Behavioral Ecology Vol. 13 No. 2: 154–159

Specialized predation on plataspid heteropterans in a coccinellid beetle: adaptive behavior and responses of prey attended or not by ants

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Two plataspid hemipteran species proliferated on *Bridelia micrantha* (Euphorbiaceae). Colonies of *Libyaspis* sp., never attended by ants, developed on branches, while *Caternaultiella rugosa* lived at the base of the trunks, mostly in association with *Camponotus brutus* that attends them in carton shelters. Both plataspid species are prey of the coccinellid beetle *Anisolemnia tetrasticta,* whose larvae always detected them by contact. When attacked the *Libyaspis* nymphs cowered, so that the hypertrophied lateral sides of their tergits made contact with the substrate, but the ladybirds slid their long forelegs under these nymphs, lifted them, and bit them on the ventral face. The *Caternaultiella* nymphs, which do not have hypertrophied extremities of the tergits, tried to escape at contact with the ladybirds, but were rarely successful. To capture them, the ladybirds either adopted the previous behavior or directly grasped then bit them. We noted a graded aggressiveness in the ants toward the ladybirds according to the situation: no aggressiveness on the tree branches; stopping the ladybirds that approached the shelters where the ants attended *Caternaultiella*; and full attack of ladybirds that tried to capture *Caternaultiella* nymphs situated outside shelters. The latter behavior can emit an alarm pheromone that triggers the dispersion of their congeners while attracting attending *C. brutus* workers. Naive workers are not attracted, so we deduce that this behavior is the result of a kind of learning. *Key words:* anti-predator behavior, ants, Heteroptera, Coccinellidae, ladybird beetles, learning, predation, trophobiosis. *[Behav Ecol 13:154–159 (2002)]*

Although many predatory insects are specialized, they can capture a relatively wide spectrum of prey; however, the suitability of the prey varies greatly. ''Essential prey'' are capable of supporting immature development and adult reproduction, whereas ''alternative prey'' only enable the predator to survive, with a mixed diet being frequent and profitable (Evans et al., 1999; Hodek, 1973).

Most ladybird species are predators. The majority of ladybirds are aphidophagous, while some others are coccidophagous. Both aphids and coccids generally live in groups, and several species have evolved trophobiotic relationships with ants (trophobiosis is a symbiotic relationship wherein ants obtain honeydew from attended insects, and in turn protect them from their natural enemies; see Hölldobler and Wilson, 1990). Aphids have developed several defenses against their predators, including the release of a pheromone that triggers the dispersal of the group when an individual is attacked. Ladybirds are therefore confronted with these defenses and in numerous cases with the aggressiveness of ants attending aphid colonies, but certain ladybird species use a kind of camouflage to obtain access to ant-attended aphids or even to live as parasites in ant nests (Corbara et al., 2001; Dixon, 2000; Majerus, 1989; Sloggett and Majerus, 2000; Sloggett et al., 1998; Völkl, 1995).

Ladybirds are also predators of plataspid heteropterans. In India the populations of *Coptosoma ostentuum,* a pest of cultivated pulses, are regulated by the ladybird *Synia melanaria,* and in Australia *Synoma seminigra* attacks nymphs of *Coptosoma* sp. (Malhotra and Krishnaswani, 1962; Pope, 1988). *Anisolemnia tetrasticta* (= *Caria shoutedeni*) has been cited as a predator of *Libyaspis* plataspids on *Sesbania* sp., a leguminous shade tree of Uganda (Hargreaves, 1925). In Cameroon we found *A. tetrasticta* preying on *Libyaspis* sp. colonies developing on several leguminous tree species and on *Bridelia micrantha* (Euphorbiaceae). *B. micrantha* can also support another plataspid, *Caternaultiella rugosa,* which is attended by ants, mostly *Camponotus brutus* (Dejean et al., 2000b). Although most of the known cases of trophobiosis concern certain lycaenid lepidoptera and Hemiptera of the former suborder Homoptera, interactions between ants and heteropterans have also been reported, but mostly through casual observations (Maschwitz et al., 1987). As a result, verifying if relationships between ants and certain heteropterans are reciprocal has become a challenging field of scientific inquiry. In this study we searched for natural predators of plataspids. We also noted that *A. tetrasticta* can prey on *C. rugosa* attended by ants outside carton shelters built by *C. brutus.*

We conducted a two-pronged study concerning firstly the predatory behavior of the ladybird *A. tetrasticta* when confronted with the two plataspid species and secondly the protective activity of the ants that attend *Caternaultiella* against the predatory pressure of this ladybird. We attempted to verify whether this ladybird is specialized on one of the plataspids by asking whether the ladybird larvae are able to counter the *Libyaspis* and/or *Caternaultiella* defenses, and whether the ladybird larvae trigger reactions by *C. brutus* workers when attempting to prey on *Caternaultiella.*

MATERIALS AND METHODS

Ant, plataspid, and coccinellid species

Camponotus brutus is a subdominant formicine ant species widely distributed in central Africa. It has been noted in pi-

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Received 1 January 2001; revised 23 March 2001; accepted 23 March 2001.

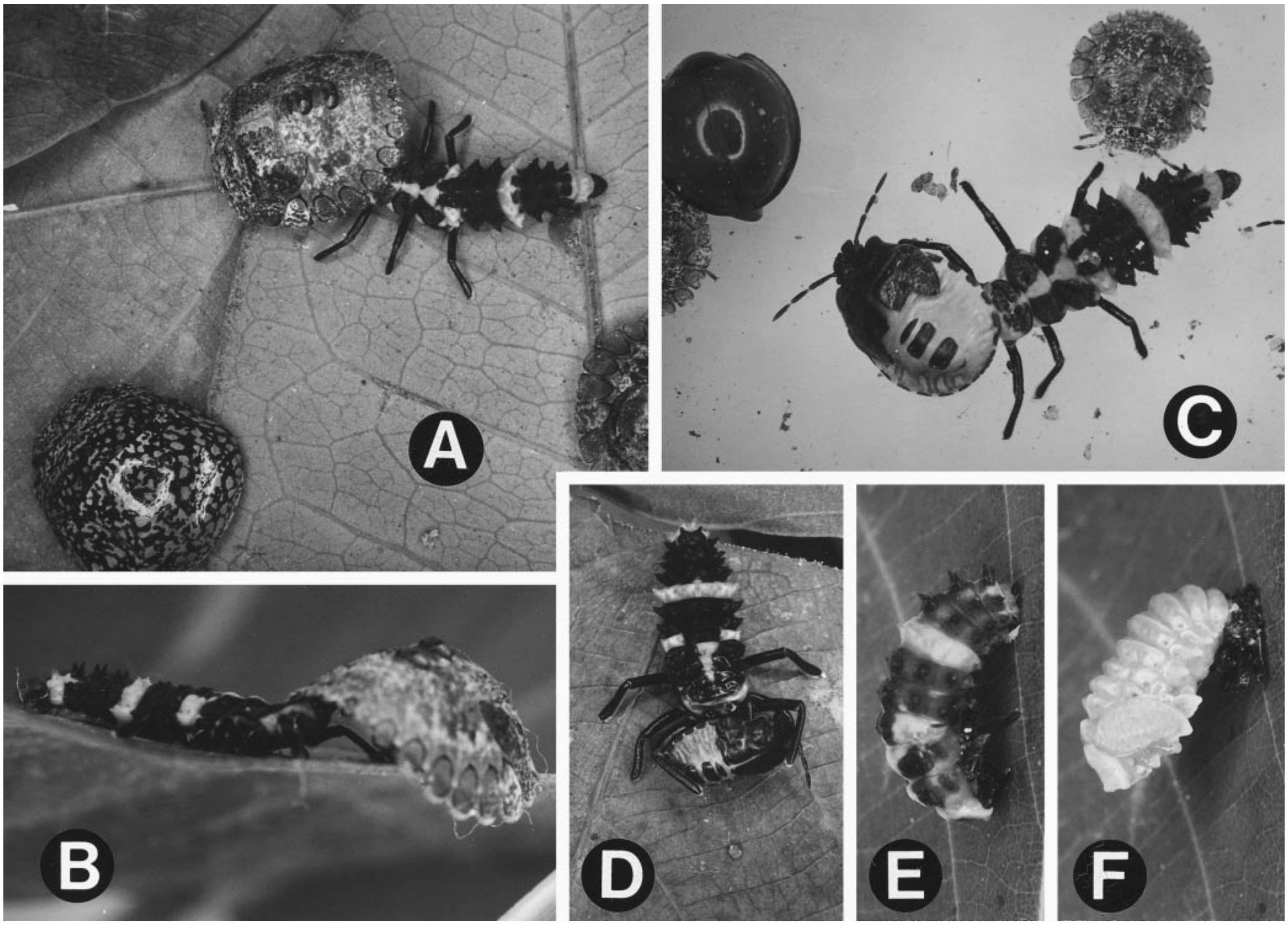


Figure 1
(A) A last-instar larvae *Anisolemnia tetrasticta* attacking a last-instar *Libyaspis* nymph by sliding the anterior part of her body under the bug; an adult is also represented in the picture. (B) Close-up of another attack. (C) Same behavior used during the attack of a *Caternaultiella rugosa* nymph; an adult ladybird is also represented in the picture as well as young nymph. (D) Grasping of a *Caternaultiella* nymph. (E) Prepupae of *A. tetrasticta.* (F) Pupae of *A. tetrasticta.*

oneer vegetal formations along forest edges, in the savanna, in cocoa tree plantations, and in the canopies of secondary and old forests. This species, which is nocturnal, can be active both day and night when exploiting large hemipterans (Dejean and Gibernau, 2000; Dejean et al., 2000a,b,c).

Caternaultiella rugosa is a plataspid heteropteran attended in shelters built by *C. brutus* or *Myrmicaria opaciventris* in the root area of *Bridelia* spp. (Euphorbiaceae). During periods of proliferation, colonies of this *C. rugosa* develop outside the shelters. In this case, the females guard their egg masses. Later, adults and last-instar nymphs place themselves above and around first instars (Dejean et al., 2000b; Gibernau and Dejean, 2000).

Libyaspis sp. is a plataspid that develops colonies without associated ants on branches of *B. micrantha* as well as on *Albizia* spp. and *Cassia* spp. (Leguminosae). In this study, colonies of 50–95 individuals generally established themselves on young branches. Adults are well protected by their pronotum and scutellum (see Figure 1). They group at the base of the branches where the colonies develop, so that it is difficult for crawling insects to access the nymphs situated on the distal part of the branches.

Anisolemnia tetrasticta subspecies *schoutedeni* (Coleoptera; Coccinellidae) was found on *B. micrantha* inhabited by *Libyaspis* sp. Females laid their eggs on the branches where *Libyaspis* proliferated. The adults and first-instar larvae fed on the eggs of *Libyaspis.* After the second moult, larvae preyed only on the first-instar nymphs of *Libyaspis,* while the larvae of later instars preyed on nymphs of a wide range of sizes. These ladybirds also explored other parts of the trees, thus enabling them to encounter the *Caternaultiella* at the base of the trunks. Last-instar larvae pupated on the branches of the trees.

Voucher specimens of ants, plataspids, and coccinellids were deposited and identified at the Museum of Natural History, London.

Preparation of experimental conditions

Colonies of *Libyaspis* sp. observed in different forests of southern Cameroon, as well as the branches supporting them, were transported in large plastic bags to the campus of the University Yaoundé I and Mvolier Valley, Yaoundé, two easily accessible sites where both *B. micrantha* and *C. brutus* were previously studied (see Dejean et al., 2000b; Gibernau and Dejean, 2000). Each branch with a colony of *Libyaspis* sp. was attached to a branch of the new supporting tree, onto which the colony spread. The coccinellids were introduced along with the *Libyaspis,* then their populations developed. In this way, we obtained 14 *B. micrantha* trees sheltering: (1) *C. brutus* attending *Caternaultiella* in shelters; (2) during periods of proliferation, *Caternaultiella* clusters developing at the base of the trunks, outside the shelters; (3) *Libyaspis* sp. colonies developing on the upper branches of the same trees; and (4) a population of *A. tetrasticta*. The latter developed first on the branches, preying on *Libyaspis,* but when the population increased some last-instar larvae foraged over entire trees and preyed on *Caternaultiella* clusters developing outside the shelters.

Predatory behavior of the coccinellid and plataspids' responses

Our studies concentrated on the predatory activity of a total of 193 last-instar larvae of the coccinellid. Ladybird larvae become more voracious and successful at capturing prey as they grow in size, with fourth-instar larvae consuming 65% of the total prey required for development (Dixon, 2000). Ladybirds were bred in petri dishes (8-cm diam) in which we introduced a 16-cm^2 piece of bark from *Bridelia*. We first conducted a series of 26 choice tests (26 different ladybirds used) by introducing into the petri dishes both a *Libyaspis* and a *Caternaultiella* nymph of the same size. We noticed each time the species of the individual attacked first. For the study of predatory behavior, the prey were introduced one by one. We recorded the behavioral sequences by direct observation. During preliminary experiments conducted under natural conditions, we noted the richest behavioral sequences, permitting us to establish data sheets that we used during experimentation to record each behavioral act performed (see Kenne et al., 2000). For each kind of prey, a flow diagram was built from observed data. We calculated percentages (transition frequency between behavioral acts) from the overall number of cases.

Ant reaction to the coccinellid larvae

We conducted observations on eight *B. micrantha* supporting both *Libyaspis* colonies on the branches and *Caternaultiella* associated with *C. brutus* at the base of the trunk. The behavior of the *C. brutus* workers when faced with the coccinellid last instar larvae were recorded (1) at the base of the trunk, near the shelters (less than 15 cm) where *C. brutus* attended *Caternaultiella*; (2) when the ladybirds attacked the attended nymphs of *Caternaultiella* outside the shelters; and (3) on the other parts of the trees.

To know whether attacked *Caternaultiella* nymphs attract their attending *C. brutus* workers, we conducted the following experiment at night. Nymphs belonging to clusters situated outside the shelters were excited during 10 s by rubbing the back part of their body with the tapered end of a graminaceous stalk. As a control, the end of a graminaceous stalk was rubbed against the bark of the trees in a zone situated close to clusters of bugs attended by *C. brutus* workers. We noted each time the number of *C. brutus* workers that approached and reached the excited bugs (experiment 1) or the brushed zone of the bark (control) among those situated within a radius of 20 cm (mostly occupied in attending bugs). We conducted the same experiment (experiment 2) with nymphs of *Caternaultiella* that we transported in petri dishes, then introduced onto the base of trees occupied by three *C. brutus* colonies that did not attend this plataspid; they were always accepted. In each case, 20 trials were conducted.

Statistical comparisons were made using the Kruskall-Wallis one-way test with post hoc pairwise comparisons (Statistix 4.1 software) for comparisons of aggressive behavior and Fisher's Exact tests (StatXact 3.1 software) for comparisons between attractiveness to attending *C. brutus* workers of clusters of bugs. We adjusted appropriate probabilities for the number of simultaneous tests using the sequential Bonferroni procedure (Rice, 1989).

RESULTS

Predatory behavior of the coccinellid last-instar larvae and reactions of the prey

A foraging ladybird larva always detected a prey by contact both under natural conditions (102 observed cases) and in the petri dishes (233 cases). Consequently, we did not note a significant difference from a random distribution during choice tests between nymphs of the two plataspid species in the petri dishes, as they attacked the *Libyaspis* nymphs first 11 times, and the *Caternaultiella* nymphs 15 times ($p = .39$).

Immediately after contact, the ladybirds tried to slide their long forelegs under the *Libyaspis* nymphs, then lifted and bit them on the ventral face (Figures 1 and 2A). Large, last-instar nymphs were never turned over, but smaller, third-instars were turned over in 42.1% of the cases ($p < .001$). In reaction to the attack, the *Libyaspis* nymphs pressed their body tightly against the plant surface, so that the hypertrophied lateral sides of the tergits came into contact with the substrate. This behavior, called "cowering" in coleopterans, permitted 27.8% of the last instars to escape the attack, but smaller nymphs were killed in all cases ($p < .001$; Figure 2A). We noted that, under natural conditions, cowering second- and third-instar nymphs are able to escape the attack of smaller ladybird larvae, and the relationship between prey and predator size thus plays an important role.

The *Caternaultiella* nymphs, which do not have hypertrophied extremities of the tergits, tried to escape at contact with the ladybird larvae. Only 12.9% of the last-instar and 3.3% of the third-instar nymphs succeeded in escaping (n.s.; $p = .095$). The behavioral sequences were more complex than for the *Libyaspis,* as the ladybirds, depending on the cases, slid their forelegs under the prey then lifted them or grasped and held them against their mouthparts, then bit them on the ventral face (Figures 1 and 2B).

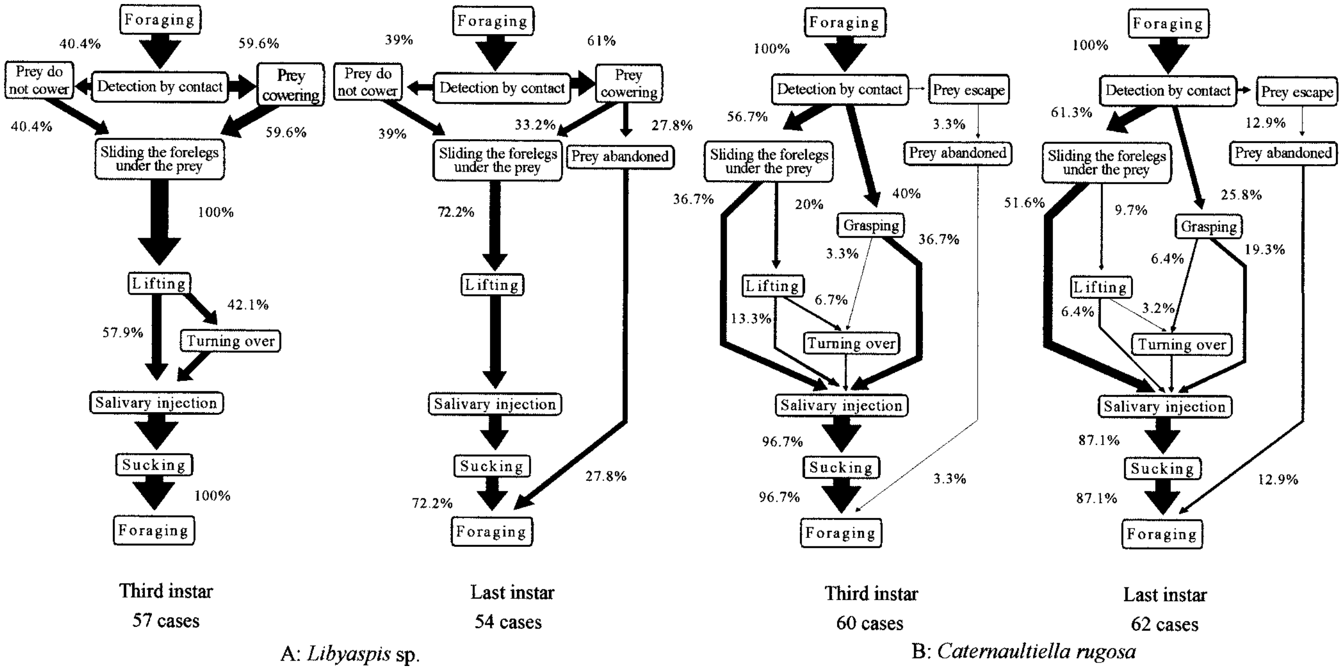
Reactions of the plataspid nymphs of a cluster when one of their congeners is attacked

When a ladybird attacked a *Libyaspis* nymph, three situations were recorded: congeners located within a radius of about 10 cm cowered and folded their antennae, while apparently continuing to suck sap (76.6% of 111 cases); the cluster broke up while only certain individuals cowered (21.6%); or only one individual left the cluster (1.8%).

In clusters of *Caternaultiella* composed only of nymphs, the congeners of a nymph attacked by a ladybird fled, and the cluster disintegrated (100% of the cases; $n = 12$). In clusters surrounded by adults, the reactions were more complex ($n = 11$). While the adults stayed in place but cowered, nymphs situated at the periphery indifferently stayed in place, moved toward the center of the cluster, fled, or dropped.

Reactions of *C. brutus* workers toward ladybirds

We observed a graded aggressiveness of *C. brutus* among the three behaviors of ladybirds (foraging on tree branches, approaching shelters, or attacking a *Caternaultiella* nymph; Figure 3). The different behaviors recorded fall into three groups: "nonaggressive behavior" (ignore; swerve; antennate with mandibles closed), "intimidation" (antennate with mandibles open; immobilization with mandibles open and antennae folded backward; immobilization with mandibles open followed by a back-and-forth movement of the body), and "aggressive behavior" (biting; venom spraying).



Third instar
57 cases

Last instar
54 cases

A: *Libyaspis* sp.

Third instar
60 cases

Last instar
62 cases

B: *Caternaultiella rugosa*

Figure 2
Diagrams of the behavioral sequences during prey capture by last-instar larvae of *Anisolemnia tetrasticta*. The percentage of escape from the ladybird attacks is significant between the last-instar larvae of (A) *Libyaspis* sp. and (B) *Caternaultiella rugosa* (Fisher's Exact test; $p = .038$), but not for third instar ($p = .26$).

When encountering ladybirds by chance on the tree branches, the *C. brutus* workers mostly ignored them or swerved (Figure 3A). Their aggressiveness was greater when a ladybird approached the shelters where workers attended *Caternaultiella*, with even cases of biting or venom spraying (Figure 3B). Nest mates were recruited in 57.6% of the cases ($n = 33$). As a result, the ladybirds turned back. Outside the shelters, *Caternaultiella* nymphs attacked by a ladybird triggered the disintegration of the cluster of congeners, while attracting one to three *C. brutus* workers (25 cases observed). Among the 78 workers situated within a radius of 20 cm of such an attack, 41 (52.6%) were attracted, while the others (47.4%) did not react. Attracted workers approached mandibles open; most of them bit the ladybirds, then cleaned their antennae and mandibles during more than one minute, or sprayed venom from a short distance (Figure 3C). All the ladybirds abandoned the prey as well as the area, but 76% of the bitten bugs died. A global statistical comparison resulted in a significant difference indicating that the *C. brutus* workers react differently according to the situation. The comparisons between the three groups also resulted in significant differences, confirming the graded aggressiveness of the workers according to the situation.

Reaction of *C. brutus* workers when a *Caternaultiella* nymph was artificially excited

When a *Caternaultiella* individual was artificially excited with the end of a graminaceous stalk, 41.9% of the workers within a radius of 20 cm were attracted and arrived with mandibles open, while most of the other nymphs flew away and the cluster disintegrated (experiment 1: 20 trials, 62 workers within a radius of 20 cm). Rubbing a graminaceous stalk on the tree bark in a similar manner as during the excitation of the bugs (about the same distance from the attending workers as in experiment 1) did not trigger a reaction from the bugs and only a slight one from the ants (12.7% of the workers attracted; control group: 20 trials; 63 workers within a radius of 20 cm), resulting in a significant difference with experiment 1 (Fisher's Exact tests and sequential Bonferroni procedure: $p < .001$). The excitation of *Caternaultiella* nymphs introduced into the hunting area of *C. brutus* colonies that did not previously attend this plataspid (experiment 2: 20 trials; 59 workers within a radius of 20 cm) only triggered slight reactions from the naive workers (16.9% of the workers). We therefore noted a nonsignificant difference with the control group ($p = .61$) and a significant difference with experiment 1 ($p < .01$).

DISCUSSION

Predatory behavior of the coccinellid last-instar larvae and reactions of the prey

This study presents a new illustration of the evolutionary arms race between prey and predators. The prey develops defenses including both morphological (hard dorsal cuticle and hypertrophied tergit extremities of *Libyaspis*) and behavioral traits (cowering), while the specialized predator foils these defenses thanks to a morphological adaptation (hypertrophied forelegs) coupled with a behavior adjusted to the situation (forelegs that the ladybird slides under the *Libyaspis* nymphs in order to lift them, then biting their ventral face). The proximity of the ventral nervous chain permits the injected saliva to act quickly, as we never observed nymphs struggling when bitten. Note that cowering is frequently cited as a defensive behavior in adult coleopterans that are protected by their thickened elytra, on which enemies' mandibles slip (Jiggins et al., 1993; Völkl, 1995).

The parsimony of the behavioral sequences when capturing *Libyaspis* versus *Caternaultiella* nymphs (Figure 2) can be interpreted as the result of evolutionary processes for a specialized predator well adapted to capture its essential prey. Sliding the forelegs under the prey body is unnecessary for the cap-

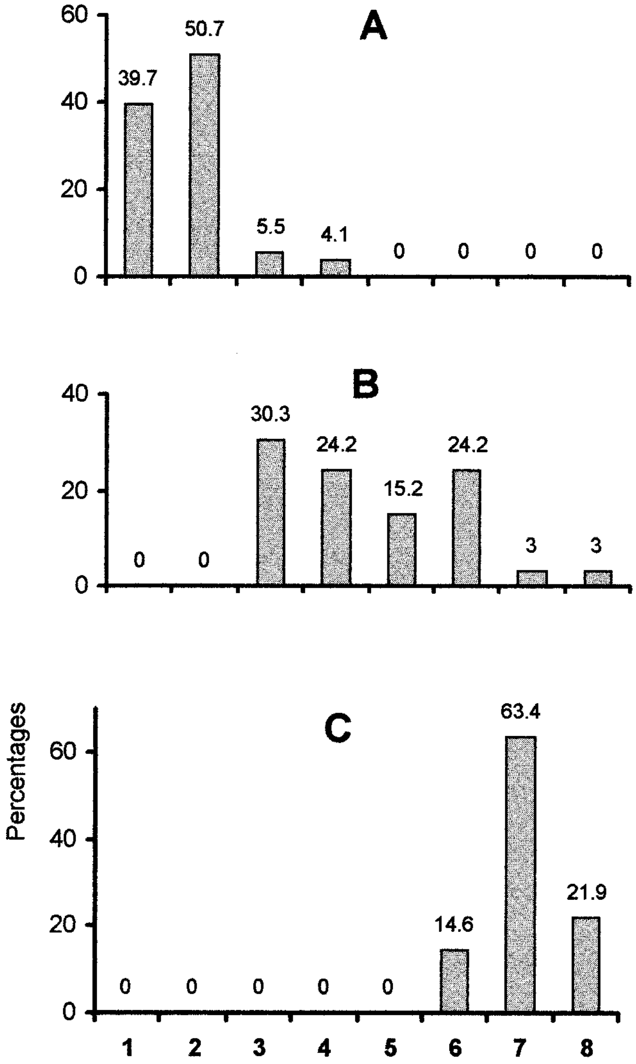


Figure 3
Graded aggressive behavior in *Camponotus brutus* workers according to the tree zone where they encountered the ladybirds: (A) encounters on the tree branches; (B) encounters at the base of the tree trunks, < 15 cm from the shelters); (C) when a *Caternaultiella rugosa* nymph attended outside the shelters was attacked by a ladybird. Bars represent, from left to right, nonaggressive behaviors: 1, ignore; 2, swerve; 3, antennate with mandibles closed (intimidation); 4, antennate with mandibles open; 5, immobilization with mandibles open and antennae folded backward; 6, immobilization with mandibles open followed by a back-and-forth movement of the body; and aggressive behaviors: 7, biting; 8, venom spraying. Statistical comparisons (nonaggressive behavior, intimidation, and aggressive behavior compared among the situations A, B, and C); Kruskall-Wallis test: 118.9; df = 2; $p < .0001$; multiple pairwise comparison of mean ranks: $p < .001$ in all cases (A × B; A × C; B × C).

ture of alternative prey, but only certain last-instar *A. tetrasticta* larvae grasped these alternative prey, while others behaved as when confronted with essential prey. The long forelegs are useful in this behavior, and the sequence, grasping/salivary injection, is strongly reminiscent of the behavior of several water bugs (Cloarec, 1974). Moreover, even when the ladybirds did slide their forelegs under the prey, in most cases they did not then lift the prey, as this behavior was unnecessary. As a result, the behavioral flexibility of the ladybirds concerned only a part of the tested individuals; the others had a tendency to react in a stereotypical manner.

Reactions of the plataspid nymphs of a cluster when one of their congeners is attacked

Although living in a group increases the risk of being detected, it is generally considered a selective advantage against generalist predators because it dilutes predation pressure and increases vigilance and defense (McEvoy, 1979). In our study, an attacked nymph emitted an alarm pheromone (see Dolling, 1991), triggering antipredator reactions from the congeners situated in the proximity in both plataspid species, but these reactions differed. The *Libyaspis* nymphs cowered in the large majority of the cases. As a result, they remained motionless even when one of their congeners was attacked and killed. This permitted the population cohesion to be maintained and so provided a better defense against further attacks. For example, cowering was sufficient against ant aggressiveness when we installed *Libyaspis* colonies on *Bridelia* for the first time in Yaoundé, and shortly thereafter the ants definitively ignored them. In contrast, the reaction of the *Caternaultiella* nymphs consisted of fleeing when a congener was attacked by a ladybird, making the clusters disintegrate. In heteropteran nymphs, the first of the three pairs of abdominal glands secretes a chemical attractive to conspecifics and causes aggregations to form, while the second and third secrete a chemical that causes aggregations to disperse (Dolling, 1991). This suggests that the two plataspid species used different glands when under attack by ladybirds, leading to different reactions from their congeners.

Response of attending ants in the case of *Caternaultiella*

Based on available evidence, we believe that the *Caternaultiella* alarm pheromone, acting as an allomone in this case, is attractive to ants, as has been recorded in aphids (Nault et al., 1976). Moreover, the action of this product is the result of a kind of learning on the part of the ants rather than due to similarities in the chemical structure between the alarm pheromones of the bug and the ant, as naive workers did not respond to stimulated nymphs. Learning in ants is well documented and concerns different behaviors (Corbara and Dejean, 2000; Hölldobler and Wilson, 1990; Johnson et al., 1994; Orivel et al., 1997).

Reactions of *C. brutus* workers toward foraging coccinellid larvae

As known for ant-attended aphids and scales (Bradley, 1973; Cudjoe et al., 1993; Jiggins et al., 1993; Nault et al., 1976; Stadler, 1991; Sudd, 1987), we noted a graded aggressiveness in *C. brutus* toward *A. tetrasticta* larvae according to the situation. When encountering *A. tetrasticta* on tree branches, *C. brutus* workers ignored them or swerved. As almost all of the perennial plants of equatorial countries are occupied by ants (see Dejean et al., 2000c), we hypothesize that the *A. tetrasticta* larvae are rather repellent to ants, permitting them to share trees with ants, as reported for other ladybird species (Sloggett and Majerus, 2000; Sloggett et al., 1998). Moreover, *A. tetrasticta* probably benefits from the ants' presence, as the latter ignored their pupae (see also Attygale et al., 1993; Völkl, 1995), while they attacked the pentatomid predator of these pupae (Orivel et al., personal observations). This situation differs from that of ladybirds that use camouflage to enter shelters where ants attend aphids (Völkl, 1995), as *C. brutus* workers are aggressive enough to force the ladybirds that approach the shelters where they attend *Caternaultiella* to flee. In this case, *C. brutus* workers can even bite the ladybirds or spray venom on them, but these behaviors are more frequent when the ladybirds attack *Caternaultiella* nymphs developing outside the shelters. In these cases, the release of a fluid from the large pores of the abdominal segments of coccinellid larvae deters the ants (see also Dejean, 1988; de Jong et al., 1991; Jiggins et al., 1993).

In conclusion, we have shown here that the ladybird *A. tetrasticta* is specialized in plataspid heteropteran predation. Although morphologically and behaviorally adapted to catch prey that cower, such as *Libyaspis* nymphs, its behavioral flexibility allows for the capture of alternative prey that escape, such as *Caternaultiella* nymphs. Moreover, this study permitted us to confirm that the relationship between *C. brutus* and *Caternaultiella* is truly mutualistic, as the attended plataspid is protected in this case against a predator (ant protection against a parasitoid wasp was demonstrated by Gibernau and Dejean, 2000). This protection seems efficacious, so that the predatory pressure of *A. tetrasticta* on ant-attended *Caternaultiella* is limited to the period of proliferation of this bug.

We are especially indebted to William R. Dolling (Brook Farm, Elstronwick, Hull, UK) for the identification of the Plataspidae and for providing helpful information on their biology. We are grateful to Amougou Akoa (University Yaoundé I, Cameroon), Barry Bolton, and Robert D. Pope (The Natural History Museum, London), for the identification of the plants, the Formicidae, and the Coccinellidae, respectively. This work was supported by the French Ministry of Cooperation (Project CAMPUS 108/CD/90).

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