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Differential efficacy of toxic pederin in deterring potential arthropod predators of *Paederus* (Coleoptera: Staphylinidae) offspring

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Abstract This study investigates the effects of pederin, a hemolymph toxin that is accumulated in the eggs of most *Paederus* females, on potential arthropod predators of the offspring of *P. fuscipes* and *P. riparius*. Insects generally do not respond to pederin present in the prey. *Paederus* larvae are sufficiently agile to escape from these predators by running away, and the eggs are hidden by the females. Unlike insects, (wolf) spiders are deterred by prey with pederin. They turn away from larvae they have already captured and exhibit cleansing behavior. Larvae containing pederin survive the attacks of spiders without damage, whereas larvae descended from females that do not transfer pederin into their eggs are often killed and eaten. In the case of sudden attacks by spiders, the larvae have no chance of escape. Their survival thus depends on chemical defense. These investigations show for the first time why pederin might be of considerable importance for *Paederus* in the field.

Key words Pederin · *Paederus* · Arthropod predators · Chemical defense · Lycosidae

Introduction

Especially in the tropics, rove beetles of the genus *Paederus* notoriously affect the health of people. Adult beetles often fly away from their natural breeding grounds and are attracted by the lighting of human habitations. In trying to drive them away, people often crush the beetles against their skin so that *Paederus* hemolymph is released. This fluid contains a unique toxic amide, called pederin (Pavan and Bo 1953), which causes itching lesions. As this kind of dermatitis

appears only several hours after topical contact with *Paederus* hemolymph, the cause is not easily recognized (Gelmetti and Grimalt 1993). Occasionally epidemics are observed when weather permits multiplication of *Paederus*, and so there is an extensive literature devoted to this phenomenon (Frank and Kanamitsu 1987).

Although attention has focused on this toxin's effects on humans, some authors have directed their effort towards the general question of the possible selective advantage of pederin. From these investigations we know that pederin is highly cytotoxic, because it inhibits mitoses in eukaryotes by blocking the synthesis of proteins at the ribosomes of eukaryotic cells, whereas prokaryotes are not impaired (Pavan 1963; Soldati et al. 1966; Tiboni et al. 1968). In spite of these severe effects, pederin has not been shown to be of selective advantage to *Paederus* beetles. Intriguingly, they do not show reflex bleeding as do other beetles that have toxins in their hemolymph (Coccinellidae, Meloidae), but have to be injured before they release the hemolymph containing pederin (Pavan and Valcurone Dazzini 1971). As most *Paederus* adults are vividly colored compared to other staphylinids, authors currently hypothesize that aposematism accounts for the presence of the toxin (Dettner 1987; Frank and Kanamitsu 1987). However, pederin, in combination with adult *Paederus* coloring, has not been proved effective in producing learned avoidance by mammals or birds. One problem with this hypothesis is that pederin is destroyed by hydrochloric acid present in the stomachs of potential vertebrate predators (Quilico et al. 1961; Pavan 1963). Therefore, pederin appears to be of no defensive value for *Paederus* (Pavan 1963), and no contradictory evidence has yet been produced (Pavan 1982).

Up to now most research has been aimed at *Paederus* adults as they are easily available. In a study of the allocation of pederin during the lifetime of *Paederus* and consequently extending the scope to all developmental stages (Kellner and Dettner 1995), we found

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that the toxin is obviously biosynthesized by females, which accumulate it in their eggs. After the larvae hatch, they retain all the toxin that was in the egg (about 1–1.5 µg pederin per specimen); it is not lost with egg-shell or exuviae. Although larval stages possess the same amount of pederin as eggs, it is diluted considerably due to growth. An unexpected aspect of this maternal pederin transfer is female polymorphism: most females (90%) transfer pederin into every egg and are thus called (+)-females whereas the others, termed (–)-females, are not capable of biosynthesizing pederin. These (–)-females lay eggs lacking the toxin, with only the first eggs sometimes containing minute quantities. Quantitative data on the two types of females and their offspring are summarized in Fig. 1. The larval developmental stages and adult males do not increase their pederin content by biosynthesis but will sequester pederin if they prey on (+)-specimens. In view of this allocation of pederin, the offspring might be the key to our understanding of the significance of this unique amide to the genus *Paederus*. It is notable that probable enemies of the offspring are quite different from the presumed enemies of adults. Arthropods are known to prey on *Paederus* offspring presented to them whereas adults are left unharmed (Kurosa 1958). The two types of offspring produced by the females provide an unprecedented opportunity to test whether pederin influences the outcome of encounters with potential arthropod predators. Therefore, we presented developmental stages of two *Paederus* species to co-occurring arthropod predators in order to determine whether they

are accepted as prey and whether the outcome of encounters with these potential predators differs between (+)- and (–)-offspring. We show that the reaction of arthropod predators is not uniform. By offering laboratory prey with artificial pederin content we show that the aversion to (+)-offspring is due to their containing the amide.

Materials and methods

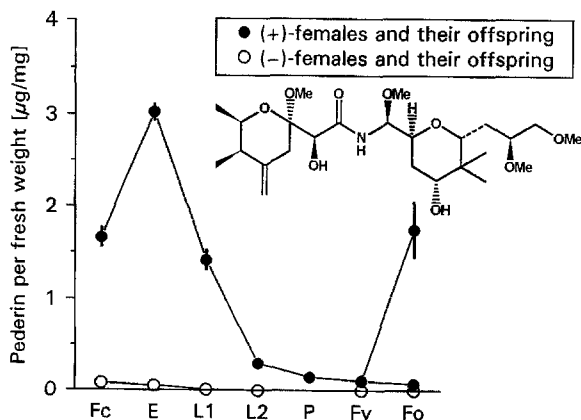
Paederus sites

In northeastern Bavaria (Germany) the two *Paederus* species chosen, *P. fuscipes* Curtis 1826 and *P. riparius* (Linné 1758), live in separate habitats. Some of the known sites were regularly visited in 1993 in order to collect adult *Paederus* and potential arthropod predators. *P. fuscipes*, which inhabits open banks, was studied in two gravel-pits near Kulmbach and Schwarzenfeld respectively, where it is found on fine-grained sediment deposited by man after washing of the gravel. These areas were bare in spring, and weeds grew there during the summer. From May to August, when *P. fuscipes* is present, the two sites were visited alternately every 2–3 weeks. By contrast, *P. riparius* inhabits marshes and swamps covered with dense vegetation. A sedgy meadow near Weiden i. d. Opf. was investigated weekly during the main active period of *P. riparius*, i.e., in April, May, and September, and also from time to time in summer.

Developmental stages of *Paederus*

After transport to the laboratory the beetles were split up into pairs. As breeding cages we used plastic boxes (10 × 10 × 5.5 cm) with a layer of plaster, some flowerpot fragments and moist cotton in a small dish. The beetles were allowed to feed ad libitum on *Drosophila melanogaster* (strain vg) and honey water. They were kept in a climate chamber at 20 °C, with a photoperiod of 15L:9D. For several weeks the females laid one to five eggs per day, preferentially into the moist cotton. The available eggs were removed from the breeding cages daily or every other day. Kept on moist absorbent paper they hatched after about one week at 20 °C. The larvae had to be separated in small petri dishes (3.5 cm diameter) in order to prevent cannibalism. Frozen *Drosophila* flies were supplied twice a day and the leavings of the last feeding were taken out. Under these circumstances the first larval stage (L1) takes about 1 week until it molts into the second stage (L2), which will pupate after two further weeks. The body length of *P. riparius* L1 is 2.1–4.3 mm, that of L2 3.8–6.8 mm, with *P. fuscipes* being negligibly smaller.

Fig. 1 Fluctuation of pederin concentration throughout the development of *Paederus riparius* ($\bar{x} \pm \text{SEM}$). Males are not represented as they simply store the toxin received maternally. Two types of females are distinguished, according to their ability to enrich pederin or not, which we designate (+)-females and (–)-females respectively. The females that are descended from (+)-females split into (+)-females and presumptive (–)-females. Pederin data are derived from Kellner and Dettner (1995), but here are presented as relative amounts because this measure has to be considered when we assess pederin efficacy in developmental stages (*E* eggs, *Fc* collected females, *Fo* older females, *Fy* young females, *L1* larvae 1, *L2* larvae 2, *P* pupae)



Biotests with arthropods

Potential arthropod predators, which were all collected from *Paederus* sites, were chosen in order to represent distinct taxa. They were determined according to the following keys: Staphylinidae (Lohse 1964), Carabidae (Freude 1976), Formicidae (Kutter 1977; Seifert 1988), Heteroptera (Wagner 1966) and Araneae (Locket and Millidge 1951; Roberts 1985; Heimer and Nentwig 1991). Species names are adopted from the most recent literature cited. It should be mentioned, however, that the ant species here called *Myrmica rubra* Linné (after Seifert 1988) is *M. laevimodis* Nylander *sensu* Kutter (1977).

Predator specimens were kept in petri dishes of different sizes (3.5 cm and 9 cm diameter) and plastic boxes (10 × 10 × 5.5 cm), all fitted out with a layer of moist absorbent paper. As standard food

we used living or frozen *D. melanogaster* flies. Predators were tested by introducing developmental stages of the respective *Paederus* species. Since these developmental stages were descended from certain females that transferred an appreciable amount of pederin either into every egg or into none, their pederin content could be predicted by extracting siblings and chemically quantifying the amount of pederin present in the extracts (Kellner and Dettner 1995). The offspring of each female were hence classified as (+)-offspring containing pederin or (–)-offspring without pederin, before using them in the experiments. These were carried out in the climate chamber already mentioned (20 °C, 15L/9D) under a lighting installation (Zumtobel) with three fluorescent tubes (Osram white L58 W/25). Statistical tests were performed using the software package CSS (StatSoft Inc., Tulsa, Oklahoma, release 2.1).

Individual specimens of insect predators were given access either to (+)-offspring or to (–)-offspring of *Paederus*. After putting (+)-offspring (eggs or larvae) into the cages, a few encounters were watched and if the respective stage was eaten readily, others were repeatedly supplied to the respective predator without watching every preying but counting the number eaten by each predator. This continued for several weeks and even months, when short spells of feeding with *Drosophila* flies were sometimes interspersed among the feeding with (+)-offspring. Some insects that did not readily prey on *Paederus* developmental stages were forced to do so by giving them no other food. If reasonable, in view of predator's size, eggs and both larval stages of *Paederus* were exposed to the predators, but the early developmental stages were used preferentially because the concentration of pederin then is highest (Fig. 1). Furthermore, foraging workers of a *M. rubra* colony were tested in the field on 26 June 1993 to see whether they recognized *P. fuscipes* eggs as prey: (+)-eggs obtained in the laboratory were put down near the trails of workers and their behavior watched. In the laboratory, ants from that colony were given access to crushed (+)- and (–)-eggs simultaneously so that they were not able to carry them away and ingestion could be watched.

As the spiders studied are not likely to search for hidden eggs they were tested only versus the larvae of *Paederus*. Each spider was confronted with (+)-larvae and (–)-larvae by turns. Shortly before the molt, larvae could not be used since they then do not rove about and thus are seldom located by the spiders. Therefore, an active larva (mean larval age for L1: $\bar{x} \pm \text{SEM} = 2.2 \pm 0.30$ days, $n = 41$, for L2: $\bar{x} \pm \text{SEM} = 1.1 \pm 0.30$ days, $n = 20$) was put into the cage of a spider and every attack was observed. These attacks are clearly observable as sudden leaps towards the larva followed by a contact. If a larva had survived one or two attacks by the spider it was removed from the arena. Individual larvae were exposed at most four times to the attacks by spiders and then left alone. Each spider was tested once or twice per day with each type of offspring and if the larvae were rejected was given one *Drosophila* between two tests in order to determine its readiness to feed.

The influence of the toxin pederin on the reaction of spiders was evaluated in two specially designed experiments. Firstly, a spider that distinguished very well between (+)-larvae and (–)-larvae was confronted with three (–)-larvae that had eaten conspecifics containing pederin, i.e., four to five eggs each. These larvae sequester the pederin ingested (Kellner and Dettner 1995) and consequently the reaction of the spider can be compared to the outcome of its attacks on true (–)-larvae, which do not contain pederin. Secondly, starved *Drosophila melanogaster* flies were allowed to feed on a solution of authentic pederin in honey water (about 1 µg/µl). Within minutes the flies ingested relatively large quantities of this solution (up to 0.5 µl per fly) until their abdomens were tight. Immediately after the feeding these flies were presented to four wolf spiders, whose behavior after capturing the flies was observed.

Results

Insects preying on *Paederus* offspring

Potential insect predators collected from *Paederus* sites and given access to developmental stages of the respective *Paederus* species all ingested eggs or larvae containing pederin (Table 1). A few beetles rejected or ignored the eggs but ate larvae. Young L1 could temporarily escape from attacks by the beetles but within the restricted range of the arenas had no chance of surviving for a prolonged period. They were therefore fed to the beetles that rejected eggs in order to evaluate the influence of pederin. L2 resisted the attacks by beetles more effectively than L1 and thus were at times presented to only the larger ones. Among the few contacts of beetles with *Paederus* larvae that were directly observed, successful escapes of the smaller larvae were noticed in one or several encounters with *Lathrobium fulvipenne*, *Philonthus atratus*, *Quedius molochinus*, *Agonum gracile*, *Platynus obscurus* and *Poecilus lepidus*, but not with *Elaphrus riparius*.

As none of the insects tested hesitated to feed on prey with pederin, experiments concentrated on the number of *Paederus* offspring fed to selected specimens rather than testing an exhaustive number of different predators (Table 2). Depending on body size, insect predators were offered one to several eggs or larvae per day, which were all ingested. This feeding on prey laden with pederin could be continued for several weeks

Table 1 Acceptability of developmental stages of a *Paederus fuscipes* and b *P. riparius* to potential insect predators that co-occur at the same sites. Representatives (n number tested, BL body length) of diverse species accepted (+, in brackets if only weak individuals could be subdued) or rejected (–) the eggs or larvae (L1 first larval stage, L2 second larval stage)

Order:family <i>n</i> Species	BL (mm)	Egg	Stage L1	L2
a Predators of <i>P. fuscipes</i>				
Coleoptera:Staphylinidae				
2 <i>Philonthus atratus</i> (Gravenhorst)	7.8	+	+	+
1 <i>Philonthus fulvipes</i> (Fabricius)	6.2	[+]	+	
Coleoptera:Carabidae				
1 <i>Elaphrus riparius</i> (Linné)	6.7	+	+	+
1 <i>Poecilus lepidus</i> (Leske)	11.3	+	+	+
Hymenoptera:Formicidae				
? <i>Myrmica rubra</i> (Linné)	~4.5	+	[+]	
Heteroptera:Saldidae				
3 <i>Saldula pallipes</i> (Fabricius)	3.5	+	[+]	
b Predators of <i>P. riparius</i>				
Coleoptera:Staphylinidae				
1 <i>Lathrobium fulvipenne</i> Gravenhorst	8.4	–	+	[+]
1 <i>Quedius molochinus</i> (Gravenhorst)	10.3	+	+	+
Coleoptera:Carabidae				
2 <i>Agonum gracile</i> (Gyllenhal)	6.2	+	+	[+]
1 <i>Platynus obscurus</i> (Herbst)	5.3	–	+	
Heteroptera:Lygaeidae				
4 <i>Scoloposthetus thomsoni</i> Reuter	3.9	+	[+]	

Table 2 Laboratory feeding of potential insect predators on developmental stages of **a** *P. fuscipes* and **b** *P. riparius*. Individual predators were fed either (+)-offspring or (-)-offspring. Some died (†) after ingestion of a few offspring

Species	Feeding on <i>Paederus</i> offspring		
	Type	No. eaten	Time (days)
a Predators of <i>P. fuscipes</i>			
<i>Philonthus atratus</i>	(+)	21	6
– " –	(+)	15	6
<i>Philonthus fulvipes</i>	(+)	29	13
<i>Elaphrus riparius</i>	(+)	48	14
<i>Poecilus lepidus</i>	(+)	24	14
<i>Saldula pallipes</i>	(+)	20	17
– " –	(+)	20	18
– " –	(–)	7	7
b Predators of <i>P. riparius</i>			
<i>Lathrobium fulvipenne</i>	(+)	47	63
<i>Quedius molochinus</i>	(+)	35	44
<i>Agonum gracile</i>	(+)	42	63
– " –	(+)	17	9
<i>Platynus obscurus</i>	(+)	7	14
<i>Scoloposthetus thomsoni</i>	(+)	4	4†
– " –	(+)	5	6†
– " –	(+)	1	1†
– " –	(–)	9	10

without most insects showing any long-term impairment (Table 2). Only the bug *Scoloposthetus thomsoni*, which sucked out *P. riparius* eggs, did not tolerate ingestion of offspring with pederin, i.e., all bug specimens died after having ingested a few (+)-eggs; the feeding of another specimen with (–)-eggs could not be continued only because these eggs were in short supply. Another bug (*Saldula pallipes*), however, shows that the susceptibility to (+)-eggs is not a feature common to all members of the order Heteroptera (Table 2). In the field, *Myrmica rubra* ants carried (+)-eggs encountered during foraging away to their colony although they had great problems in grasping these round objects and spent a lot of time in doing so. In the laboratory, when they had a choice between pulps of (+)-eggs and (–)-eggs, the ants did not prefer one of the two types and both samples were repeatedly ingested completely.

Table 3 Attacks by potential spider predators on first and second stage larvae of **a** *P. fuscipes* and **b** *P. riparius*. Each spider attacked (+)-larvae and (–)-larvae, of which the numbers eaten and rejected are given separately. For further legends see Table 1

Order:family <i>n</i> Species	BL (mm)	Stage		No. eaten:rejected	
		L1	L2	(+)	(–)
a Predators of <i>P. fuscipes</i>					
Araneae:Lycosidae					
2 <i>Pardosa amentata</i> (Clerck)	6.8		+	0:19	5:11
1 <i>Pardosa</i> cf. <i>amentata</i> (Clerck)	5.7	+		0:10	5:5
1 <i>Pirata piraticus</i> (Clerck)	5.5	+		0:11	1:9
b Predators of <i>P. riparius</i>					
Araneae:Lycosidae					
1 <i>Pardosa pullata</i> (Clerck)	6.4	+		0:12	8:1
1 <i>Pirata hygrophilus</i> Thorell	5.5	+	+	0:7	3:11
Araneae:Salticidae					
1 <i>Evarcha arcuata</i> (Clerck)	7.0	–	+	0:2	1:0

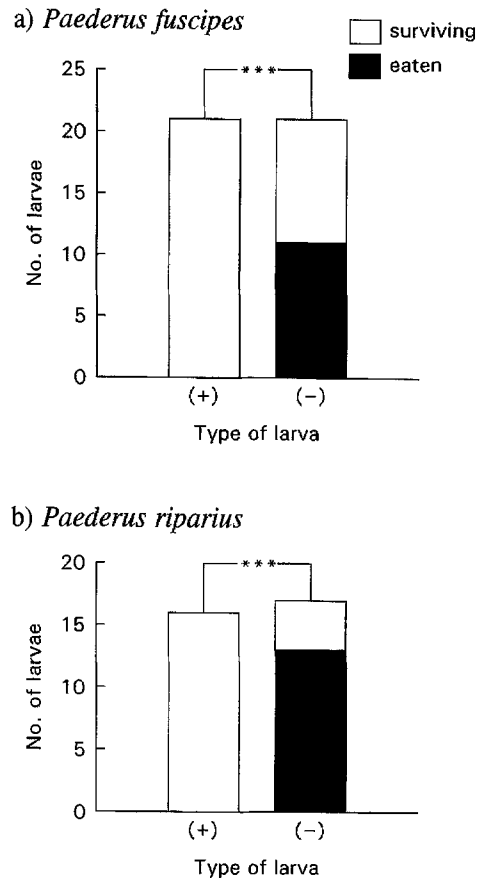


Fig. 2 Individual fate of **a** *P. fuscipes* and **b** *P. riparius* larvae (L1 and L2 combined) that were attacked by spiders (Lycosidae, Salticidae). (+)- and (–)-larvae differ significantly (***) χ^2 -test $P < 0.001$, for values see text)

Spiders preying on *Paederus* offspring

All spiders collected from *Paederus* sites (Lycosidae, Salticidae) attacked the *Paederus* larvae presented to them and, unlike insects, distinguished between larvae with and without pederin: (+)-larvae were rejected and never eaten while (–)-larvae were either eaten or also rejected, some spiders ingesting most and others few of the larvae captured (Table 3). *Drosophila* flies presented to the spiders were eaten in every case. The jump-

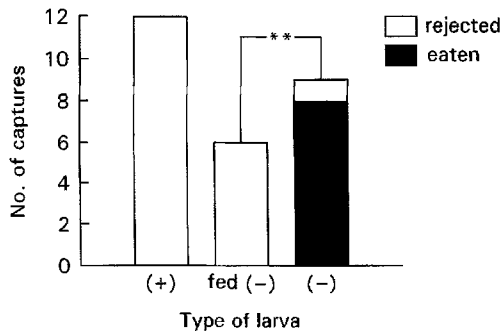


Fig. 3 Reactions of a *Pardosa pullata* female after attacks on different types of *Paederus riparius* larvae. These had received pederin either by birth [(+)-larvae] or by feeding on 4–5 conspecifics that contained pederin [fed (-)-larvae] or they had no pederin [(-)-larvae]. Fed and true (-)-larvae differ in spite of their common descent (**Fisher’s exact test $P < 0.01$)

ing spider *Evarcha arcuata* only attacked the larger L2 of *P. riparius*, but it refused to attack more larvae and *Drosophila* after having eaten a (-)-larva.

In both *Paederus* species the two types of larvae clearly differ in their ability to withstand attacks by spiders (Fig. 2). A considerable fraction of the (-)-larvae did not survive the attacks while (+)-larvae always were unharmed (*P. fuscipes*: $\chi^2 = 14.90$, $df = 1$, $P < 0.001$, *P. riparius*: $\chi^2 = 20.19$, $df = 1$, $P < 0.001$).

If (-)-larvae are given access to conspecifics containing pederin, on which they prey and thus acquire pederin as well, they will be treated like (+)-larvae (Fig. 3). That is, no distinction can be made between (+)-larvae and (-)-larvae fed with pederin, which are clearly distinguished from true (-)-larvae (Fisher’s exact test, $P = 0.0014$). The ability to withstand attacks by spiders may hence be transferred from (+)-larvae to (-)-larvae.

The sudden attacks by spiders are too rapid for *Paederus* larvae to show any escape reaction. Therefore, the larvae can survive only if they are unpalatable and thus are rejected by the spider. Larvae that the spiders decided to eat were reduced to small balls of cuticular remains. When rejected, however, the larvae were released unharmed even if they had been grasped by chelicerae for some time. In only one of the many attacks observed did the larva walk with a limp after being released by the spider, and later this handicap disappeared. Grasped and rejected larvae thus survive and develop normally (Table 4). Their mortality was no higher than that of their siblings that did not encounter spiders (*P. fuscipes*: $\chi^2 = 0.67$, $df = 1$, $P = 0.416$, *P. riparius*: $\chi^2 = 1.16$, $df = 1$, $P = 0.284$). The shortest life-span observed after attacks was 4 days, when some larvae died because they were accidentally drowned (1 L1 of *P. fuscipes*)

Table 4 Further development of a *P. fuscipes* and b *P. riparius* larvae [(+)- and (-)-larvae combined] that had survived the attacks of spiders in comparison with their siblings (control)

Case	Control No.	Larvae attacked by spiders	
		No.	Life span after attack (days, \pm SEM)
a <i>P. fuscipes</i> larvae			
Successful development	23	14	
Imaginal stage not reached	27	11	20.1 \pm 2.33
Eaten by insect predators		3	
Preserved for pederin analysis		3	
b <i>P. riparius</i> larvae			
Successful development	28	9	
Imaginal stage not reached	30	5	12 \pm 3.9
Eaten by insect predators		2	
Preserved for pederin analysis		4	

Table 5 Results of attacks by spider individuals on untreated *Drosophila melanogaster* flies (control) and others that were fed with either honey water or pederin dissolved in honey water immediately before the test

Spider species	<i>Drosophila</i> (control) No. eaten:rejected	<i>Drosophila</i> fed with	
		Honey water No. eaten:rejected	Honey water + pederin No. eaten:rejected ^a
<i>Pardosa amentata</i> (female)	14:0	1:0	0:1
<i>P. cf. amentata</i> (subadult female)	10:0	–	0:1
<i>P. pullata</i> (female)	10:0	1:0	0:1
<i>Pirata piraticus</i> (male)	11:0	1:0	0:1

^aThe flies were captured as usual and the predators commenced feeding on thorax muscles. But as soon as they progressed to the tightly filled abdomen, the spiders immediately turned away from the prey. Although the spiders came back to the prey one to four times to try it again, they in the end left the abdomens and often also the heads of the flies uneaten

or could not shed their larval cuticle (2 L1 of *P. riparius*). *Paederus* larvae, especially L2 that do not pupate successfully, typically survive for long periods (Table 4).

After releasing (+)-larvae, the spiders often showed some special cleansing behavior: They lowered their whole body and moved forward either by slanting the legs without steps or by walking a short distance, while they dragged their chelicerae over the moist paper covering the bottom of the arena. Subsequently they usually cleaned their mouth-parts. Pederin is really the cause of spiders' aversion, as shown by presenting four wolf spiders with *Drosophila* flies that contained a mixture of authentic pederin and honey water in their gut (Table 5). Palatable prey is deterrent if it is artificially supplemented with pederin, but is abandoned only after several trials. Every time the spiders turned away from *Drosophila* flies fed with pederin, they showed the cleansing behavior already known from attacks on (+)-larvae.

Discussion

The predatory insects we tested are not deterred by the presence of pederin in their prey. Beetles that did not feed on eggs accepted young L1. As these were offered just after hatching and before they had grown, their amount of pederin was not diluted as compared to the eggs. Therefore, it is not a difference in the concentration of pederin that led to eggs being spared, but some other preference of prey type or an inability to pierce round objects. It appears, then, that insect predators generally are not poisoned by pederin. The only exception we found is the lygaeid bug *Scoloposthetus thomsoni*: the bugs died when they had been fed with a few (+)-offspring, which indicates a toxic effect of pederin. Lygaeids, however, normally feed on plants and rarely take dead insects (Wagner 1966), and *S. thomsoni* was probably forced by starvation to suck out *P. riparius* eggs. Insects belonging to families with greater ecological importance as predators appear not to be affected by pederin. This supports the finding of Kurosa (1958) that eggs and larvae of *P. fuscipes* are taken as prey, especially by carabid and staphylinid beetles.

Unlike insects, the spiders we tested rejected all larvae containing pederin and never ate them. The substance thus acts as a strong and selective feeding deterrent. Pederin itself causes the deterrence of spiders, since turning away and the characteristic cleansing behavior are also observed after contacts with pederin in the gut of *Drosophila* flies. The amide obviously renders already captured prey unpalatable. In contrast to *Paederus* larvae containing pederin, (–)-larvae risk being killed and eaten after an attack by a spider. It cannot be ruled out that these (–)-larvae contain traces of pederin that can hardly be measured but suffice to deter spiders, which might account

for the rejection of some (–)-larvae. Furthermore, the rejection of (–)-larvae might depend on the constitution of the hunting spider, i.e., whether it has heightened food requirements during growth or reproduction or has already had experience with (+)-larvae. Testing naive spiders may reveal the possible influence of learning by contacts with (+)-larvae. In our experiments, however, the aim was to present larvae to predators collected from *Paederus* sites, which consequently could already have had contact with *Paederus* larvae.

Spiders may come into contact with pederin by biting *Paederus* larvae. That one larva was limping and others were grasped for some time by the spiders suggests this possibility. By means of their chelicerae, spiders could perceive pederin located in the hemolymph. Dispersion of a deterrent in the hemolymph is interpreted as an adaptation to prevent predation by spiders, because these predators are able to handle prey that store defensive chemicals in exocrine glands (Nentwig 1987). If they do bite *Paederus* larvae, however, the spiders apparently do not use their venom, because the larvae would then die even if they were not eaten. This has been observed for moth larvae (*Utetheisa ornatix*), which contain pyrrolizidine alkaloids and thus are not eaten by wolf spiders (*Lycosa ceratiola*) (Eisner and Eisner 1991). Of 30 moth larvae tested, 2 died after rejection by the spiders in Eisner and Eisner's study; in contrast, no *Paederus* larva out of 51 that survived spider attacks died as a result of the attacks in our study.

While four spider species tested by Kurosa (1958), which belong to different families, did not prey on *P. fuscipes* and its offspring, the wolf spider *Lycosa T-insignata* was recorded as a predator of larvae. In view of our experiments the larvae eaten were probably (–)-larvae. Apart from this exception the findings of Kurosa (1958) accord with our results and indicate a general efficacy of pederin against spiders.

As *Paederus* eggs are laid singly or in small numbers and are hidden (in the laboratory in cotton, in nature probably in plant debris), they are not liable to be found by insect predators that would eat them. The larvae are agile and have many projecting setae that enable them to perceive attacking insects, often in time. This may suffice for escaping from insect predators in most cases, so that there is no need of chemical protection. All observed wolf spider attacks, however, were so quick that larvae had no chance to escape. Their agility even makes them more vulnerable because wolf spiders ambush their prey and prefer fast-moving animals (Ford 1978; Yeorgan 1975). *Paederus* larvae then rely on their chemical defense to survive the attacks by spiders. Therefore, the efficacy of pederin is primarily related to the larval means of defense.

Prey spectra of wolf spiders are not well known (Turnbull 1973; Stratton 1985) but these spiders are considered to be generalist predators, which feed on small, soft-bodied arthropods (Nentwig 1986; Nyffeler

and Benz 1988). Larvae of staphylinid beetles have been found among the prey of wolf spiders, e.g., *Pardosa ramulosa* (Yeagan 1975) and *P. amentata* (Nyffeler and Benz 1988). *Paederus* larvae, too, could fall prey to wolf spiders because the two taxa often live in the same habitat (El-Heneidy and Abbas 1984; Plachter 1986). Spiders are often limited by food resources and prey on arthropods that use the same resources, but the extent of this intraguild predation is unclear (Wise 1993). It is on the open banks of rivers and other waters that the greatest number of *Paederus* species, including *P. fuscipes*, occur naturally (Koch 1989). There lycosid spiders outnumber the members of other spider families, while in adjacent areas covered with vegetation and litter there are several families more important than wolf spiders (Uetz 1976; Plachter 1986). The latter are thus the main threat to *Paederus* specimens on open banks. As shelter is scarcer on these banks than in leaf litter, potential prey might be more exposed to attacks by wolf spiders (Uetz 1976). Although the spider fauna of swamps and moist meadows, where *P. riparius* and other species are found, is not dominated by Lycosidae, they are present in large numbers (Cordes 1991).

Adults of several wolf spider species are active in early summer, with juveniles replacing them in late summer (Cordes 1991). Both *Paederus* species studied lay eggs in May and larvae develop in summer, so that a new generation emerges at the end of summer (Bohác 1985; R. Kellner, unpublished work). Therefore, during the reproductive season of these *Paederus* species there are always a lot of predaceous wolf spiders. As no adults lacking pederin were collected from the field (Kellner and Dettner 1995), the offspring of (–)-females may not reach adulthood there. They might either prey on conspecifics containing pederin and thereby compensate for the deficiency of pederin or they might be eliminated. Spiders are the predators which potentially are responsible for such a selection.

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