Positional biases in leg loss of spiders and harvestmen (Arachnida)

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Abstract: Missing legs of spiders and harvestmen were counted in the field. Differences between sexes, species, and larger taxons may give clues to behavioural or anatomical causes of leg loss. Three araneid species (*Zygiella x-notata*, *Lariniodes sclopetarius* and *Araneus diadematus*) showed a significant 1.6 times higher leg loss than a group of 26 spider species from other families and a significant 3.0 times lower leg loss than harvestmen (Opiliones). *Zygiella x-notata* had a significant 1.8 times higher leg loss than *L. sclopetarius*. The araneid group had a significant 2.3 times more frequent anterior-long-leg than posterior-short-leg loss. *A. diadematus* deviated in showing a significantly smaller anterior-posterior difference in leg loss than each of the two other araneids. In harvestmen also a long leg (second or fourth leg) was lost significantly more (2.5 times more frequently) than a short one (first or third leg). In contrast to the front-rear-axis there was not a significant leg loss bias in the left-right axis if the data of the three araneid species were combined. However, *Z. x-notata* alone had a significant 2.6 times higher left than right leg loss. This separate analysis of *Z. x-notata* was justified because the overall divergence between the lateral biases of the three araneid species was significant. In *L. sclopetarius* the females were significantly more (13.6 times) left-biased than males in their leg loss. The significant bias of spiders to lose anterior or long legs rather than posterior or short legs confirms the results of an earlier study on Thomisidae, Lycosidae and Agelenidae (Bauer, 1972).

The present study is the first to show a significant laterality in leg loss of a spider species (*Z. x-notata*) and a significant sex difference in leg loss laterality of another spider species (*L. sclopetarius*).

Keywords: spiders, harvestmen, Arachnida, leg loss, positional biases.

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Introduction

Wild animals that have lacking or lesioned left or right body parts due to predation have been reported e.g. in Cambrian trilobites (significant bias to lesions on the right body side) and whitefish (significant bias to left side lesions due to lamprey attack: see Bradshaw & Rogers, 1993: 18-20). Other than predation-induced lesions such as asymmetric abrasions of the feeding apparatus produced by lateral biases during feeding have been reported from whales (Clapham et al., 1995). A behavioural lateral bias has been suggested to be on the basis of these body lesions but it is not known whether the bias comprises a preferential attack direction of the predators and/or asymmetric coiling of the prey during the attack (Bradshaw & Rogers, 1993).

A behavioural lateral bias in invertebrates that is not related to predation has been reported at the population level in a crab species (right-claw "dominance" with respect to size and behaviour) but since there are many invertebrates known to possess purely anatomical asymmetry at the population level (such as enlarged genital claspers in male bedbugs: see Bradshaw & Rogers, 1993) we suspect that behavioural studies of these invertebrates will show many more behavioural asymmetries at the population level.

In "symmetric" invertebrates of the Apidae (Hymenoptera) a preference in making holes in the left or right side of flowers was demonstrated, i.e. a laterality with reference to the insects' body orientation in space irrespective of the (natural or experimentally changed) orientation of the flowers (Herschel, 1883;

Schmucker, 1930, 1931; Kugler, 1943; Gerner, 1972; Koeman-Kwak, 1973; Westerkamp, 1993). This significant preference (laterality) which may exist at the population level, or only at the individual level, often changes from left to right, or vice versa, in consecutive years, and the change was explained by genetic factors residing in the colony queens and/or by individual experience of the workers. However, the locomotory movements of the apids on the (left-right-symmetric) flowers were right-handed (significant at the population level: Herschel, 1883; Schmucker, 1930).

Westerkamp (1993) points to left-right-asymmetries in the morphology of some flowers that might also lead to asymmetric scent production. This might have caused locomotory left-right asymmetries in the movements of his megachilid, anthophorid, and apid bees once they have landed on the asymmetric flowers (although Westerkamp did not present quantitative data on these movements).

We further refer to Ludwig (1929) who reviewed anatomical morphological and locomotory lateralizations of invertebrates up to protozoans. Chyba (1997) gives a recent account on the ultimate origin of left-right asymmetries of living organisms in general.

In wild spiders (Philodrominae, Lycosidae, and Agelenidae) leg loss has been studied, without, however, distinguishing left from right, by Bauer (1972). He assumes that the original cause of the leg loss has to be sought in an elevated degree of locomotory activity since a much higher frequency of autotomized legs in the highly active *Philodromus* and *Pardosa* was found than in the website bound *Tegenaria*. Also in each of these three spider genera the longest legs were missing most often irrespective of their position on the cephalothorax. Thus, e.g. in *Philodromus* the long second legs were missing most often while the long first and fourth legs were missing most often in *Pardosa*.

Apart from being caused by physical accidents related to high locomotory activity and to predator-attack, biases in leg loss of wild spiders could be caused by attacks from other spiders in inter- and intraspecific fights. Non-behavioural factors residing in the anatomy of the spiders might also be a cause. Thus, the strength with which the different leg types are attached to the cephalothorax could differ and/or there could be a bias in the nerve command producing leg loss (autotomy, i.e. a device by which a leg that is seized or squeezed at the tibia or any more proximal point, is broken off between the coxa and trochanter). Bauer (1972) clarifies autotomy as a “behavioural-positional” factor: “Irritation” initiates autotomy, with the coxa, trochanter, and femur taking up a particular position, whereas the pull of an aggressor at one leg or the counter-pull of the spider does not play a decisive part in the production of autotomy.

In a first attempt to clarify the original cause of the missing legs we counted the number of lesioned or missing legs in three araneid species and many other related and non-related spiders in the wild, keeping records of the position of the legs in the front-rear and in the left-right dimension. This leg loss was further compared with that of wild harvestmen (Opiliones). Furthermore the inter-sexual difference in leg loss was studied in the araneid *Lariniodes sclopetarius* (Clerck).

Materials and methods

Leg loss of harvestmen (Opiliones) and spiders (Araneae) was studied from specimens in their natural habitat without touching or catching them in order to exclude that the missing legs were the result of human interference. In each case the position of the missing legs on the front-rear and on the left-right axis was noted. Intact spiders were also counted in order to compare the proportion of intact specimens in different species. However, only specimens with a single missing leg were considered here, i.e. a small minority of individuals that missed more than one leg was discarded in the present study. Young spiders prior to sexual differentiation were disregarded.

We did not discriminate between different

Table 1. Numbers of wild spiders versus wild harvestmen that missed one leg (incomplete) versus the numbers that did not miss any leg (complete).

	Incomplete	Complete	
Spiders	94	423	$p < 0.001$
Harvestmen	60	76	ns

Table 2. Number of wild spiders missing a left versus the number missing a right leg in three Araneid species.

	Left	Right	
Zygiella x-notata	21	8	$p < 0.05$
Araneus diadematus	14	18	ns
Lariniodes sclopetarius	16	18	ns
Total	51	44	ns

species of harvestmen because we only wanted to compare spiders to harvestmen in general. The most extensive data came from three araneid spider species, i.e. *Zygiella x-notata (*Clerck), *Araneus diadematus* Clerck and *Lariniodes sclopetarius*. The other spider species were mostly determined at species level except for taxa such as *Philodromus* and *Clubiona* which are difficult to discriminate in the field. These spider species are mentioned in table 5. The study was conducted over all seasons in 1995 and 1996.

For statistical testing we used Siegel (1956). Yates-correction was always used in the Chi-square-test applications. Significance was accepted if p was < 0.05 in a two-tailed test.

Heimer & Nentwig (1991) and Roberts (1984, 1995) served as guides to species determinations and relative leg length measurements.

Results

We found a bias in the leg loss of spiders to one side or to front legs depending on the species.

Table 1 shows that there were significantly more complete wild spider specimens than incomplete spiders that lost one leg, i.e. 423 complete versus 94 incomplete specimens ($p < 0.001$). In wild harvestmen, however, this difference was not significant, i.e. 76 complete versus 60 incomplete individuals. The complete/incomplete ratio was significantly higher in spiders than in harvestmen ($p < 0.001$; spider species specified in Materials and methods, and in table 5).

The three investigated araneid spider species *Zygiella x-notata*, *Araneus diadematus* and *Lariniodes sclopetarius* significantly more often lost a leg than the remaining spider species (all from other families) in the wild, i.e. 61 incomplete and 228 complete araneid specimens versus 33 incomplete and 195 complete non-araneid specimens ($p < 0.05$; $\chi^2 = 4.2$; data not shown).

Table 2 shows that there was no significant laterality in the leg loss of the three araneid species as a group, i.e. 51 wild specimens missing a left versus 44 specimens missing a right leg. It can further be seen in table 2 that the araneids *Z. x-notata*, *A. diadematus* and *L. sclopetarius* significantly diverged from each other in the loss of a left versus a right leg (significant interaction between the three species categories and the left-right position of the missing legs: $p < 0.05$; $\chi^2 = 6.0$; df = 2). This significant general disparity between the three araneid species allows for further significance tests concerning only a part of the data set in table 2. It then appears that *Z. x-notata* was significantly left-biased in its leg loss (21 specimens losing a left versus 8 specimens losing a right leg: $p < 0.05$). It further appears that the left-right ratio of missing legs was significantly larger in *Z. x-notata* than in *A. diadematus* (21/8 and 14/18 ratio respectively; $p < 0.05$; $\chi^2 = 4.0$). The difference between *Z. x-notata* and *L. sclopetarius* was only marginally significant ($0.05 < p < 0.10$) and the difference between *L. sclopetarius* and *A. diadematus* was not significant.

Table 3 shows that leg loss laterality significantly depended on the front-rear position of the legs in the three araneid species as a group ($p < 0.05$; $\chi^2 = 11.3$; df = 4 after pooling of the second and third data column). Both in *Z. x-notata* and *L. sclopetarius* there was a significant tendency towards leg loss in the frontal direction ($p < 0.01$) but in *A. diadematus* there

Table 3. Number of wild spiders missing a first, second, third or fourth leg in three Araneid spider species.

	First legs	Second legs	Third legs	Fourth legs	
Zygiella x-notata	17	7	3	2	$p < 0.05$
Araneus diadematus	10	6	5	11	ns
Lariniodes sclopetarius	22	4	2	6	$p < 0.05$
Total	49	17	10	19	$p < 0.05$

was no such tendency. It can further be seen in table 3 e.g. that long (first and second) legs were significantly more often lost than short (third and fourth) legs in the araneids as a group, i.e. 66 long versus 29 short legs ($p < 0.01$; these combined data not shown). Even within the long legs the difference between first and second legs was significant, e.g. 49 first versus 17 second legs in the araneids as a group ($p < 0.01$) and 22 first versus 4 second legs in *L. sclopetarius* alone ($p < 0.01$).

Like spiders harvestmen also had their heaviest losses in the longer (second and fourth) legs, i.e. after pooling left and right losses in each of the four leg loci on the front-rear axis 7 specimens lost a first leg, 25 a second leg, 9 a third leg, and 15 a fourth leg, giving $p < 0.01$ in a X^2-test (df = 3; left and right losses not significantly differing from each other in any of the four body loci; data not shown).

Table 4 shows that wild male *L. sclopetarius* significantly more often lost a right relative to a left leg than wild females of the same species ($p < 0.02$) although the laterality in each sex apart was only marginally significant ($0.05 < p < 0.10$ both in females and in males). The males and females did not significantly differ from each other in the probability of losing an anterior (first or second) relative to a posterior (third or fourth) leg, i.e. the anterior/posterior ratio was 8/3 in females and 12/4 in males (not shown).

Only one other spider species provided enough data for a meaningful analysis of a possible difference in left-right bias (laterality) between females and males, i.e. *Z. x-notata*. In this species the sex difference was far from significant (not shown).

Table 5 gives the leg loss of all investigated spider species in the left-right and the front-rear axis (while including also data of spiders missing a leg after they had been caught). The most important result is the difference in leg loss on the front-rear axis between three-dimensional-web-building species and "hunting" species, i.e. between araneids, linyphiids, tetragnathids, pholcids (web builders) and lycosids, pisaurids, zorids, gnaphosids, clubionids, salticids (hunters). Thus, in the three-dimensional-web builders the front-rear ratio of leg loss (four front legs versus four rear legs) was 140/64, whereas in the hunters this ratio was 12/15 (difference between the two ratios significant: $p < 0.05$), i.e. the web-builders were more likely than the hunters to lose a front relative to a rear leg (see table 5; hunters(h); web-builders(wb)).

Furthermore, the leg losses of the 8 different legs (losses combined for all spiders) below in table 5 significantly deviate from equal losses on all eight body loci (χ^2-test; df = 7; $p < 0.05$). This general difference allows for a further significance test on parts of these data. It then appears that there were significantly more losses of second left than of second right legs (33 versus 16). These significant results show that there is a significant interaction between the influence of the leg position on the front-rear axis and the influence of the leg position on the left-right axis on the causation of leg loss, i.e. the probability of losing a left or right leg is specific for (possibly depends on) the locus of the leg on the front-rear axis, or it is the other way round, i.e. the probability of

Table 4. Number of wild female and male *Lariniodes sclopetarius* missing a left or right leg.

	Left	Right	
Female	9	2	$0.05 < p < 0.10$
Male	4	12	$0.05 < p < 0.10$

Table 5. Number of individuals losing single legs on different positions and number of intact individuals of all spider species observed in the wild (L1 indicating the first \leg on the left side, R1 the first leg on the right side, etc,). Not only spiders missing a leg before capture but also spiders showing single-leg loss after capture were included in this table. The number of the post-capture specimens was only substantially large in *Enoplognatha ovata*. A few spiders having one leg that was hurt (leg held in an abnormal orientation while not moving and often lost afterwards in captivity) were also included (while always excluding spiders that had two or more legs hurt and/or lost). wb = web builder; h = hunter; oc = outside category (species falling outside h and wb categories)

Species	Leg Positions								Sum		
	L1	R1	L2	R2	L3	R3	L4	R4	Incomplete	Intact	
Zygiella x-notata (Clerck)	15	5	4	3	3	0	1	1	32	70	wb
Araneus diadematus Clerck	6	10	7	2	1	6	7	8	47	126	wb
Lariniodes sclopetarius (Clerck)	8	14	3	1	0	2	5	2	35	139	wb
Nuctenea umbratica (Clerck)	0	2	0	0	0	0	0	0	2	4	wb
Linyphia hortensis Sundevall	1	0	0	0	0	0	0	0	1	41	wb
Neriene montana (Clerck)	0	3	0	0	0	0	0	0	3	171	wb
Gonatium rubellum (Blackwall)	0	1	0	0	0	0	0	0	1	7	wb
Diplostyla concolor (Wider)	0	0	0	1	0	0	0	0	1	4	wb
Diplocephalus cristatus (Blackwall)	0	0	1	1	1	0	0	0	3	29	wb
Lepthyphantes nebulosus (Sundevall)	1	1	0	1	0	0	0	0	3	20	wb
Tetragnatha montana Simon	0	0	0	0	0	0	1	0	1	157	wb
Pachygnatha clercki Sundevall	0	0	0	0	1	0	0	0	1	38	wb
Theridion sp.	3	2	0	0	1	1	0	0	7	24	wb
Enoplognatha ovata (Clerck)	6	9	6	1	0	1	6	4	33	145	wb
Achaearanea tepidariorum (C. L. Koch)	1	0	0	0	0	1	2	1	5	22	wb
Steatoda grossa (C. L. Koch)	1	1	0	0	1	0	0	0	3	32	wb
Steatoda phalerata (Panzer)	0	0	0	0	0	0	0	1	1	0	wb
Pholcus phalangioides (Fuesslin)	9	7	2	3	0	1	2	1	25	38	wb
Segestria bavarica C. L. Koch	1	0	0	0	0	0	0	0	1	11	oc
Nigma puella (Simon)	1	0	0	0	0	0	0	0	1	0	oc
Amourobius similis (Blackwall)	0	0	0	1	0	0	0	0	1	16	oc
Tegenaria sp.	3	1	1	1	2	0	0	0	8	37	oc
Textrix denticulata (Olivier)	0	0	0	0	1	0	2	0	3	26	oc
Pardosa sp.	0	0	1	0	0	0	1	2	4	51	h
Trochosa sp.	1	2	0	0	0	1	0	1	5	15	h
Pisaura mirabilis (Clerck)	0	0	2	0	0	0	0	0	2	6	h
Zora spinimana (Sundevall)	0	0	0	0	1	0	0	1	2	21	h
Xysticus sp.	0	1	1	0	0	0	1	0	3	39	oc
Philodromus sp.	2	1	5	0	3	1	0	0	12	49	oc
Micaria pulicaria (Sundevall)	0	0	0	1	0	0	0	0	1	11	h
Zelotes latreillei (Simon)	0	0	0	0	0	0	1	0	1	10	h
Clubiona sp.	1	1	0	0	0	0	2	1	5	569	h
Marpissa muscosa (Clerck)	0	1	0	0	0	1	0	0	2	9	h
Salticus scenicus (Clerck)	1	0	0	0	0	0	1	1	3	29	h
Heliophanus sp.	1	0	0	0	0	0	0	0	1	3	h
Salticid sp.	0	0	0	0	0	1	0	0	1	3	h
Sum	62	62	33	16	15	16	32	24	260	1993	

losing a leg on a particular locus of the front-rear axis depends on whether it is a left or a right leg.

Discussion

The frequency of leg loss per se without regard to leg position (table 1) was significantly higher in wild harvestmen than in three wild araneid spider species as a group, which on their turn had a significantly higher leg loss than a group of 26 wild spider species from other families. In harvestmen this finding could be expected because they even lose legs when gently handled by humans. But we have no explanation for the unexpected higher incidence of leg loss in the three araneid species than in other spiders, nor do we have an explanation for the fact that some spiders (especially so *Meta segmentata* (Clerck), *Steatoda grossa* (C.L. Koch), *Steatoda bipunctata* (Linnaeus), *Pachygnatha degeeri* Sundevall, and *Pachygnatha clercki* Sundevall, showed an extremely low, if not completely non-existing, incidence of leg loss in the wild. The *Pachygnatha*-species even did not show leg loss when fighting inter-specifically in the wild or in the laboratory (experiments presently conducted).

With regard to the position of the leg losses the main findings were as follows:

(1) The three main investigated araneid species in the wild, i.e. *Zygiella x-notata*, *Araneus diadematus* and *Lariniodes sclopetarius*, did not show a significant laterality of leg loss as a group. However, they significantly diverged from each other in degree of leg loss laterality (table 2). In one of them, i.e. *Z. x-notata*, the laterality was significant and consisted of a higher left than right leg loss. A significantly higher left than right leg loss was also found in the second legs of all spider species combined (table 5).

(2) There was a significant divergence between the three araneid species in the incidence of leg loss on the front-rear axis (table 3). The long legs (first and second legs) were lost significantly more often than the short legs (third and fourth legs) both in the araneids as a group and in *Z. x-notata* or *L. sclopetarius* alone, but not so in *A. diadematus*. In *L. sclopetarius* the inclination towards a frontal bias in leg loss was extreme since its first legs were more than 5 times as often lost as its second legs. In harvestmen the long legs (second and fourth legs) were also lost significantly more often than the short (first and third) legs. In all three-dimensional-web-building spiders combined (more than 15 species in table 5) the bias towards front-leg loss was significantly larger than in all "hunting" species combined.

(3) *L. sclopetarius* was also extreme in the difference between males and females because there was a significantly stronger bias towards right- relative to left-leg loss in males than in females (table 4), whereas such a sex difference was far from significant in the two other araneid species (*A. diadematus* and *Z. x-notata*). Although the sexes in *L. sclopetarius* did differ in leg loss laterality, they did not importantly differ from each other in the positions of leg loss on the front-rear axis.

The finding of laterality of leg loss at species level (left-leg loss preponderance in *Z. x-notata*) is new to spiders. It may also be new to invertebrates possessing anatomical symmetry because the invertebrate lateralities that have been demonstrated at species level pertain only to species possessing a clear anatomical asymmetry (such as the genital claspers of male bedbugs: see the review of Bradshaw & Rogers, 1993). Although large anatomical differences between left and right legs of spiders are not known, small differences might still exist. We have no explanation for the general higher incidence of second left than of second right leg loss in the data of all our investigated spider species combined (table 5).

A bias to long-leg loss in the wild as in the present study has also been found in three spider families in which the longer legs are not always the anterior legs (thomisids, lycosids, and agelenids: see Bauer, 1972). Our study sustains the importance of leg length as a factor that increases the probability of leg loss. The non-araneid families that we investigated as a group (11 families comprising 26 species) also shared a significant bias to losing anterior legs (in spite of the fact that in a minority of these non-araneid species the four anterior legs were not the longer legs). But if "hunting" species (which typically have long rear legs) were contrasted to three-dimensional-web-building species (having typically short rear legs) the hunters, indeed, appeared to be significantly more prone to lose a long rear leg than the web-builders did (table 5).

Harvestmen (Opiliones) were similar to spiders in that they also showed a significant bias to lose a long (second or fourth) leg. Also the weak (non-significant) bias to left-leg loss of harvestmen resembled the weak left bias of spiders in general.

Perhaps the most unexpected finding was

that female *Lariniodes sclopetarius* were significantly more left-biased than males in their leg loss. Do females of this species have relatively longer left legs than males? This is one thing that should be investigated in the future. But, of course, there are other factors than leg size that could explain the differential leg loss, i.e. (1) differences in the strength of the joints connecting the left and right legs to the cephalothorax, (2) differences between nerve inputs on the left and right legs, (3) "behavioural" factors involving a different orientation of the left and right legs (or their joints) with respect to the cephalothorax axis so as to facilitate autotomy (see Bauer, 1972), and (4) other types of behavioural factors such as a preferential exposure of a particular body side to potential predators when the spiders or harvestmen are attacked in the wild, a preference in the predators themselves to attack from one side, or simply a bias to move the legs of one side more than the other. There are no data or suggestions so far on left-right or front-rear differences in the joint strength or nerve command in spiders or harvestmen that could explain the high incidence of left-leg and long-leg loss that were found. A possible factor that should perhaps be investigated first is related to the particular orientation of leg parts that is needed in order to produce autotomy (Bauer, 1972) because this author explicitly mentions that neither a strong force put on a spider leg (probably mimicking a predator attack) nor a strong counter-pull of the spider itself, is important for producing autotomy. Autotomy has been reported from several spider families (e.g. lycosids, thomisids, agelenids: Bauer, 1972; oxyopids: Formanowicz, 1990; salticids: Jackson, 1990; pholcids: Maughan, 1978; salticids and others: Wells, 1988).

Breland (in Bauer, 1972) hypothesized that legs broken off at the patella-tibia joint would occur especially often in spider species with relatively long legs, whereas whole legs that are broken off at the coxa-trochanter joint would be more typical for shorter-legged spiders. A small part of our leg losses were in fact partial (legs broken off at the patella-tibia joint). A striking peculiarity of these partial leg losses was that they occurred significantly more often in linyphiid spiders than in the remainder of the spider species combined. We do not know whether this sustains the hypothesis of Breland because our partial leg loss was especially frequent both in a rather short-legged linyphiid (*Diplocephalus cristatus* (Blackwall)) and in a rather long-legged linyphiid (*Lepthyphantes nebulosus* (Sundevall)). Clearly the hypothesis is contradicted by the extremely long-legged *Pholcus phalangioides* (Fuesslin) (Pholcidae) in which we and also Bauer (1972) only found cases of whole legs that were broken off and never partial leg loss.

Before going further into differences in leg loss between spider taxa our current research concentrates on the proximate causes of leg loss of spiders in two ways: (1) how the lost legs' position on the body of wild specimens differs from specimens that were victimized in laboratory fights with other spiders, and (2) how the leg loss of spiders before capture from the wild differs from the legg loss after capture. If the fighting-induced leg loss resembles the natural loss more than the capture-induced loss, this would sustain the importance of natural fights between spiders as a cause of their leg loss. Alternatively, if the leg loss of captured spiders would mimic their natural loss more than the leg loss of fighting spiders, this would point to the importance of physical accidents (and perhaps also capture attempts by large predators) as causes of the natural leg loss. The leg loss of a species showing very few leg losses *(Tetragnatha montana* Simon) may be instructive here because wild specimens showed only losses of rear legs (two males: one missing the four rear legs, and the other missing a part of the fourth left leg) whereas the only specimen with a capture-induced leg lesion out of several hundreds of conspecifics, i.e. a juvenile *T. montana*, showed a first right leg with a severely hurt coxa-trochanter joint, i.e. the leg was directed backwards and completely motionless when the spider was running. The difference between natural and capture-induced leg lesion in *T. montana* supports the assumption that the causes of natural leg loss are not physical accidents (that were probably mimicked by our capture procedure) but have to be sought elsewhere, i.e. probably in aggressive encounters with other spiders. We do not see how other invertebrates than spiders could cause leg loss in spiders except perhaps for ants. Spiders that encounter other spiders as well as ants in the laboratory should tell us more about the causes of their natural leg loss.

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