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New Prey-predator Association in Aposematic Pyrrhocorid Bugs: *Antilochus coqueberti* as a Specialist Predator on *Dysdercus* Species

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Abstract. We investigated the prey-predator relationship between aposematic pyrrhocorid bugs, *Antilochus coqueberti* and *Dysdercus cingulatus*. They are similar in appearance and often found in the same habitat simultaneously. Carnivory of *A. coqueberti* on *D. cingulatus* and *D. decussatus* was observed in the field, and *A. coqueberti* could not develop when experimentally fed on only plant materials, strongly indicating the obligate carnivory of *A. coqueberti*. While *A. coqueberti* did not prey on bugs in the families Lygaeidae, Largidae, Coreidae, and Rhopalidae that share the aposematic body coloration with *A. coqueberti* and *D. cingulatus, A. coqueberti* preyed on all the pyrrhocorids and alydids provided, regardless of their body coloration. Visual resemblance is only partially involved in the prey preference of *A. coqueberti*. We conclude that *A. coqueberti* is the obligate predator specialized to *Dysdercus* species.

Key words: Pyrrhocoridae, *Dysdercus cingulatus*, mimicry, carnivory, phytophagy, prey preference.

Introduction

Among heteropterous bugs, strong resemblance or mimicry is occasionally observed between a putative prey and its predator when both are aposematic and live in the same habitat (Edmunds, 1974; Iwata, 1975, 1978a, b; Ahmad & Schaefer, 1987; Schaefer, 1997, 1999; Nishida, 1999; Nishida *et al.*, 2001). This type of mimicry can be theoretically divided into Müllerian mimicry and aggressive mimicry (Wickler, 1968). The former refers to a situation in which both participants are noxious and the common aposematic signal is enhanced by living together; the latter refers to a prey-predator association where the specialist predator mimics the aposematic prey as a 'the wolf in sheep's clothing'.

Schaefer (1997) reported several cases of prey-predator associations in heteropterous bugs, in which preys were herbivorous pyrrhocorids and the predators were predacious reduviids; he suggested Müllerian mimicry for those pyrrhocorid-redviid associations. Iwata (1975, 1978a, b) reported a similar prey-predator association, but the prey and predator were both pyrrhocorids. However, almost all evidence for prey-predator association in pyrrhocorids has been anecdotal until Nishida *et al.* (2001) showed the first convincing evidence for the prey-predator association in pyrrhocorids in West Java, Indonesia: *Raxa nishidai* Schaefer fed exclusively on *Melamphaus faber* (Fabricius), and both are similarly aposematic. As the authors pointed out, the absence of common predators on these two pyrrhocorids suggests that Müllerian mimicry is no longer exerting selection pressure on maintaining this association.

Our preliminary observations suggested that *Antilochus coqueberti* (Fabricius) (Pyrrhocoridae) dwelled near aggregations of the cotton stainer *Dysdercus cingulatus* (Fabricius) (Pyrrhocoridae), particularly in and around *Hibiscus* shrubs on Ishigaki-jima Island, the southernmost part of the Ryukyu Islands. These two species look very similar, having aposematic red and black coloration. *Antilochus coqueberti* has been reported as a predator of the cotton stainers, *Dysdercus* spp. (Pyrrhocoridae) (Corbett, 1923; Chauthani & Misra, 1966; Iwata, 1975, 1978a, b; Quayum & Nahar, 1980; Dhiman, 1985), whereas some reports treated *A. coqueberti* as a herbivore attacking malvaceous plants such as *Hibiscus tiliaceus* and cotton

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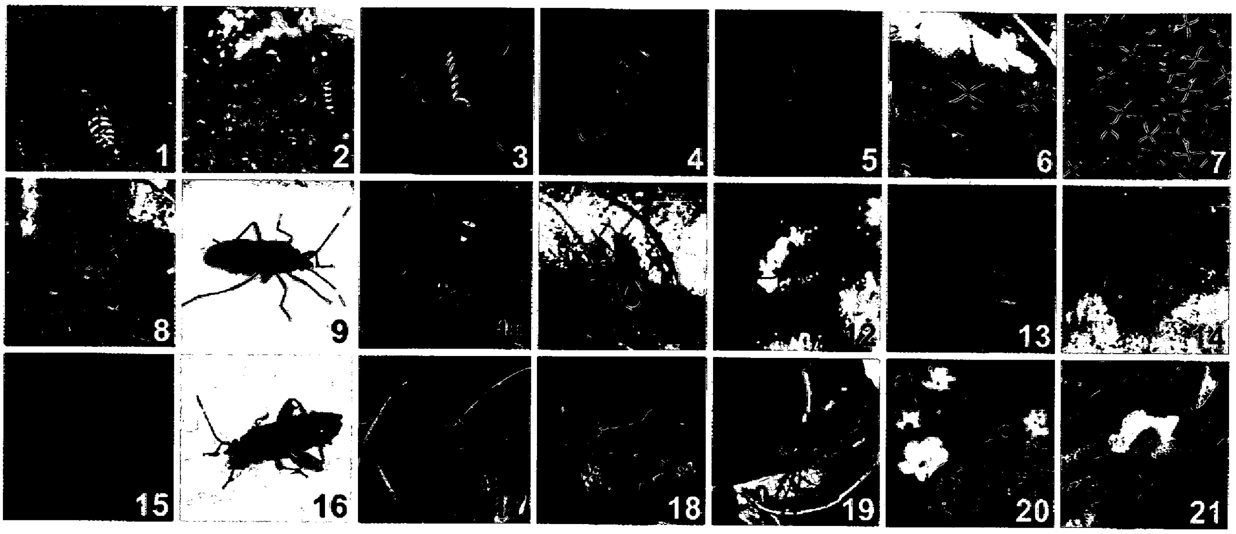

Fig. 1–21. Bug and host plant species used in the experiments. 1, *Antilochus coqueberti*, Pyrrhocoridae; 2, *Dysdercus cingulatus*, Pyrrhocoridae; 3, *D. poecilus*, Pyrrhocoridae; 4, *Dysdercus* sp. probably *D. solenis*, Pyrrhocoridae; 5, *Dysdercus* sp. probably *D. mesiostigma*, Pyrrhocoridae; 6, *D. decussatus*, Pyrrhocoridae; 7, *D. philippinus*, Pyrrhocoridae; 8, *Physopelta cincticollis*, Largidae; 9, *P. gutta*, Largidae; 10, *Oncopeltus nigriceps*, Lygaeidae; 11, *Graptostethus servus*, Lygaeidae; 12, *Spilostethus hospes*, Lygaeidae; 13, *Thunbergia sanguinaria*, Lygaeidae; 14, *Armatillus* sp., Pyrrhocoridae; 15, *Riptortus clavatus*, Alydidae; 16, *Daclera levana*, Alydidae; 17, *Dasynus coccocinctus*, Coreidae; 18, *Leptocoris augur*, Rhopalidae; 19, *Leptocoris rufomarginata*, Rhopalidae; 20, *Hibiscus makinoi*, Malvaceae; 21, *H. tiliaceus*, Malvaceae.

plant (Kawasawa & Kawamura, 1977; Singh & Tomar, 1977). In spite of the relatively detailed description of the predatory habit of *A. coqueberti* by Iwata (1975, 1978a, b), quantitative and experimental tests are still necessary before concluding that *A. coqueberti* is predaceous, as there are several records of predation or cannibalism by pyrrhocorids which are recognized to be basically phytophagous (Ahmad & Schaefer, 1987).

We carried out field observations and laboratory experiments to clarify to what extent *A. coqueberti* is predacious, and to evaluate the prey preference of *A. coqueberti* for various heteropterous bugs inhabiting the southwest islands of Japan.

Materials and Methods

Antilochus coqueberti, *the putative predator*

Antilochus coqueberti is rather rare but widely distributed in Southeast Asia, Taiwan and up to Ishigaki-jima Island (Kawasawa & Kawamura, 1977; Miyamoto & Yasunaga, 1989; Yasunaga *et al*., 1993). Its body color is highly aposematic, bright red except for the black tips of its forewings (see Fig. 1). Its appearance and body size are similar to those of the cotton stainer *Dysdercus cingulatus* (see Fig. 2).

Dysdercus *species, the putative prey*

In the Ryukyu Islands, we found at least six species of *Dysdercus*. All these *Dysdercus* are aposematic, but they can be divided roughly into two groups based on their body colorations. *Dysdercus cingulatus* (Fabricius), *D. poecilus* (Herrich-Schaeffer), *Dysdercus* sp. probably *D. solenis* (Herrich-Schaeffer) and *Dysdercus* sp. probably *D. mesiostigma* Distant are red and black, often with black spots on the forewings (see Figs. 2–5), while *D. decussatus* Boisduval and *D. philippinus* Herrich-Schaeffer are red and black with a large white cross on the forewings (see Figs. 6, 7). The genus *Dysdercus* includes many critical pests of cotton and other malvaceous crops in the world, especially in the tropics to subtropics (Freeman, 1947; van Doesburg, 1968). Among them, *D. cingulatus* is regarded as the most serious cotton pest in Southeast Asia (Miwa, 1944; Iwata, 1975, 1978a, b; Ahmad & Kahn, 1980; Ahmad & Schaefer, 1987; Farine, 1987; Yasuda, 1992). On Ishigaki-jima Island, where there is no commercial cotton cultivation, this species is usually observed on various malvaceous plants, especially *Hibiscus makinoi* (Kohno, unpublished). *Dysdercus poecilus* is, on the other hand, principally dependent on *Sida rhombifolia*, a wild malvaceous species, on Ishigaki-jima Island (Kohno, 2001). *Dysdercus solenis* and *D. mesiostigma* are very rare on Ishigaki-jima Island and there is no information on their host plants. *Dysdercus decussatus* is principally observed on *Hibiscus tileaceus* on Ishigaki-jima Island (Kohno, unpublished). With the exception of *D. philippinus*, which was collected on Okinawa Island, all species were collected on Ishigaki-jima Island.

Other heteropterous bugs used in the study

Other than *Dysdercus,* we used 12 species of heteropterous bugs belonging to six families for the prey preference experiment. These included Largidae (*Physopelta cincticollis* Stål, *P. gutta* (Burmeister); Figs. 8, 9), Lygaeidae (*Oncopeltus nigriceps* (Dallas), *Graptostethus servus* (Fabricius), *Spilostethus hospes* (Fabricius), *Thunbergia sanguinaria* (Stål); Figs. 10–13), Pyrrhocoridae (*Armatillus* sp.; Fig. 14), Alydidae (*Riptortus clavatus* (Thunberg), *Daclera levana* Distant; Figs. 15, 16), Coreidae (*Dasynus coccocinctus* (Burmeister); Fig. 17), and Rhopalidae (*Leptocoris augur* Fabricius, *L. rufomarginata* Fabricius; Figs. 18, 19). Except for three species with dull coloration (*Armatillus* sp., *R. clavatus* and *D. levana*), all other species selected have aposematic red and black coloration. With the exception of *Thunbergia sanguinaria*, which was collected on Iriomote-jima Island, all species were collected on Ishigaki-jima Island.

Field observation on habitat use

Field observation was executed in various vegetations including various malvaceous and bombacaceous plants at more than 20 sites on Ishigaki-jima Island for about 150 days intermittently from October 1998 to August 2001 to identify the habitat of *A. coqueberti.*

Preliminary experiment on entomophagy of A. coqueberti

We examined whether *A. coqueberti* can develop into adults feeding only on *D. cingulatus*. The rearing experiment was carried out under room temperature (ca. 25–30℃) and natural day length throughout the experimental period. About 80 eggs deposited in the laboratory on September 10, 1998 by a field-collected adult female of *A. coqueberti* were kept in a plastic container provided only with moistened filter paper until molting to the second instar on September 20. These second instar nymphs were kept together in a plastic container fed only with nymphs of *D. cingulatus* and water until the fifth instar and then fed with *D. cingulatus* adults and water. No plant materials were given at all throughout the nymphal development.

Entomophagy vs. phytophagy in A. coqueberti

Hibiscus plants (Figs. 20, 21), especially *H. makinoi*, are common habitat plants and a suitable food resource for *D. cingulatus* (Kohno, unpublished). Second instar nymphs of *A. coqueberti* were reared individually under 25℃ and 14L–10D and provided with moistened filter paper. Each *A. coqueberti* nymph was provided one of three diets: five *Hibiscus makinoi* seeds (N=22), five *H. tiliaceus* seeds (N=22), or one full-grown second instar nymph of *D. cingulatus* (N=18). When the *D. cingulatus* nymph was consumed, an additional nymph was supplied. As a control, 30 second instar nymphs of *A. coqueberti* were reared with only water. Survival until the third instar and nymphal development were recorded every day.

Prey preference of A. coqueberti

The laboratory experiment was carried out with ten adult males of *A. coqueberti* reared in the laboratory with *D. cingulatus* as food. Two *Dysdercus* species (*D. cingulatus* and *D. decussatus*), recorded as natural prey of *A. coqueberti* in the field during this study, and two Physopelta species (*P. cincticollis* and *P. gutta*), which look like *A. coqueberti and D. cingulatus*, were used as potential preys. Each *A. coqueberti* individual was tested to see if it had consumed an individual from a randomly selected potential prey species within a 24 hour time frame. This test was repeated four times on each predator, once for each of the prey species.

To elucidate potential effects of visual resemblance and taxonomic relationships of preys on diet breadth of *A. coqueberti*, we observed the foraging behavior toward various bug species in the laboratory. The bugs used as potential preys were four *Dysdercus* species (*D. poecilus*, sp. probably *D. solenis,* sp. probably *D. mesiostigma, D. philippinus*) and ten species listed in the section "Other heteropterous bugs used in the study"—all except for the two largid species.

Results

Field observation on habitat use

Antilochus coqueberti was found only on and near *Hibiscus* or *Chorisia* shrubs or trees that were infested by *Dysdercus* bugs (Table 1), whereas *Dysdercus* species were often found alone. *Antilochus coqueberti* was most abundant during winter when *Hibiscus makinoi* fruited and a large number of *D. cingulatus* aggregated on and around it. *Antilochus coqueberti* was usually found on the ground and at lower parts of the host plants less than 1 m above the ground, while *D. cingulatus* inhabited various parts of the host plants and nearby vegetation or on the ground, forming aggregations at various parts of the plant including fruits formed at the tips of shoots. On Ishigaki-jima Island, *D. cingulatus* had a wide rage of host plants: *Hibiscus makinoi, H. mutabilis, H. tiliaceus, H. syriacus, H. rosa-sinensis, H. cannabinus, Gossyppium arboreum, Malvastrum coromandelianum, Abelmoschus moschatus, A. esculentus, Chorisia speciosa* and *Bombax* *ceiba*. *Dysdercus decussatus* was usually associated with *H. tiliaceus* and in winter often formed aggregations on the undersides of its leaves, but was occasionally found on the fruits and leaves of *H. makinoi*, *G. arboreum* and *Thespesia populnea*. *Dysdercus poecilus* was usually found on various parts of *Sida rhombifolia* and rarely on *H. syriacus*.

Antilochus coqueberti adults killed adults and nymphs of *D. cingulatus* and *D. decussatus*, either on *Hibiscus* shrubs, on the ground or at lower parts of various nearby plants. Nymphs of *A. coqueberti* killed and fed principally on nmphs of *D. cingulatus* and *D. decussatus* in the similar manner as the adults. We observed no herbivory for *A. coqueberti*.

Preliminary experiment on entomophagy in A. coqueberti

Fourteen males and eight females of *A. coqueberti* emerged during October 22–30, 1998 fed only with *D. cingulatus*. This suggests that *A. coqueberti* is carnivorous to a considerable degree. Cannibalism sometimes occurred among younger instars.

Entomophagy vs. phytophagy in A. coqueberti

The second instar nymphs could develop to the third instar only when they were fed with *D. cingulatus* nymphs (Table 2). No individuals fed with *Hibiscus* seeds and water survived and developed to the next instar. The longevity of the individuals fed with *Hibiscus* seeds and water did not differ significantly from that fed with water alone.

Table 1. Habitat plants and *Dysdercus* bugs associated with *Antilochus coqueberti* on Ishigaki-jima Island.

Plant species	*Dysdercus* bugs
Malvaceae	
Hibiscus tiliaceus	*D. cingulatus* & *D. decussatus*
H. makinoi	*D. cingulatus*
	D. cingulatus & *D. decussatus*
H. rasa-sinensis	*D. cingulatus*
H. syriacus	*D. cingulatus*
	D. cingulatus & *D. poecilus*
Bombacaceae	
Chorisa speciosa	*D. cingulatus*

Prey preference of A. coqueberti

Adult males of *A. coqueberti* immediately attacked within few minutes and consumed within 24 hours all the *Dysdercus* species, but neither attacked nor fed on any *Physopelta* bugs. Additional experiments revealed that *A. coqueberti* attacked and consumed almost all the pyrrhocorids and alydids, whereas no predation was observed on the lygaeid, coreid, and rhopalid species provided (Table 3).

Discussion

The results of our observations and experiments clearly exhibited that *A. coqueberti* is predacious, as pointed out by Iwata (1975, 1978a, b), and an obligatory predator. Previous reports on herbivory of *A. coqueberti* (Kawasawa & Kawamura, 1977; Singh & Tomar, 1977) could be erroneous or at best exceptional.

The experiments on prey preference for heteropterous bugs of various families revealed that *A. coqueberti* attacked and fed on pyrrhocorids and alydids immediately, regardless of the degree of their visual resemblance to the predator, but never attacked largids, lygaeids, coreids and rhopalids even if they looked similar in body coloration to the predator and its natural preys. Among these families, Pyrrhocoridae and Largidae are in the superfamily Pyrrhocoroidea (Schuh & Slater, 1995), but the prey preferences by *A. coqueberti* markedly differed between them. A similar phenomenon was observed for Alydidae, Coreidae and Rhopalidae, all of which are in the superfamily Coreoidea; only the Alydidae was preferentially attacked and consumed by *A. coqueberti*.

In the field, however, *A. coqueberti* preyed on only specific pyrrhocorids and no alydids. One reason may be the existence of some association between *A. coqueberti* and the malvaceous and bombacaceous plants listed in Table 1. If so, there must be very few

Table 2. Duration or longevity of the second instar nymphs of *Antilochus coqueberti* fed on the second instar nymphs of *Dysdercus cingulatus* or *Hibiscus tiliaceus* or *H. makinoi* seeds.

Feeding treatment	Diet	N	Molting	Died	Survival rate to 3rd instar	2nd instar duration Mean days±SE	Longevity Mean days±SE[a]
Animal material	*D. cingulatus* nymph+Water	18	18	0	100%	5.6±0.1	—
Plant material	*H. tiliaceus* seeds+Water	22	0	22	0%	—	6.2±0.2a
	H. makinoi seeds+Water	22	0	22	0%	—	5.1±0.2b
(Control)	Water	30	0	30	0%	—	5.8±0.3ab

[a] Values followed by the same letter were not significantly different (Tukey-Kramer test, $P > 0.05$).

Table 3. Feeding experiment on prey preference of *Antilocus coqueberti*.

Prey species	Appearance (See Figs.)	N	*A. coqueberti*	Result
Lygaeidae				
Oncopeltus nigriceps	Fig. 10	1	5th instar nymph	not consumed within 5 days
Graptostethus servus	Fig. 11	6	Adult	not consumed within 7 days
Spilostethus hospes	Fig. 12	1	5th instar nymph	not consumed within 24 h
Thunbergia sanguinaria	Fig. 13	3	Adult	not consumed within 3 days
Pyrrhocoridae				
Dysdercus poecilus	Fig. 3	6	4th instar nymph	all attacked within 15 min and consumed
Dysdercus sp.[1]	Fig. 4	2	Adult	all attacked within 1 min[3]
Dysdercus sp.[2]	Fig. 5	3	Adult	2 of 3 attacked within 10 min and consumed
D. philippinus	Fig. 7	11	Adult	all attacked within 25 h and consumed
Armatillus sp.	Fig. 14	4	Adult	all attacked within 10 min and consumed
Alydidae				
Riptortus clavatus	Fig. 15	2	Adult	all attacked within 5 h and consumed
Daclera levana	Fig. 16	1	Adult	attacked within 18 h and consumed
Coreidae				
Dasynus coccocinctus	Fig. 17	2	Adult	not consumed within 5 days
Rhopalidae				
Leptocoris augur	Fig. 18	1	5th instar nymph	not consumed within 5 days
L. rufimarginata	Fig. 19	1	Adult	not consumed within 5 days
		1	5th instar nymph	not consumed within 5 days
		1	4th instar nymph	not consumed within 5 days

[1] Probably *Dysdercus solenis* (Herrich-Schaeffer) according to Freeman (1947).

[2] Probably *Dysdercus mesiostigma* Distant according to Freeman (1947).

[3] Interrupted when *A. coqueberti* attacked the prey.

opportunities for *A. coqueberti* to encounter alydids or *D. poecilus* in the field, as alydids are primarily dependent on Leguminosae (Schaefer, 1980) and *D. poecilus* is exclusively dependent on the malvaceous plant, *Sida rhombifolia* (Kohno, 2001) and is rarely observed on another malvaceous plants. Four other pyrrhocorids are difficult to discuss because *Dysdercus* sp. probably *D. solenis*, *Dysdercus* sp. probably *D. mesiostigma* and *Armatillus* sp. are very rare and *D. philippinus* may be absent from Ishigaki-jima Island.

Another possible reason for the selectivity in the field may be the population density of each putative prey species. *Dysdercus cingulatus* was observed to reproduce in large numbers, especially during winter, on *H. makinoi*; predation on *D. cingulatus* by *A. coqueberti* was often observed there. Predation on *D. decussatus* by *A. coqueberti* was usually observed when *D. decussatus* occurred in the same habitat simultaneously with *D. cingulatus* (Table 1). In contrast, the alydids, *D. poecilus*, and other pyrrhocorids found on Ishigaki-jima Island were not observed in large numbers. If *A. coqueberti* is attracted to the prey in high density, there may be very few opportunities for *A. coqueberti* to prey on the bugs other than *D. cingulatus* and *D. decussatus*.

Our findings suggest that the *A. coqueberti–D. cingulatus* system is similar to the *Raxa nishidai–Melamphaus faber* system (Nishida, 1999; Nishida *et al.*, 2001). A notable difference is that *A. coqueberti* is oligophagous whereas *R. nishidai* is monophagous, specializing to *M. faber*. The difference in the diet breadth between the two predators may be based on that of the prey species. Both *D. cingulatus* and *D. decussatus*, especially the former, seasonally change host plant species (Kohno, unpublished) and they sometimes occur together in the same habitat simultaneously. In contrast, *M. faber* is virtually monophagous and stays within the same habitat throughout the year (Nishida, 1999; Nishida *et al.* 2001). In this respect, the *A. coqueberti–D. cingulatus* system could be more similar to the pyrrhocorid-reduviid system (Fuseini & Kumar, 1975; Schaefer & Ahmad, 1987) or the tingid-mirid system (Henry *et al.*, 1986; Neal *et al.*, 1991), in which the predators and prey exhibit considerable mobility and the predators are oligophagous.

It still remains to be explored whether these predator-prey associations are Müllerian mimicry or aggressive mimicry. In both the *A. coqueberti-Dysdercus* and the *R. nishidai-M. faber* systems, the predators are more brightly aposematic than are the prey, and both seem to be distasteful (Kohno, unpublished; Nishida, personal communication). This suggests that in both systems the predators species are models and the prey species are mimics, forming a Müllerian mimic ring. However, no common predators have so far been observed. Before elucidating the mimicry types, a further study is necessary, particularly on the selection pressure that maintains the mimicry system.

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