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Stick insects (Phasmida) as prey of spiders: size, palatability and defence mechanisms in feeding tests

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Summary. The maximum body length of the phasmid *Carausius morosus* which the ctenid spider *Cupiennius salei* can overwhelm is 2–3× larger than the length of crickets. Eight phasmid species were offered to *Cupiennius salei* in feeding tests. Among them, *Carausius morosus* was raised on 4 different food plants. All species of prey items were accepted by the spider predator very readily (>80%). This indicates that phasmids are a highly palatable prey group for spiders. The possible importance of chemical defence and its obvious lack under laboratory conditions are discussed.

Key words: Phasmida – Spiders – Araneae – Ctenidae – Feeding tests

Phasmida occur in most terrestrial ecosystems with the exception of the northern and southern parts of the globe in approx. 2500 species and with locally high densities (Carlberg 1986). Nevertheless, field observations on enemies of stick insects are only anecdotical and concern primarily parasites and vertebrate predators (e.g. Bedford 1978). For spiders, a polyphagous and common group of invertebrate predators, practically no prey records of phasmids are known. Robinson and Robinson (1973) and Robinson and Lubin (1979) report single cases of predation by psechrids and the araneid *Nephila maculata* (1 phasmid among >6000 prey items) in New Guinea. During a 12-month-investigation of the prey of 4 orb weaving spiders in Panama, no phasmids could be found among >12000 prey items (Nentwig 1985). In the literature no records at all exist for wandering spiders. Some phasmid species possess very powerful chemical defensive glands against predators (e.g. Eisner 1965), some are able to vomit their gut contents when attacked (Sivinski 1980) and additional techniques of chemical defence are known from other insect groups and could occur in phasmids as well (Blum 1981). However, probably a majority of species are a suitable food for a wide range of insectivorous animals (if the observations which have often been made in zoos with some species can be generalized). It remains, therefore, somewhat enigmatic as to why nothing is known about predation by spiders upon phasmids. To clarify this point feeding experiments were performed with several phasmid species and one spider species which are reported here.

Material and methods

Eight species of stick insects were included in the feeding experiments: *Carausius morosus* (de Sinéty) (Lonchodidae); *Sipyloidea sipylus* (Westwood) (Necrosciidae): *Anisomorpha buprestoides* (Houttuyn in Stoll), *Paraphasma rufipes* (Redtenbacher) (Bacunculidae); *Baculum thaii* Hausleithner, *Baculum extradentatum* (Brunner von Wattenwyl), *Extatosoma tiaratum* (MacLeay) (Phasmatidae); *Heteropteryx dilatata* Parkinson (Bacillidae). The phasmids derived from several laboratory cultures, were kept under suitable conditions in wide screen cages and fed primarily with bramble (*Rubus* sp., Rosaceae). *Paraphasma rufipes* could only be fed with privet (*L igustrum vulgare* L., Oleaceae). To test a possible influence of the stick insects' food plant on the acceptance rate of stick insects by predators, groups of *Carausius morosus* were alternately fed with lime (*Tilia* sp., Tiliaceae), hazel (*Corylus avellana* L., Corylaceae) or ivy (*Hedera helix* L., Araliaceae). As spider predator we used *Cupiennius salei* Keyserling (Ctenidae), a neotropical wandering spider of which a permanent laboratory culture exists.

Spiders (total N 80–100) were kept individually in plastic boxes and fed for several days with a small cricket (*Acheta domesticus* (L.)) to bring them to an "average degree of hunger". When the feeding experiment started one phasmid per spider and day was offered, the next day the remains or the refused insect were replaced by a new phasmid. A refused phasmid was followed by a smaller item, an accepted phasmid was followed by a larger one. For the palatability tests different species or differently fed *Carausius morosus* were offered on consecutive days and the phasmids varied between 50 and 150% of the spiders' body length. This led to a feeding regime in which prey sizes and prey composition tended to cluster around the optimum prey size or palatability range. The days in which a spider moulted and the days before and after moulting were not taken into consideration. For more technical details, see Nentwig and Wissel (1986).

Table 1. Acceptance rate (%, N) of the phasmid *Carausius morosus* raised with 4 different food plants by the spider *Cupiennius salei* in feeding tests

Phasmid instar	Food plant species			
	Tilia	*Rubus*	*Corylus*	*Hedera*
1	85.5 (55)	96.0 (25)	90.9 (22)	–
2	91.3 (23)	87.0 (23)	88.5 (26)	–
3	96.4 (28)	100 (16)	95.0 (40)	95.2 (21)
4	82.2 (45)	100 (17)	100 (10)	92.0 (25)
5	100 (11)	100 (4)	–	–
$\bar{x}$	88.3 (162)	95.3 (85)	93.9 (98)	93.5 (46)

Table 2. Acceptance rate (%, N) of 8 phasmid species by the spider *Cupiennius salei* in feeding tests

Phasmid species	Instar	%	N
Carausius morosus	1–adult	91.6	391
Baculum thaii	1–3	87.5	72
Baculum extradentatum	1–adult	80.0	25
Sipyloidea sipylus	1–adult	82.2	45
Anisomorpha buprestoides	1–adult	81.8	11
Extatosoma tiaratum	1–3	84.6	13
Heteropteryx dilatata	1–4	73.7	28
Paraphasma rufipes	3	100	2

Results

Palatability

The first 5 instars of *Carausius morosus* were accepted by *Cupiennius salei* with an average of 91.6% (range 88.3–95.3%) and no significant difference (chi^2-test of Brandt and Snedecor) between the 4 food plant groups or between instars could be found (Table 1). In a comparison of 8 phasmid species high acceptance rates from 74–92% (when excluding the 100% ($N=2$) for *Paraphasma rufipes*) were found (Table 2). *Heteropteryx dilatata* (73.7% accepted; $p<0.001$) and *Sipyloidea sipylus* (82.2% accepted; $p<0.05$) showed significantly lower acceptance rates then the most frequently accepted *Carausius morosus* (91.6%); the other phasmid species did not differ significantly (chi^2-test of Brandt and Snedecor).

Body size

A cricket of 200 mg body weight has an average body length of 20 mm. Stick insects of 200 mg measure 50–70 mm in length (Fig. 1). The acceptance rate of crickets decreases between 100 and 150% of the spider's body length from approx. 50% to zero (Fig. 2). This indicates that *Cupiennius salei* prefers prey items which are smaller than the spider itself and that it is not able to overwhelm items which are much larger than the spider. In the case of stick insects, however, *Cupiennius salei* preys successfully on much larger items. Phasmids up to 350% of the spider's body length are accepted in more than 80% of cases, only items larger than 400% cannot be subdued (Fig. 2).

Discussion

Palatability and chemical defence

The herein reported feeding experiments show that several phasmid species are obviously a palatable food for

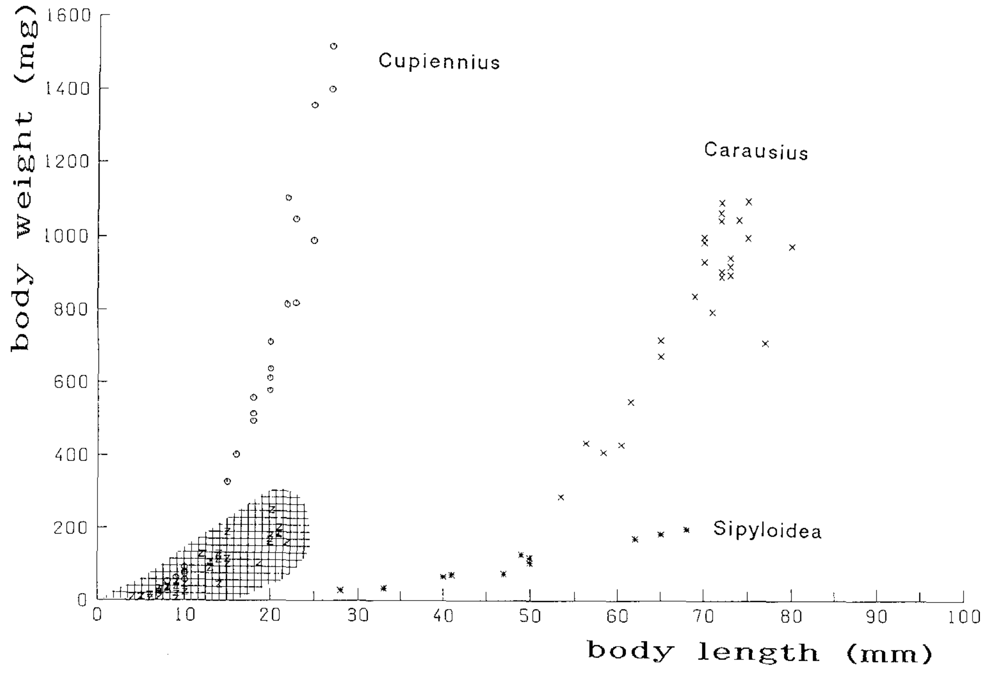

Fig. 1. The relation between body weight (mg) and body length (mm) for the phasmids *Carausius morosus* and *Sipyloidea sipylus*, the spider *Cupiennius salei* and the cricket *Acheta domesticus* (*hatched area*)

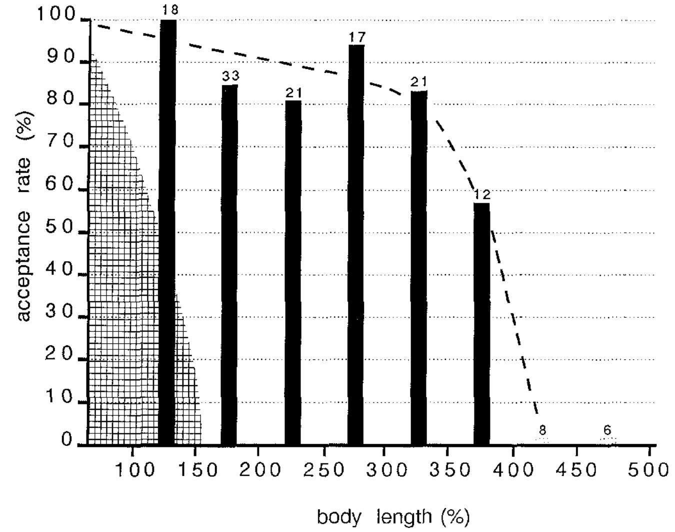

Fig. 2. Acceptance rate (%) of the phasmid *Carausius morosus* by the spider *Cupiennius salei* versus body length (measured as % of body length of the spider) in feeding tests (*black bars*); the hatched area indicated the acceptance rate of the crickets *Acheta domesticus* by the spider *Cupiennius salei* (from Nentwig and Wissel 1986)

Cupiennius salei. Additionally, a nutrition with different food plants does not influence the acceptance rate of *Carausius morosus*. Although the chemistry of food plants may affect the poisoness of phytophagous arthropods (e.g. Emden 1972; Blum 1981) and although the polyphagous species *Carausius morosus* shows a remarkable inducable food plant preference (Cassidy 1978) no repellent or avoidance effects could be found which affected the spider predator. Some of the tested food plants (e.g. *Hedera helix*) contain chemical substances which are able to deter potential predators (Blum 1981; Abrahamson 1988); in the here presented study, however, no effect could be found. In earlier feeding tests *Cupiennius salei* was compared with 6 other wandering spiders and was shown to be an extremely polyphagous predator with an overall acceptance rate of 77.5% in a test of 30 arthropod groups (Nentwig 1986). Thus, even the less-preferred phasmid species (e.g. *Heteropteryx dilatata*) are still eaten to a relatively high amount.

The complete lack of an effective chemical defence of the phasmid species tested here is astonishing because several phasmids are known to secrete strong and irritating substances. *Sipyloidea sipylus, Extatosoma tiaratum* and *Anisomorpha buprestoides* defend themselves successfully against laboratory rats (Carlberg 1987); Carlberg (in press) mentions the chemical defence secretion of *Heteropteryx dilatata* and Eisner (1965) found the *Anisomorpha buprestoides* secretion to deter ants, beetles, mice and jays. According to Table 2, these species have a lower acceptance rate (73.7–84.6%, mean value 80.6%) by *Cupiennius salei* than the *Caurausius* and *Baculum* species which lack any chemical defence (acceptance rates 80.0–91.6%, mean value 86.4), this difference, however, is neither convincing nor significant.

One explanation for this discrepancy may be the ontogenetic stage of the phasmids tested: it could be possible that a species produces its defensive secretion only as adults and that juveniles are relatively unprotected. But *Sipyloidea sipylum* and *Anisomorpha buprestoides* were tested by me also as adults (and eaten by *Cupiennius salei*) and *Anisomorpha buprestoides* prossesses functional defence glands already in the first instar (Eisner 1965). According to Carlberg (personal communication) all species studied by him were equipped with chemical defence from the first day when they left the egg.

Another explanation concerns the physiological difference between stick insects raised in captivity and those which grow up in the field. It is possible that the (at least partly unknown) food plant spectrum influences the chemical defence of phasmids and that phasmids in captivity never produce the same quantity (and quality) of defensive secretion as they do under natural conditions (Eisner, personal communication). It is, therefore, necessary to know more about the food plant range of phasmids and about their chemical defence under natural conditions.

Probably a much more effective defence mechanism of phasmids is their cryptic appearance and their thanatosis (reviewed in Bedford 1978; Carlberg 1986). Under laboratory conditions especially feigning death prevented the stick insects for many hours from being attacked. In field situations this could mean that phasmids are less often preyed upon by spiders than their palatability suggests.

Body size

Feeding tests of phasmids of varying body size reveal that spider predators do not treat them like other insects such as crickets. Phasmida are several times longer than crickets of the same body weight. The successful predation of *Cupiennius salei* on very large stick insects indicates, therefore, that the factor body weight is probably much more important than the factor body length. According to Nentwig and Wissel (1986) the maximal body length of prey items (crickets) is 300% for wandering spiders (excluding mygalomorph spiders), 500% for web-building spiders and 1000% for social spiders (spiders' body length = 100%). Since these spiders measure (approx. maximal values) 2–3 cm, 2–3 cm and 1 cm, respectively, the largest prey items measure (maximal values) 6–9 cm, 10–15 cm and 10 cm. Since *Cupiennius salei* accepts phasmids which are 2.5 × larger than crickets the largest phasmid prey for the other spider groups (if this extrapolation is justified) may measure up to 37.5 cm (2.5 × 10 – 15 cm). This includes nearly all phasmid species and indicates that the extreme body size of phasmids will not prevent most spider group from preying on them. Feeding experiments with these spider groups could prove these calculations, field observations, however, are required much more.

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