using one leg to stroke another. The spider often manipulates the prey extensively before initiating a sustained bite and feeding.

Methods

Study area and subjects

The study was conducted at the F. Edward Herbert Center of Tulane University, which has been described by Christenson & Goist (1979). Data were collected between 0700 and 1400 hours during June-July 1979 and April-May 1980.

Prey were presented to 122 subjects selected according to the following criteria: (1) intact orb entirely free of prey, with no holes or other evidence of recent prey capture and (2) estimated cephalothorax-abdomen length of approximately 2-3, 5, 7, or 9 mm. Actual mean sizes of these groups were 2.5 mm (n = 26), 5.1 mm (n = 40), 7.1 mm (n = 33) and 9.1 mm (n = 23). Mean weights for five randomly selected spiderlings from each class were 3.20 mg (2-3 mm), 10.03 mg (5 mm), 21.39 mg (7 mm) and 39.98 mg (9 mm). A second group of 2-3 mm spiderlings was tested ($\overline{X}$ = 2.35 mm, n = 15) omitting our habituation procedure (see below) to determine its effects on predatory behaviour.

Procedure

Two experimenters collaborated for each prey test. Order of size class tested and experimenter presenting prey were counterbalanced. One experimenter blew a *D. melanogaster* from a pipette to the viscid spiral. Twelve randomly selected prey weighed 0.72 mg and measured 2.25 mm in cephalothorax-abdomen length and 2.06 mm in wing length. Prey were aimed at a point 1/2 to 1/3 the distance from the hub to the lowest concentric strands.

As the first experimenter observed and reported behaviour, the other recorded the following responses and latencies timed by stopwatch: latency to contact, removal from the viscid spiral, return to the hub, onset and completion of wrapping, completion of attaching prey to the hub, initiation of feeding, and termination of postural adjustments and cheliceral examination of prey. Also recorded were the numbers of wrapping and attaching movements, grooming behaviour, and plucking responses. After testing, the spiderlings were measured with calipers while on their orbs.

To ensure that spiderlings were responding to prey rather than to our method of presentation, we habituated subjects to soft puffs of air directed through a

small pipette to the target area of the viscid spiral. Inter-puff interval was 5 s. The habituation criterion was three successive puffs that elicited no response from the spiderling. Test prey were presented within 15 s of the final puff. When the prey was not propelled from the pipette on the first attempt (n = 32), spiderlings were rehabituated if they showed any response to the associated air puff (n = 10). Spiderlings were also rehabituated if the first *Drosophila* either passed between the web strands or immediately glanced off the orb (n = 24) or if wind conditions prevented another *Drosophila* from being presented within 30 s (n = 3). To determine the effects of this procedure on subsequent behaviour, we tested 15 spiderlings without prior habituation.

Analyses of variance (one-factor) and subsequent Scheffe comparisons were used to test differences in response latencies between size groups. Differences in frequencies and conditional probabilities of responses were evaluated by chi-square tests. The effects of the habituation procedure were tested by comparing responses of the nonhabituated 2-3 mm spiderlings with the 2-3 mm spiderlings that were habituated. This nonhabituated group was not included in the overall analysis of size differences.

Of the immature subjects in this study, 18% were differentiated males when tested. Since the size at which sexual differentiation occurs is variable, subjects that were undifferentiated at testing cannot be assumed to be females. Following individuals to maturity is difficult because of the mobility of juveniles. Consequently, the sex of most subjects tested is unknown. Therefore, this paper does not consider variations in behaviour resulting from sex or differentiation that are independent of size differences.

Results

Size differences in spiderling predatory responses

Approach and initial contact with prey

Upon striking the web virtually all *Drosophila* exhibited sustained wing and leg movements. Spiderlings typically oriented immediately to the location

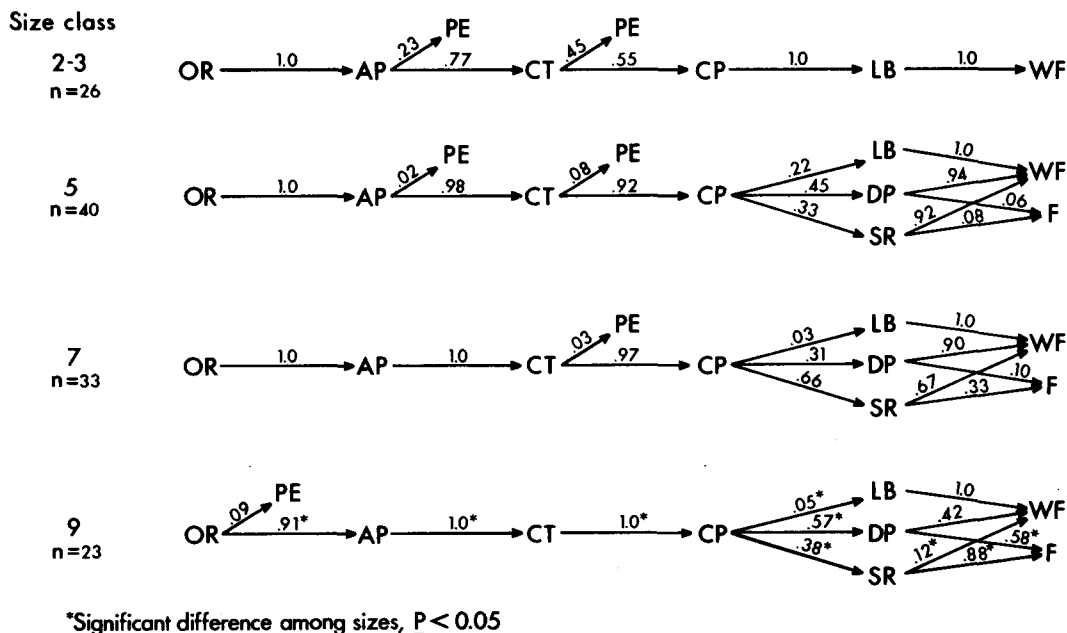*Significant difference among sizes, P < 0.05

Fig. 1: Predatory sequences used by spiderlings of different sizes. Conditional probabilities are shown for transitions between the following behaviours: orient (OR), approach (AP), contact (CT), escape of prey (PE), capture (CP), long bite maintained at capture site (LB), discrete pull-out movement (DP), unitary seize in chelicerae and return to hub (SR), wrapping before feeding (WF), and feeding upon return to hub, omitting wrapping (F).

of impact and rapidly approached the prey. Size differences in the basic components of capture sequences are summarised in Fig. 1. The manner in which juveniles approached prey varied with size, although latencies in orienting and approaching did not differ significantly (Table 1). Only the smallest subjects paused or hesitated while descending towards the prey (19.2% 2-3 mm). On occasion, large animals overran the prey, then backed up to contact it (0% 2-3 mm; 2.5% 5 mm; 24.2% 7 mm; 4.4% 9 mm), or first approached a mislocated site on the orb (0% 2-3 mm; 2.5% 5 mm; 6.1% 7 mm; 8.7% 9 mm). Some of the smallest and largest animals used the first pair of legs to pluck the web radii before approaching (11.5% 2-3 mm; 0% 5 mm; 9.1% 7 mm; 26.1% 9 mm).

The manner of approach affected the likelihood of contacting prey, particularly for the smallest animals. Only one of the five 2-3 mm juveniles which hesitated succeeded in contacting the prey before it freed itself. All of the animals over 3 nm which approached also contacted prey, although one 7 mm animal returned to the hub after approaching, leaving the prey entangled in the orb (Fig. 1). Plucking (n = 10), initial overruns (n = 10), and mislocations (n = 5) did not impair the spiderlings' ability to locate and contact prey, except for one 2-3 mm juvenile that failed to reach the prey before it escaped. Of the six smallest subjects failing to contact prey, four interrupted their approaches with one or two pauses, one descended continuously but slowly, and one plucked. In these cases the prey escaped in 3 s to 6.5 s ($\overline{X}$ = 4 s). Two 9 mm juveniles did not approach the *Drosophila* after plucking; these prey remained in the orb for 41 s and 270 s.

The largest animals were not faster in locating and contacting prey (Table 1); the median interval from approach to contact was about 1 s in all size groups. More of the larger animals showed extremely long latencies to contact, including 8 s, 23 s and 27 s for 7 mm subjects, and 19 s and 69 s for 9 mm subjects. Four of these latter five subjects plucked during approach ($\overline{X}$ = 4 plucks). The average duration of the approach phase for spiderlings which plucked was 19 s, significantly longer than for those which did not pluck ($\overline{X}$ = 1.7 s; $F(1,111)$ = 67.95, $p < 0.001$).

Capture of prey

Larger animals were faster (Table 1) and more effective (Fig. 1) in clasping prey and initiating an immobilisation bite. Virtually all the juveniles over 7 mm bit the prey immediately after contact. The 5 mm animals were only slightly less effective; two lost the prey after contacting it with their anterior legs, failing to move over the prey body to engage the cheliceral bite. In contrast, many 2-3 mm animals which contacted *Drosophila* failed in capture (Fig. 1), and small spiderlings frequently had to struggle with a prey before subduing it. Eight lost the prey immediately, including one that backed away, allowing the *Drosophila* to escape. One prey escaped after a 7 s struggle with the spiderling during; which both were hanging free from the viscid spiral on a silk strand from the hub. The 11 successful captures included struggles of 18.5 s, 8 s and 6.5 s. A biting posture with the first and second pairs of legs flexed back over the prosoma was displayed by three of these small spiderlings; this behaviour was not shown by any larger juveniles.

Immobilising prey

Different sized spiderlings employed varying methods of immobilising prey (Fig. 1), resulting in a differing interval between engaging a bite and attempting to pull prey away from the orb (Table 1). Many juveniles larger than 3 mm seized the prey in their chelicerae and, in a continuous motion, lifted it away from the silk strands and returned to the hub (Fig. 1). Most of the other large spiderlings freed prey by a discrete pull-out behaviour (Fig. 1). In contrast, all the 2-3 mm spiderlings held their cheliceral bites at the capture site for more than 25 s, remaining up to 208 s before removing the prey (Table 1). Only six subjects of various sizes pulled more than once to remove prey.

After freeing the prey, spiderlings turned and carried it to the hub in their chelicerae. Only three had an impeded ascent, entangling the *Drosophila* or one of their own legs in the orb strands. Smaller animals, however, ascended more slowly to the hub (Table 1). One nonhabituated 2-3 mm subject deviated from this sequence; it held a bite on the prey's wing for 188 s and an abdominal bite for 131 s, then freed the prey, proceeding to enswathe

it in silk at the capture site rather than transporting it to the hub before wrapping.

Wrapping prey

With the prey in their chelicerae, spiderlings attached themselves with silk to the hub, assuming the head-down predatory posture. Smaller animals were more likely to enswathe the prey in silk before feeding (Fig. 1). Smaller juveniles spent more time enswathing prey (Table 1) and executed more wrapping motions ($\overline{X}$ = 70.0 2-3 mm; 32.7 5 mm; 26.6 7 mm; 22.4 9 mm; $F(3,72) = 41.5, p < 0.0001$). Wrapping usually continued uninterrupted; only three subjects wrapped, paused, then initiated another wrapping bout.

The occurrence of wrapping was related to the type of behaviour spiderlings used in freeing prey from the web (Fig. 1). Animals of all sizes which held the capture bite for more than 5 s also wrapped. Spiderlings in the 7 and 9 mm sizes were more likely to omit wrapping, and those that used a continuous motion to seize prey tended to feed immediately

upon returning to the hub (Fig. 1; $F(1,47) = 3.89$, $p = 0.05$). Of the eight 7 mm animals which did not wrap, seven had used the seizing motion, simply lifting prey away from the orb. More of the 9 mm spiderlings using the continuous movement fed without wrapping (7/8; 87.5%), compared with those needing a discrete pull-out response to free the prey (7/12; 58.3%).

Feeding

Spiderlings attached the prey to the hub while holding it in their legs. Smaller juveniles spent more time securing prey (Table 1) and made more attachments ($\overline{X}$ = 9.6 2-3 mm; 6.9 5 mm; 5.7 7 mm; 5.7 9 mm; $F(3,72) = 9.99, p < 0.0001$). Feeding usually commenced after spiderlings had again assumed the head-down posture at the hub, first pulling the prey up with the anterior legs and manipulating it with their chelicerae. Twenty of the 76 (26.3%) which wrapped prey also groomed their appendages before investigating the prey. Most of the smallest animals (9/11; 81.8%) groomed, which resulted in a longer

Responses	2-3		5		7		9		(df)	p
	MN	SD	MN	SD	MN	SD	MN	SD	F	
Approach to contact	0.8	1.0	0.6	1.5	1.4	3.1	4.1	14.7	(3,109) 1.44	0.235
Contact to bite	4.8*	5.1	0.0	0.0	0.0	0.0	0.0	0.0	(3,96) 28.02	0.000
Bite to pull-out	81.7*	64.2	3.2	3.3	0.7	1.1	1.2	1.5	(3,96) 48.05	0.000
Pull-out to return to hub	17.0*	8.0	2.4	2.3	2.3	1.5	2.1	2.1	(3,96) 68.94	0.000
Return to hub to feed (w/o wrapping)			0.0	0.0	8.8	10.0	8.8	10.2	(2,21) 0.73	0.495
Return to hub to wrap	54.6	53.4	24.6	24.0	48.7	77.1	49.7	86.3	(3,71) 1.31	0.279
Begin to finish wrapping	43.7*	21.4	15.2	4.9	11.8	6.4	10.4	3.1	(3,72) 33.41	0.000
Finish wrapping to finish attaching	22.1*	7.5	11.4	5.8	10.0	2.3	8.5	1.5	(3,72) 17.39	0.000
Finish attaching to begin feeding	51.3*	29.3	14.3	14.9	8.8	6.5	6.7	4.3	(3,72) 21.80	0.000

Table 1: Size differences in mean intervals (s) between predatory responses.

*Differs from other groups, subsequent Scheffe tests, $p < 0.05$.

interval between attaching prey to the hub and initiating feeding (Table 1). Those spiderlings which did not wrap began feeding in an average of 8.1 s after returning to the hub, while the complete wrapping and attaching sequence generally lasted about 85.7 s.

Responses to successive prey

In nine cases natural prey flew into a juvenile's orb after it had returned to the hub with the test *Drosophila*. Spiderlings which had wrapped the test prey (n = 5) attacked and captured the additional prey item; the test *Drosophila* remained suspended on silk at the hub. Test prey had not been wrapped in the other four cases. One 9 mm juvenile dropped the *Drosophila* remains from its chelicerae to approach and capture a small moth. The other three subjects had the *Drosophila* in their chelicerae while locating and approaching the second prey. One 9 mm captured a mosquito, returning to the hub to wrap both simultaneously. Another, a 5 mm, immobilised the new prey, returned to the hub, wrapped the original *Drosophila*, then brought the new prey to the hub and wrapped it separately. In the remaining case, a 2-3 mm spiderling did not capture the additional prey; it approached halfway but returned to the hub, proceeding to wrap the *Drosophila*.

Responses to habituation

Size Differences

When puffs of air were directed through a small pipette to the viscid spiral, spiderlings usually responded with postural adjustments, orientations, or approaches. Smaller spiderlings executed more responses before reaching our habituation criterion of no response for three consecutive puffs ($\overline{X}$ = 5.9 2-3 mm; 8.8 5 mm; 5.9 7 mm; 3.2 9 mm; $F(3,118)$ = 2.8, p = 0.043). In addition, more second habituations were necessary with the smallest group ($\overline{X}$ = 2.2 2-3 mm; 1.3 5 mm; 1.3 7 mm; 1.3 9 mm; $F(3,118)$ = 6.45, p < 0.001). This difference probably resulted from our testing criteria. We rehabituated and retested a subject if its prey escaped within 3 s and the spiderling had not yet contacted it; many small spiderlings which paused during approach failed to contact the *Drosophila*.

Effects of the habituation process

We found no significant differences in the predatory behaviour of nonhabituated versus habituated spiderlings. All 2-3 mm juveniles oriented to the prey and most approached it (100% habituated; 93% non-habituated; χ^2_1 = 1.78, p = 0.18). The *Drosophila* was contacted by 93% of the nonhabituated spiderlings and 77% of the habituated ones (χ^2_1 = 1.81, p = 0.18). An equivalent proportion of both groups succeeded in immobilising the prey (42% habituated; 40% nonhabituated; χ^2_1 = 0.02, p = 0.88).

Discussion

Spiderling capture sequences were consistently composed of discrete behaviours in predictable temporal relationships. Sequences differed with juvenile size in the duration of the capture bite and the frequency of wrapping prey. These variations may principally reflect changes in the spiderling-to-prey size ratio; Robinson & Mirick (1971) have demonstrated that prey weight and size parameters affect the type of attack strategy employed by adults. Predatory patterns of many spiderlings in the larger sizes tested resembled those of mature *Nephila* capturing small, lightweight prey that are exhibiting sustained vibration (Robinson & Mirick, 1971), that is, a unitary response of seizure in the chelicerae, lifting from the orb, and transport to the hub. Harwood (1974) noted that rapid immobilisation of light insects may be advantageous since their tenuous attachment to few strands of viscid silk might allow escape.

While most spiderlings approached the prey immediately, some larger juveniles showed latencies to approach longer than 20 s. Slow approach latencies could result either from rejecting prey or difficulty in locating prey. Suter (1978) examined *Cyclosa turbinata* (Walckenaer) predatory responses to small prey and found that the rate of approach was correlated positively with prey mass. As the relative calorific value of small prey decreases, benefits of preying may change (Suter, 1978), and it may become advantageous to remain at the hub to monitor for larger prey. We plan to examine responses to prey that are maintained at a constant proportion of spiderling body weight.

Slow approaches by juveniles were associated

with plucking, which is thought to provide vibratory information useful in prey location (Robinson & Mirick, 1971). Differences in ease of prey location may be influenced by size changes in the orb. Maturational increases in body size, weight, and leg length coincide with increases in web size, decreases in the number of radial strands, and a corresponding increase in openness of the silk mesh (Benforado & Kistler, 1973; Brown, 1981; Turnbull, 1962; Witt & Baum, 1960; Witt et al., 1972). Perception of prey-impact vibrations could be attenuated in larger webs, since vibration amplitude changes with distance from the vibration centre (Liesenfeld, 1956). In addition, smaller prey may contact fewer silk strands in orbs of larger animals. Szlep (1964) found that tuning fork vibration of more than one radius maintained responses at higher levels. These influences could be tested by presenting prey at a constant distance from spiderlings of various sizes and by testing spiderlings of different sizes on webs of the same mesh size.

The behaviour of smaller juveniles was similar in some respects to responses of mature spiders confronting large prey. Robinson & Mirick (1971) observed that adult Nephila capturing heavy insects often sustain a capture bite with their anterior legs flexed far back over the prosoma. This posture was displayed by only a few small juveniles in this study. Many small subjects held the cheliceral bite at the capture site, rather than executing a unitary seize or pull-out movement. Robinson & Robinson (1976) suggested that the capture bite is held until prey are immobilised and can be released for wrapping. Because bite durations were longer in adult Argiope that had no experience with live prey, they hypothesised that spiders may have to learn to gauge the effect of a bite. In addition, small spiderlings may release a smaller quantity of venom, possibly producing a less effective bite than larger spiderlings.

Small spiderlings were more likely than large to wrap prey before feeding. All but two spiderlings smaller than 7 mm wrapped prey, as did three-fourths of the 7 mm group. Nephila usually wrap all prey at the hub; Robinson & Mirick (1971) noted the omission of wrapping only with very small prey transported to the hub in the chelicerae. The possible functions of wrapping may relate to these size differences. Attaching prey to the hub has been considered an adaptation that prevents loss when subsequent

prey are attacked (Eberhard, 1967; Robinson, 1975). Diguetid spiders wrap prey only after they return to the retreat to feed; some are not wrapped until other prey contact the web (Eberhard, 1967). Robinson (1975) suggested that performing additional attacks while holding prey in the chelicerae would be inefficient. Most N. clavipes tested with several prey in succession did attempt this manoeuvre, and many lost the original prey (Robinson et al., 1969). The degree of interference a Drosophila produces in subsequent attacks could influence the decision to wrap; in the few cases that we observed, it appeared easier for larger animals to capture additional prey while holding a Drosophila in the chelicerae. The responses to successive prey of juvenile Nephila are being investigated in detail (Brown, 1981).

About half the smallest juveniles failed to capture the Drosophila, while 5 mm spiderlings effectively immobilised the test prey, which were about half their size. The development of precise and efficient behaviours adapted to particular groups of stimuli depends on morphological changes and experience. Since this field study examined spiderling responses resulting from several concommitant developmental processes, the effects of a changing predator-to-prey size ratio are difficult to separate from the effects of experience.

In previous work with Nephila, Drosophila prey were presented to juveniles (approximately 2-3 mm) removed from predispersal communal groups and transferred to orbs constructed by solitary individuals. The majority of third instars tested approached prey, but less than half contacted and few captured the Drosophila (Hill & Christenson, 1981). When the same animals were retested after one day's residence on the foreign orb, all approached prey and over three-fourths made contact; most of these still failed in capture (Hill, 1979). Several that contacted prey withdrew, and the rest lost prey during bite attempts. The smallest juveniles tested in the present study were of comparable size, and while the nature of postdispersal experience is unknown, they displayed similar difficulty subduing prey. In contrast, only two 5 mm juveniles and none larger failed to capture prey that they attempted to bite. When morphologically mature but experientially naive Argiope were tested with live prey for the first time, they showed unimpaired clasping and

cheliceral insertion, although bites were prolonged (Robinson & Robinson, 1976). Experience may enhance the ability to localise and contact prey, but larger size may facilitate prey capture, increasing a spiderling's physical capacity to hold the prey with the legs or to reach over an insect's body to deliver the cheliceral bite. Further tests with inexperienced spiders of different sizes are necessary to elucidate the contribution of experience in the development of predatory behaviour.

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