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## The effect of leg loss on prey capture in *Nephila clavipes*

Monika Weissmann and Fritz Vollrath\*

Department of Zoology,  
South Parks Road, Oxford, OX1 3PS

### Summary

Efficiency of prey capture in *Nephila clavipes* suffered as a result of leg loss in two ways. Spiders that had lost legs built webs which retained prey less well than normal webs. Moreover, spiders with missing legs oriented less accurately and caught prey more slowly, even when placed in the more regular webs built by intact spiders.

### Introduction

The golden-web spider *Nephila clavipes* (L.), like many other orb spiders, builds its webs across insect flight paths (Castillo & Eberhard, 1983). Because of a very tight mesh, the huge webs are capable of intercepting rather small prey; thus tiny Hymenoptera and Diptera, minute relative to the spider, may constitute a major part of *Nephila*'s diet (Robinson & Mirick, 1971; Hill & Christenson, 1981; Rypstra, 1985; Nentwig, 1985). Mesh size (spacing of the capture spiral) typically influences the predatory success of spiders: narrower meshes retain smaller insects (Chacón & Eberhard, 1980) and thus prey interception is correlated with thread density (Eberhard, 1986; ap Rhisiart & Vollrath, 1994). However, there are costs as well as benefits of a fine mesh: the size of a web, the area covered by the capture spiral, the number of load-bearing radii, the spacing and regularity of the capture spiral, and the total amount of silk in a web can all be interrelated and traded off against one another (Craig, 1987). Further costs and trade-offs are found in the metabolism, speed and accuracy of the building process that leads to the final structure, i.e. the building behaviour with its

complex manipulation, locomotion and orientation behaviour patterns (Vollrath, 1992).

The behaviour of most animals would be affected by the loss of a leg. Especially so, one would have thought, a highly tuned and interactive behaviour such as the orb spider's web-building (Vollrath, 1987). Leg loss does indeed cause altered geometry of webs in *Araneus diadematus* Clerck (Jacobi-Kleemann, 1953; Reed *et al.*, 1965) and *Zygiella x-notata* (Clerck) (Le Guelte, 1965) as well as in *Nephila clavipes* (Weissmann & Vollrath, in prep.). In all three species the webs of spiders with missing legs were smaller and less regular, and had fewer radii and spiral turns (Weissmann & Vollrath, in prep.). Regularity, in particular, could be strongly affected if more than one leg was missing. Thus leg loss can indirectly affect a spider's prey-capture success through its effect on web geometry (Weissmann & Vollrath, 1998). In addition, leg loss might also directly affect prey capture by partially incapacitating the spider and thus slowing it down. Prey attack is an important part of the integrated system spider+web dealing with the incoming prey, and it is the part of the capture sequence where speed and accuracy of orientation can matter tremendously (Klärner & Barth, 1982; Landolfi & Barth, 1996). Our study was designed to examine specifically this aspect in *Nephila clavipes*. In nature, leg loss is typically found in 5–10% of a given species, thus compensating for leg loss is a realistic selection pressure for web spiders (Vollrath, 1990, 1995; Weissmann & Vollrath, 1998), with *Nephila* being no exception.

### Material and methods

*Nephila clavipes* is common in tropical and subtropical regions of South and North America. It builds a large and tightly meshed web (c. 60 cm diameter) at the edges of forest clearings and across paths and streams. The web is U-shaped with the hub close to the upper rim. Often the web is surrounded by a three-dimensional structure of threads that connect to the surrounding vegetation.

\*Corresponding author and present address: Department of Zoology, Universitetsparken B 135, DK 8000 Aarhus C, Denmark.

All our observations and experiments were made on 15 juvenile *Nephila clavipes* (4th to 5th instar after hatching) in the laboratory, where these spiders had been reared from eggs. The spiders were kept under standard laboratory conditions (LD 16:8,  $25 \pm 2^\circ\text{C}$ , RH  $50 \pm 5\%$ ) and reared in individual cages on wild-type *Drosophila melanogaster* raised on enriched baby-food (Milupa formula).

*Drosophila* were released from rearing bottles which were held slightly tilted close behind the web. The web, spider, and flies within 2 cm of the web plane were filmed on  $\frac{1}{2}$  inch video-tape, which was later analysed frame by frame. The recorder was fitted with an electronic clock (1/100 s units) which, with a film speed of 50 frames/s, gave an accuracy of  $\pm 20$  ms per observation. Measurements of distances and angles were made directly on the screen of a 45 cm monitor. Each spider was filmed until it had caught 5 or 6 flies in rapid sequence. The spider was then allowed to feed and the web was destroyed afterwards. When the spider had built a completely new web (*Nephila* often repairs a web), it was used again for the next set of trials. The spiders were filmed three times in each of three states: (i) intact, (ii) with one leg removed, and (iii) with a second leg removed (either the neighbouring leg or the corresponding leg on the other side of the body). Leg loss was effected by inducing the spider to autotomise by squeezing the leg with forceps (Vollrath, 1990).

The first five catching sequences to be completed in each session were incorporated into the analysis. Analysed were:

- reaction times=the time between the moment a fly touches the web and the spider's first slight reaction: tensing up, moving a leg or turning;
- catching times=the time between a fly touching the web and the spider's bite into it;
- reorientation stop distances=every few cm the spiders stopped, tensed their legs, obviously to feel again the vibrations of the fly, and adjusted their direction of pursuit (minimal accuracy: 1 mm);
- initial orientation errors=the deviation of the spider's direction after turning around to face the fly from the true direction of the fly (minimal accuracy:  $1^\circ$ );
- running speed=mean velocity of the spider between starting and catching time, regardless of slowing down for orientation stops, etc. (=distance/(catching time-starting time)) (minimal accuracy: 0.5 cm/0.02 s);
- proportion of flies stuck in the web out of all flies in the vicinity. The camera focused from c. 2 cm before to 2 cm behind the web; all the flies within this distance were likely to either fly into the web or sense it in time to avoid it, and were therefore counted as the total of available flies;
- retention time=(in cases where a fly escaped from the web) the time between the instant of getting stuck and the instant of flying out of the web;
- proportion of reactions to flies "stuck" in the web=only includes those flies that were disturbed in their flight by contact with the web; flies that flew straight through were not counted.

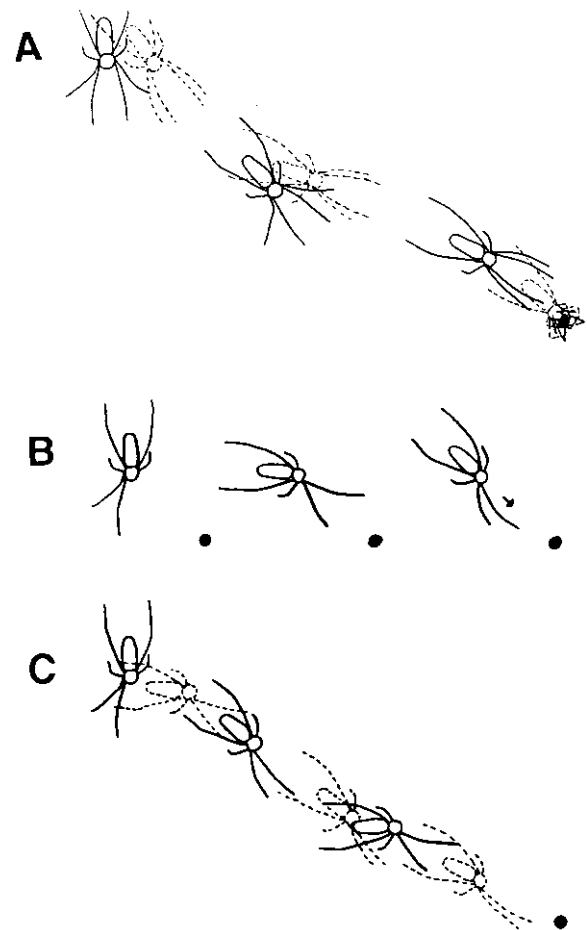


Fig. 1: Prey capture sequence of normal and missing-leg *Nephila clavipes*. **A** Normal with all legs present and occasional reorientation (dotted); **B** Orientation with the two existing front legs; **C** Run towards prey (large dot) with frequent reorientation (dotted) using the existing front legs.

Reaction times and catching times were also measured for intact spiders put into webs built by six-legged spiders (C in ML) and for six-legged spiders put into webs built by intact spiders (ML in C).

Unless indicated otherwise, the data were analysed non-parametrically, usually by Kruskal-Wallis tests, and—unless otherwise indicated—the data on six-legged spiders (–2 legs) refer to spiders that were missing any combination of legs. The data on fly behaviour were collected by playing the tape slowly (1/20 of normal speed) and counting the flies flying, getting stuck in the web, and being caught by the spider.

Our data on reaction times and running speeds with intact *Nephila* conform with one data set collected on *Nephila clavipes* prey-catching behaviour (Klärner & Barth, 1982) but fail to conform with another data set (Hill & Christenson, 1981; Hill *et al.*, 1982). The conforming study used a vibrator and bigger (apparently subadult) spiders. The non-conforming studies used a range of smaller spiderlings and recorded much longer catching times than we did (four to ten times longer with a positive correlation between body size and approach latency). However here *Drosophila* were blown into the webs and the discrepancy from our data probably results from the different method of presenting the flies. We discarded blowing or throwing flies into the webs

because then the flies did not move immediately when they touched the web; and the spiders usually only noticed flies when they started struggling. By letting the flies fly into the web on their own we used an arrangement for examining the spider's behaviour and web functions which was more realistic, albeit extremely time-consuming. Note that using this method we could not determine the weight or size of the flies that came into contact with the web.

### *Nephila* capturing *Drosophila*

With *Drosophila* as prey *Nephila clavipes* uses the catching sequence typical for attacking small Diptera (Robinson & Mirick, 1971; Klärner & Barth, 1982). This is as follows (Fig. 1A): the spider sits in the hub of the web, legs evenly distributed around the body (*c.* 15: 55: 95: 150°). When a fly touches the web the spider is alerted: it flexes the legs pointing towards the prey to tension the relevant radii and improve the transmission of vibratory signals (Klärner & Barth, 1982). If the strength of the vibration matches with the appetitive threshold then the spider turns towards the source of vibration and grips the four leading radii with its two front pairs of legs stretched out far ahead.

If the vibrations are weak or if the fly just sits in the web without moving, then the spider may pluck the radii with its two front pairs of legs to locate it by creating sufficient vibrations itself and “listening” for the “echo” (Klärner & Barth, 1982). When this allows the spider to identify a direction, it starts running towards the prey, stopping frequently (*c.* every 1–4 cm in our spiders) to reorient towards the stimulus with the first two pairs of legs stretched forward, and continues running in the new

Range°	Mean	S.D.	<i>n</i>
0–30	284	385	274
31–80	259	329	226
81–130	234	332	31
131–180	184	140	5

Table 1: Reaction times (ms) of intact *Nephila* towards flies presented at different angles to the spider's body axis. Time resolution 1/100 s;  $\chi^2=9.47$  (12 df), n.s. ( $\chi^2$  calculated for 0–30, 31–80 and 81–130, the group 131–180 contained too few data for this test).

direction until it either reaches the fly or has to reorient again. The fly is then bitten and held with the first three pairs of legs until it ceases to struggle (“long bite”, see (Robinson & Mirick, 1971)). Now the spider pulls the fly out of the web, wraps it and usually carries it up to the hub suspended on a thread held off the web with a fourth leg. Alternatively (rarely in our spiders), the fly may be carried up in the jaws and wrapped at the hub; the carrying behaviour is size dependent and we used smallish immature *Nephila*, not the much larger adults. Finally, the spider fixes the wrapped fly near the hub, cleans its legs and feeds on one of the bundles of prey. The main elements of this sequence are: (1) receiving a vibratory stimulus, (2) turning to face the stimulus and finely adjusting the direction with the front two pairs of legs, (3) running towards the stimulus (reorient, run, etc.), (4) catching the fly, without losing it again, (5) transporting it back to the hub, wrapping, feeding. The following experiments show the influence of leg loss on prey capture. The overall sequence of the main behavioural elements during a capture run did not change when legs were missing. The spider oriented, ran with reorientation, bit, wrapped and returned to the hub.

## Results

Overall there was little difference in the prey capture success of intact spiders and spiders with one or two legs missing (Fig. 2) although there were behavioural differences in attack and prey handling.

*Reaction times:* Normal (8-legged) spiders reacted quickly to flies touching the web, regardless of the angle

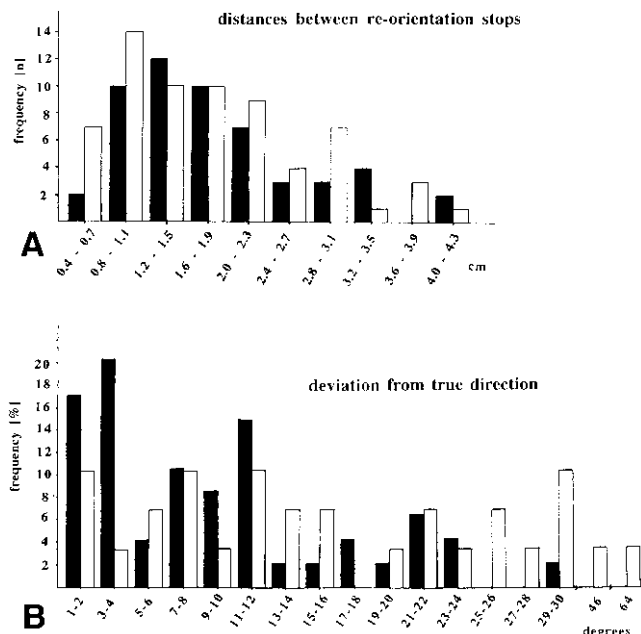


Fig. 2: Reorientation and deviation in normal and missing-leg *Nephila*. Control animals (with all 8 legs) are shown by hatched bars, experimental animals (legs 1 and 2 on the same side missing) by white bars. **A** Distances between reorientation stops in cm; **B** Deviation from the “true” direction pointing from the spider's head towards the prey, in degrees.

	Median	Range	<i>n</i>	<i>N</i>
Normal	120	20–2060	180	15
– 1 leg	140	20–1920	155	12
– 2 legs	120	20–2080	180	15
C in ML	80	20–1680	100	5
ML in C	120	20–3220	36	3

Table 2: Reaction times (ms) of missing-leg *Nephila* towards flies. Because of the non-normal distribution of the data we used non-parametric connotation and tests (Kruskal–Wallis test; normal/– 1/– 2 legs:  $H=5.61$  ( $v=2$ ), n.s.; normal/C in ML/ML in C:  $H=5.05$  ( $v=2$ ), n.s.). “– 1 leg” means that a first leg is missing; “– 2 legs” means that a pair of legs or the first and second leg on the same side are missing; “C in ML” means intact control spiders in webs built by missing-leg (– 2 legs) spiders and “ML in C” means the opposite;  $n$ =trials,  $N$ =spiders.

	Median	Range	n	N
Normal	1180	80–10,810	180	15
– 1 leg	1650	300–12,160	155	12
– 2 legs	1815	260–60,280	180	15
C in ML	1300	220–10,160	100	5
ML in C	1670	460–10,630	36	3

Table 3: Catching times (ms) of normal and missing-leg *Nephila* towards flies. Kruskal–Wallis test; normal/– 1/– 2 legs:  $H=24.03$  ( $v=2$ ),  $p<0.001$ ; normal/C in ML/ML in C:  $H=7.12$  ( $v=2$ ),  $p<0.05$ .

which the fly had to the spider’s longitudinal axis ( $0^\circ$ =straight in front of the spider, Table 1). Thus for these spiders the direction of the stimulus did not influence the reaction speed.

Spiders with legs missing were not slower than normal spiders in detecting a fly (Table 2). It seemed that a spider always covered the area around it as evenly as possible with its legs. So, if there were legs missing, the neighbouring legs shifted their positions a little to fill the “hole”. If only one leg was missing, no real “hole” was visible in the pattern of leg placement when the spider waited for prey. If a first and a second leg on the same side were missing, the remaining legs (especially the small third leg) could not fill the hole properly. Nevertheless, with the remaining legs the spider still reacted extremely quickly to most vibrations (Table 2). Indeed, they reacted equally as fast in good webs made by intact spiders as in inferior webs made by experimental spiders with 2 front legs missing. That these webs were inferior is demonstrated in detail elsewhere (Weissmann & Vollrath, in prep.).

*Catching times:* Spiders with legs missing took significantly longer to catch prey, and it made a difference whether they were lacking 1 or 2 legs (Table 3). Moreover, it seemed that web quality had an effect: (i) control spiders in webs built by ML six-legged (– 2 legs) spiders took longer than control spiders in webs built by control spiders, and (ii) six-legged ML spiders in control webs took about as long as “– 1 leg” spiders in “– 1 leg” webs. Thus, spiders with equal numbers of missing legs did better in normal webs than in irregular webs. This was not due to reorientation stops *en route* but to initial orientation error coupled with differences in running speeds.

*Orientation towards prey:* The distances between reorientation stops in our samples (10 captures each for intact and six-legged spiders) ranged from 0.4 to 4.3 cm ( $n=119$ , both medians 1.6 cm). They did not differ significantly between control and “– 2 legs” spiders

	Median	Range	n	N
Normal	6	0–48	219	12
– 1 leg	8	0–52	259	12
– 2 legs	9	0–114	231	12

Table 4: Initial orientation errors (deviation from “true” direction, degrees). Kruskal–Wallis test: normal/– 1/– 2 legs:  $H=11.13$  ( $v=2$ ),  $p<0.001$ ; all six-legged spiders with a missing pair of legs.

	Median	Range	n	N
Normal	7.89	0.57–29.0	120	12
– 1 leg	5.68	0.73–49.4	120	12
– 2 legs	5.25	0.32–20.4	120	12

Table 5: Running speed (cm/s). Friedman test: normal/– 1/– 2 legs:  $\chi^2=17.03$  ( $v=2$ ),  $p<0.001$ .

(Fig. 2A). There was a significant initial “orientation error” on the hub: usually a spider turned less than was necessary to face the fly precisely. Since the spider’s waiting posture was always head downwards, this meant that the spider faced below the fly; this could be advantageous for the spider should the fly free itself and tumble down the web. There was a clear increase in deviation from the “true” direction if the spider had fewer legs (Table 4, Fig. 2B). The data in Table 4 for “– 2 legs” include only turning angles of six-legged spiders with a pair of legs missing, whereas those in Fig. 2B refer to spiders with 2 legs missing on the same side.

The spiders that lacked legs 1 and 2 on the same side showed an interesting deviation from the behaviour exhibited by all other spiders: they did not try to face the fly directly, but oriented so that the fly was between their remaining first and second legs (Fig. 1B). Clearly, this was not an orientation problem, but can be interpreted as their most efficient alternative for exact determination of directions, since they all turned again and headed straight towards the fly, making their way with the usual reorientation stops. So, what looked like severe deviation (Fig. 1C, Fig. 2B), in reality was a very efficient method of compensation.

*Running speed:* Our data on the spider’s capture behaviour clearly showed that running speed was negatively correlated with the number of missing legs (Table 5).

*Web regularity and prey retention:* A web is supposed to catch and hold prey until the spider can attack and immobilise it. But, as shown elsewhere (Weissmann & Vollrath, in prep.), webs built with fewer than eight legs are wider meshed and less regular than normal webs. Thus differences in web structure are likely to affect a web’s performance and add to any disadvantages the spider encounters because of missing legs.

The first question to ask is whether potential prey (i.e. flies in close proximity to the web), come into prolonged contact with the web. We found that in our experimental set-up 17% of the available flies were trapped by normal *Nephila* webs. Therefore more than 80% of the flies

	Median	Range	n
Normal	17.0	9.2–22.0	14
– 1 leg	21.3	11.6–25.6	25
– 2 legs	18.0	13.1–20.5	9

Table 6: Proportion (%) of flies stuck in web to flies in the vicinity of a web. Vicinity is defined as within 2 cm either side of the web plane. Kruskal–Wallis test: normal/– 1/– 2 legs:  $H=5.499$  ( $v=2$ ), n.s.

	Median	Range	<i>n</i>
Normal	340	20–39,960	226
– 1 leg	380	20–13,240	149
– 2 legs	260	20–11,240	225

Table 7: Retention times (ms). Kruskal–Wallis test: normal/–1/–2 legs:  $H=68.24$  ( $v=2$ ),  $p<0.001$ .

flying around such a web (within a distance of about 2 cm before and behind it) recognise the web in time to avoid it. There was no difference in prey-capture ability between the normal webs and webs built with seven or six legs (Table 6).

Next we examined the length of time that a fly was actually trapped in a web; this is the time available for a spider to run and catch the prey. These retention times decreased significantly (Table 7) in webs which were built with seven or fewer legs (compared with the webs of intact spiders). Retention times were especially short for webs built by spiders with six legs. Note the overlap between retention and catching times for control and six-legged spiders (Fig. 3): normal spiders caught only about the “slower” 50% of trapped flies. Six-legged spiders would catch even fewer flies; this was mainly because (i) the spiders took longer to reach a fly (Table 3), and (ii) the less regular web did not hold the flies as long (Table 7). In none of the following categories did Kruskal–Wallis tests for differences yield significant results; proportion of: (i) spider reactions/flies

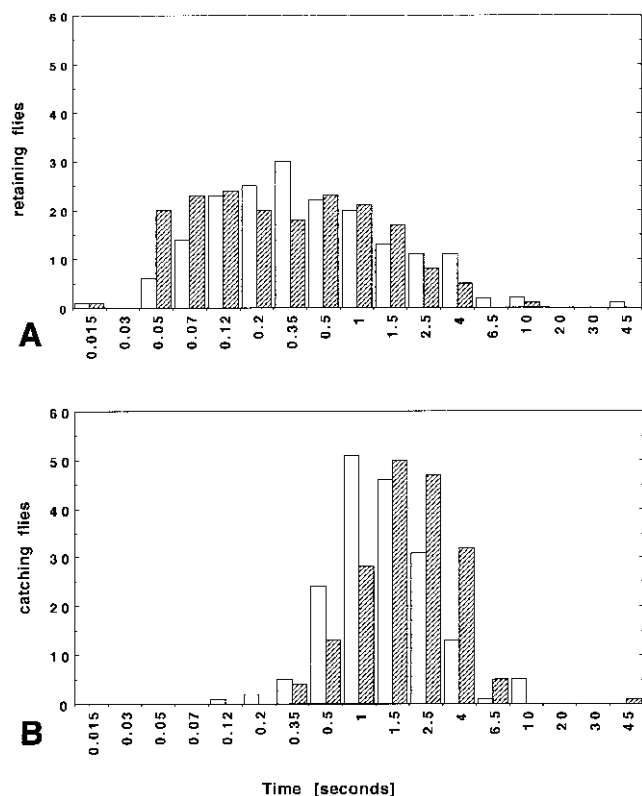


Fig. 3: Number of flies caught by control and experimental *Nephila*. Overlap between retention times of flies in web (A) and capture times of flies by spiders (B) for 8-legged control spiders (white bars) and 6-legged experimental animals (hatched bars). The experimental animals were missing a pair of legs. More details given in Tables 3 and 7.

stuck in the web (28–35%,  $H=2.64$ ,  $v=3$ , n.s.); (ii) flies caught by spider/all flies reacted to (19–25%,  $H=2.68$ ,  $v=2$ , n.s.); and (iii) flies caught/flies stuck in the web (9–11%,  $H=1.69$ ,  $v=3$ , n.s.). Note that all spiders appeared to react to a comparable percentage of arriving flies (c. 28–35%), which suggests (i) that a web transmitted vibrations reasonably independently of its regularity, and (ii) that these vibrations were equally well sensed by the spiders.

## Discussion

Webs built by spiders that had legs missing appeared to fulfil their function well enough to allow the loss of one or two legs not to significantly affect the overall predatory success. Nevertheless, a web built with fewer legs did not hold flies as long as did a normal web. The changes in web quality (irregular spiral geometry, wider average mesh) documented elsewhere (Weissmann & Vollrath, in prep.) can be explained by the lack of building precision shown by spiders with missing legs. This difference is small when only one leg is missing, but it is more apparent when several legs are missing (Weissmann & Vollrath, in prep.). We have shown that such webs are still reasonably good traps. But we have also shown that leg loss has a more depressing effect on the spider's prey-catching behaviour. In particular, three parameters were significantly affected: catching times increased because of higher initial orientation errors and slower running speeds. In brief, although the reaction speed was not impeded, the spider was less accurate in its perception and moved more slowly.

Our data did not show a difference in prey-capture ability between normal webs and webs built by spiders missing either one or two legs. However, our observations gave us the impression (not quantified) that flies may have somehow recognised normal webs a little earlier and therefore avoided them more often than webs built with six legs. This “recognition” effect was apparently counteracted by the “gap” effect, i.e. the relative coarseness of the “missing legs” webs which allowed more flies simply to fly through.

We can conclude that the predatory success of an orb-web spider depends on a variety of identifiable parameters, some of which show significant degradation when a spider loses legs.

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