

QUINONE MIXTURE AS ATTRACTANT FOR NECROPHAGOUS DUNG BEETLES SPECIALIZED ON DEAD MILLIPEDES

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Abstract—2-Methyl-1,4-benzoquinone (toluquinone) and 2-methoxy-3-methyl-1,4-benzoquinone are the most common components of defensive secretions of juliform millipedes (Diplopoda: Juliformia). A natural and a synthetic millipede-defensive secretion composed of these two substances attract dung beetles of a few *Onthophagus* species (Coleoptera: Scarabaeidae) that feed mainly on freshly dead millipedes. This olfactory mechanism and adaptation to the toxic effects of quinones enables them to be the first and exclusive users of this resource.

Key Words—Quinones, attractants, diplopod-defensive secretions, benzoquinones, dung beetles, necrophagy, Diplopoda, Scarabaeidae.

INTRODUCTION

1,4-Benzoquinones are the main components of defensive secretions of various groups of Arachnida and Insecta as well as of juliform millipedes (Diplopoda: Juliformia, orders Spirostreptida, Spirobolida, and Julida) (Blum, 1981; Huth, 2000). They are effective repellents for both invertebrate and vertebrate predators (Eisner et al., 1978; Weldon et al., 2003) and may take up more than 1% of the total body weight of a millipede (Demange, 1993; Huth, 2000). Even predators specialized on juliform millipedes may follow sophisticated strategies to avoid the quinones (Eisner et al., 1998). Because of the strong quinonoid smell of freshly

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dead Juliformia, they are unattractive for most necrophagous animals. However, in tropical regions, some dung beetles regularly feed on this resource (Cambefort, 1984; Krell et al., 1997; Krell, 1999; Brühl and Krell, 2003). They even copulate in the millipede carcasses, bring them in parts into their nest burrows, and use them as food for their offspring (personal observation).

We found that the defensive secretions of diplopods serve as an attractant for the beetles of some of these species (Krell et al., 1997, 1998; Krell, 1999; Brühl and Krell, 2003). In this study, we present further results on the attractive effect of defensive secretions of the millipede *Pelmatojulus tigrinus* (Hoffman and Mahsberg) (Spirobolida: Pachybolidae), analyze their chemical composition, and test whether benzoquinones are actually the attractive components.

METHODS AND MATERIALS

Study Area. We conducted our experiments from 1996 to 1998 in the Parc National de la Comoé in the north-eastern Côte d'Ivoire (Ivory Coast, West Africa) around the research camp of Würzburg University (Lola-Camp). This area is at the border between Guinea and Subsudan savanna attributed by Porembski (1991) to the former and by, e.g., Poilecot (1991), to the latter. Traps were set in the gallery forest of the Comoé river around the camp ($3^{\circ}48'58''\text{W}$, $8^{\circ}45'07'' - 14''\text{N}$) and in the savanna between the Lola creek and the Kongo river ($3^{\circ}45'58''\text{W}$, $8^{\circ}46'20''\text{N}$). Two traps were set in the wet gallery forest of the Iringou river ($3^{\circ}46'16''\text{W}$, $8^{\circ}50'21''\text{N}$), but included in the data set of the Comoé gallery forest (Table 1), because the studied millipede and beetle species occur in both habitats.

Traps. We used pitfall traps made of a blue (1996) or transparent (1997, 1998) plastic funnel (about 10 cm diam.; polyethylene) placed on the top of a transparent plastic cup (polystyrene) without conservation fluid. The bait was placed beneath the funnel at the bottom of the cup. Although no rain cover was installed, no trap suffered from flooding.

Bait. (a) Diplopod-defensive secretions: We used uninjured individuals of the large millipede *Pelmatojulus tigrinus* (Hoffman and Mahsberg, 1996) (Spirobolida: Pachybolidae) as donors of the defensive secretions. Rubbing the diplopods with toilet paper induced the animals to emit their defensive secretions. Such paper soaked by the secretions was used for the baiting experiments. In the control traps, we used unsoaked toilet paper. *P. tigrinus* is the most abundant diplopod species in the gallery forest of the Iringou river near our study area and forms a small population directly in the study area in the Comoé gallery forest as well (Mahsberg, 1997).

(b) Chemicals: The following substances were tested as attractants, sometimes dissolved in ethanol p.a. (Riedel de Haën, Germany, product number 32221): 1,4-benzoquinone, >98% (Fluka, Buchs, Switzerland, 12310; lot 341571 595

TABLE 1. NUMBERS OF INDIVIDUALS OF *Onthophagus latigibber* CAPTURED BY PITFALL TRAPS BAITED WITH DIFFERENT QUINONES IN THE GALLERY FOREST OF THE COMOÉ RIVER, COMOÉ NATIONAL PARK, IVORY COAST

Baits	Number of traps	Number of specimens of <i>Onthophagus latigibber</i>
1,4-Benzoquinone	29	0
2-Methyl-1,4-benzoquinone	16	0
1,4-Benzoquinone + 2-methyl-1,4-benzoquinone	2	0
2-Methoxy-3-methyl-1,4-benzoquinone	7	2
2-Methoxy-3-methyl-1,4-benzoquinone + 2-methyl-1,4-benzoquinone	12	73
2,3-Dimethoxy-1,4-benzoquinone	4	0
2,3-Dimethoxy-5-methyl-1,4-benzoquinone	4	0
2,5-Dihydroxy-1,4-benzoquinone	2	0
2-Methyl-1,4-hydroquinone	8	0
Control	26	0

and 358421/1 1296); 2-methyl-1,4-benzoquinone (toluquinone), >98% (Fluka, Buchs, Switzerland, 89590; lot 298563/1 795 and 358564/1 297); 2,3-dimethyl-1,4-benzoquinone (synthesized, procedure see below); 2-methoxy-3-methyl-1,4-benzoquinone (synthesized, procedure see below); 2,3-dimethoxy-5-methyl-1,4-benzoquinone, >99% (Fluka, Buchs, Switzerland, 38775; lot 256800/896); 2-methyl-1,4-hydroquinone (toluhydroquinone), >98% (Fluka, Buchs, Switzerland, 89600; lot 339925/1 595); 2,5-dihydroxy-1,4-benzoquinone, 98% (Sigma-Aldrich, Steinheim, Germany, 19,546-4; lot 10643-077). As the dispenser, we used white unperfumed toilet paper of Ivorian production. In the control traps, toilet paper without quinones but, whenever appropriate, with ethanol was exposed.

Synthesis of 2-Methoxy-3-Methyl-1,4-Benzoquinone. The benzoquinone was synthesized after Godfrey et al. (1974) and Luly and Rapoport (1981). The Vilsmeier complex for a Vilsmeier-Haack reaction was made by adding 82.5 ml phosphoryl chloride slowly to 150 ml dry *N,N*-dimethylformamide at 0°C. The complex was then added slowly to a solution of 93.1 g of 2,6-dimethyltoluene in 150 ml *N,N*-dimethylformamide at 110°C and was stirred at 110°C for 2 hr. The reaction mixture was diluted with aqueous sodium carbonate and extracted with ethyl acetate. After washing and drying of the organic layer the crude product was purified by crystallization. 2,4-Dimethoxy-3-methylbenzaldehyde (13.5 g) and *m*-chloroperbenzoic acid (25.3 g) were heated under reflux in 400 ml methylene chloride for 24 hr. ¹H NMR (CDCl₃) δ 1.95 (s, 3H), 4.02 (s, 3H), 6.61 (d, *J* = 9, 1H), 6.68 (d, *J* = 9, 1H).

Synthesis of 2,3-Dimethyl-1,4-Benzoquinone. The benzoquinone was synthesized as described by Sharma et al. (1985). 2,3,4-Trimethoxybenzaldehyde (10 g) and *m*-chloroperbenzoic acid (22.5 g) in 175 ml methylene chloride was stirred for 2 hr at room temperature. One hundred milliliters of 10% sodium thiosulfate solution were added, and stirring was continued for a further 45 min. The mixture was extracted with methylene chloride, washed, and dried. Solvent was removed under vacuum and 50 ml of a mixture of THF and methanol (1:1) were added at 0°C. Ice-cold 10% KOH (25 ml) was added in two portions while shaking. After 15 min, the solution was acidified with 5% HCl, extracted with methylene chloride, washed, and dried. After evaporation of the solvent, the crude oil was dissolved in 250 ml acetonitrile and was added slowly to a solution of ceric ammonium nitrate (25 g) in 250 ml water. Water (500 ml) was added and the mixture was shaken for 5 min. The mixture was extracted with methylene chloride, washed, and dried. The residue was purified by column chromatography and gave orange colored crystals (1.8 g). ¹H NMR (CDCl₃) δ 4.00 (s, 6H), 6.60 (s, 2H).

Chemical Analysis of the Defensive Secretions. We irritated living millipedes (*Pelmatojulus tigrinus*) mechanically till droplets of defensive secretion were visible on the cuticle, took the substance with filter paper, and extracted it immediately in methylene chloride (chromatography grade). Capillary gas chromatography–mass spectrometry (GC–MS) was performed on a Carlo-Erba HRGC 5160 gas chromatograph (now Fisons, Engelsbach, Germany) coupled with a Varian CH7 mass spectrometer (Varian, Palo Alto, CA). The GC was equipped with a DB-1 fused silica capillary column (30 m × 0.25 mm ID; df = 0.25 μm; J & W, Folsom, CA) using the following temperature program: 50°C for 2 min, increased at a rate of 20°C/min to 70°C, then 6°C/min to 200°C, and 20°C/min to 300°C, and held for 5 min at 300°C. Injection of 1 μl was carried out in the splitless mode for 1 min with an injection temperature of 300°C and a helium flow rate of 2 ml/min. Electron impact mass spectra (EI-MS) were recorded with an ionization voltage of 70 eV.

Experiments. (a) Natural defensive secretions (Figure 1): During the periods of April 4–May 8, 1996, June 10–August 8, 1997, and April 1–7, 1998, 57 traps baited with defensive secretions of *Pelmatojulus tigrinus* and 33 control traps were exposed before dusk (between 16:30 and 18:00) and collected between 21:00 and 23:00. The flight activity peak of the target species is between 18:00 and 19:00 (personal observations; for *O. latigibber*, see Krell et al., 1998). Our 1996 experiments (included in the present evaluation) have already been described by Krell et al. (1997).

(b) Artificial defensive secretions (Table 1): During the periods of March 20–April 11, 1996, May 6–August 9, 1997, January 31–February 1, 1998, and March 31–April 17, 1998, 84 traps with different quinones and mixtures of quinones (soaked in toilet paper) and 26 control traps (with untreated toilet paper) were

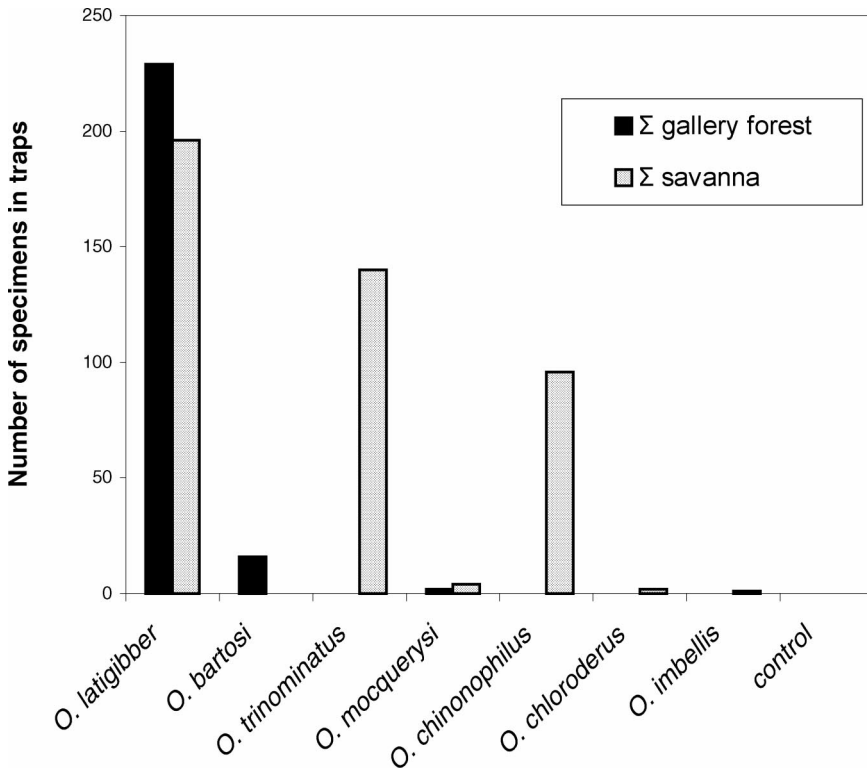


FIG. 1. Numbers of individuals of *Onthophagus* species captured by pitfall traps baited with defensive secretions of *Pelmatojulus tigrinus* (Diplopoda: Spirobolida).

exposed before dusk (18:00, some between 16:00 and 18:00) in the Comoé gallery forest and collected between 20:00 and 22:00.

Beetles. Beetles were identified by F.T.K. and specimens are deposited in The Natural History Museum, London.

RESULTS

Attracting Effect of Diplopod-Defensive Secretions. In 57 traps baited with defensive secretions of the millipede *Pelmatojulus tigrinus*, we found 686 specimens of seven species of the dung beetle genus *Onthophagus*. With the 33 control traps, no *Onthophagus* specimens were caught (Figure 1).

Millipede-defensive secretions act as attractants for these beetles both in the savanna and in the gallery forest. In the savanna parkland, 439 specimens of six species were caught in the baited traps, while in the gallery forest, 247 specimens

belonging to three species (Figure 1) were caught. *Onthophagus bartosi* Balthasar was only present in the gallery forest. *O. trinominatus* Goidanich, *O. chinophilus* Krell, *O. chloroderus* d'Orbigny, and *O. imbellis* d'Orbigny were present in the savanna parkland. The most abundant species, *O. latigibber* d'Orbigny, was dominant in both habitats. One of the abundant species is new to science and will be described as *O. chinophilus* in a separate paper.

Chemical Composition of the Defensive Secretions. We found by GC-MS analysis that the defensive secretions of *Pelmatojulus tigrinus* consist mainly of 2-methyl-1,4-benzoquinone (toluquinone) (EI-MS (70 eV): m/z (%) 39 (53), 54 (77), 66 (71), 82 (81), 94 (93), 122 (100)) and 2-methoxy-3-methyl-1,4-benzoquinone (EI-MS (70 eV): m/z (%) 39 (21), 53 (67), 66 (65), 82 (48), 94 (12), 109 (53), 122 (79), 137 (11), 152 (100)). Consequently, we tested these and related substances for attraction of beetles. The proportion of the two components differed between individuals, but 2-methyl-1,4-benzoquinone always occurred in higher concentration.

As minor components, we identified 2-hydroxy-3-methyl-1,4-benzoquinone (EI-MS (70 eV): m/z (%) 39 (8), 55 (25), 82 (35), 110 (10), 124 (29), 138 (100)), 2-methylhydroquinone (EI-MS (70 eV): m/z (%) 39 (8), 55 (6), 67 (11), 77 (10), 95 (20), 107 (11), 124 (100)), and 2,4-dihydroxy-6-methylbenzaldehyde (EI-MS (70 eV): m/z (%) 40 (30), 53 (20), 65 (10), 81 (18), 92 (17), 109 (12), 121 (11), 138 (100), 152 (72)). These components were not present in every sample and may be degradation products of the unstable 2-methoxy-3-methyl-1,4-benzoquinone rather than synthesized by the millipedes.

Attracting Effect of Quinones. In our comparison of the attraction of different quinones on *Onthophagus* dung beetles in the gallery forest, the mixture of the two main components of the defensive secretion (2-methoxy-3-methyl-1,4-benzoquinone and 2-methyl-1,4-benzoquinone) was most successful (Table 1). This mixture attracted 73 *O. latigibber* and 2 *O. bartosi*. The individual components attracted only singletons (2-methyl-1,4-benzoquinone: 2 *O. cyanochlorus* d'Orbigny; 2-methoxy-3-methyl-1,4-benzoquinone: 2 *O. latigibber*, 1 *O. bartosi*, and 1 *O. trinominatus*), whereas the other tested quinones did not attract a single beetle. Hence, the beetles were attracted specifically by the mixture of the two main quinonoid components of the defensive secretions.

DISCUSSION

Repellents as Attractants. Exploitation of olfactory signals, e.g., pheromones, by predators is a common phenomenon (Stowe et al., 1995; Zuk and Kolluru, 1998). However, defensive secretions of arthropods rarely have an attractive effect on other organisms. Single cases are known in which specialized predators use the defensive secretions of their prey to find them. Köpf et al. (1997) found a syrphid fly (Diptera: Syrphidae) to be attracted by the generally noxious salicyl aldehyde

produced by its prey, a leaf beetle larva (Coleoptera: Chrysomelidae). Crab spiders (Araneae: Thomisidae) were attracted by (*E*)-2-octenal and (*E*)-2-decenal, which are components of the defensive secretions of true bugs (Heteroptera) (Aldrich and Barros, 1995). Attraction of *Onthophagus* species to freshly dead millipedes is the first reported case of necrophages being attracted to a resource by its repellents.

Diplopod-defensive secretions did attract *Onthophagus* dung beetles effectively as we have already stated (Krell et al., 1997). It is highly improbable that a considerable number of beetles went into the baited traps by chance, since dung beetles generally do not walk randomly on the ground and do not land in numbers at a place where no resource is present.

Millipede Carcasses as Resource. Quinonoid-defensive secretions are effective repellents to vertebrates and invertebrates (Eisner et al., 1978; Hopkin and Read, 1992), but they do not protect the millipedes perfectly against predators. Beetles, assassin-bugs, ants, scorpions, centipedes, spiders, dormice, shrews, hedgehogs, mongooses, frogs and toads, lizards, turtles, birds, and monkeys are recorded to prey upon quinone-producing diplopods (Lévieux, 1972; Baker, 1985; Lawrence, 1987; Hopkin and Read, 1992; Valderrama et al., 2000; Mahsberg, personal communication). Wedge-capped Capuchin monkeys (*Cebus olivaceus* Schomburgk) anoint themselves with millipedes presumably using the quinonoid-defensive secretion as repellent for flies and mosquitoes (Valderrama et al., 2000; Weldon et al., 2003). Many animals may kill millipedes accidentally by trampling or deliberately as potential food, but neglect them afterwards because of the repellent smell. Phorid flies parasitize juliform millipedes (Disney, 1994). These facts result in fresh millipede carcasses or unused parts of them being available for exploitation by necrophages. If large juliform millipedes are abundant, their carcasses are a regularly available resource for necrophages. However, they contain quinones in high concentrations (Demange, 1993; Huth, 2000) and are, therefore, an unattractive and unsuitable resource for most necrophages.

2-Methyl-1,4-benzoquinone (toluquinone) and 2-methoxy-3-methyl-1,4-benzoquinone are the most common compounds in defensive secretions of juliform Diplopoda (Eisner et al., 1978; Blum, 1981; Attygalle et al., 1993; Huth, 2000). The seven dung beetle species we found in our baited pitfall traps are not only able to cope with the deterrent and toxic quinones, but to use the most common of them as a cue in resource-location. This mechanism enables dung beetles to be recruited to cadavers more rapidly than competitors that use the scent of decomposition when locating them because the quinonoid smell emerges immediately when a millipede is killed, whereas the smell of rotting appears later.

Since large juliform millipedes are abundant in the African tropics (Dangerfield, 1990; Mahsberg, 1997) specialization on their fresh carcasses, which are unattractive for most necrophagous competitors, is probably an advantageous strategy. Indeed most of the individuals found in our traps belong to species specialized on millipede carcasses (*O. latigibber*, *O. bartosi*, *O. trinominatus*,

O. chinophilus, *O. chloroderus*, and *O. imbellis*; Cambefort, 1984; personal observation). As with most “specialized” dung beetle species, this means that they strongly prefer the particular resource, but are occasionally found on other resources. Singletons of *O. latigibber* have been found on reptile and amphibian carrion and on human feces and buffalo dung (Cambefort, 1984; personal observation). *O. bartosi* was caught in traps with fish and amphibian carrion by Cambefort (1984). *O. mocquerysi*, which was only occasionally attracted to defensive secretions (Table 1), and *O. cyanochlorus* d’Orbigny, which was found once in a trap with toluquinone, seem to be generalists. Cambefort (1984) considered the former to be a satellite species in coprocenoses of human feces and other “petits excréments les plus divers,” and it was even found in elephant dung (Frey, 1961). However, 99.0% (758) of the 767 specimens captured in all experiments belonged to specialist species.

High abundance and permanent availability of a resource during the activity period of potential users may cause specialization of the users involving complex adaptations (i.e., coping with the toxicity of quinones). Are there users of dead millipedes if this resource is rare?

Attraction of dung beetles by quinonoid-defensive secretions of diplopods is not limited to the Afrotropical region. In Borneo, where large millipedes are rare, we found *Onthophagus penicillatus* Harold, *O. rudis* Sharp, and two species of Hybosoridae (Scarabaeoidea) attracted by the quinonoid-defensive secretions of Harpagophoridae (Brühl and Krell, 2003). All of these beetle species are generalist necrophages. At least for *O. penicillatus*, necrophagy on juliform millipedes is known (Masumoto, 2001). Although the resource is rare, these beetles are adapted on and even attracted by the quinonoid-defensive secretions. However, since the resource is rare, specialization was obviously not an advantageous strategy.

Attractants for Dung Beetles and Other Scarabaeoidea. Odorous components of feces that attract coprophagous dung beetles (including *Onthophagus* species) most efficiently, particularly as a bouquet, are 2-butanone, cresol, indole or skatole, and butyric acid (unpublished results; Inouchi et al., 1988). Phenol is also attractive (Inouchi et al., 1988). It is conceivable that receptors for cyclic compounds might have been modified in evolution to become sensitive to benzoquinones, since, for instance, phenol and cresol are structurally closely related to benzoquinones. Recently, benzoquinones were found to attract phytophagous and xylophagous Scarabaeidae of other clades: 1,4-benzoquinone is a sexual pheromone of a European cockchafer (*Melolontha hippocastani* Fabricius, Melolonthinae; Ruther et al., 2001) and an attractant for males of the chafer *Rhizotrogus vernus* Germar (Melolonthinae; Imrei et al., 2002). The same substance and different substituted benzoquinones, among them toluquinone and 2-methoxy-3-methyl-1,4-benzoquinone, attracted an Afrotropical rhinoceros beetle (Dynastinae; Krell et al., 1999). Because of the possible modification of receptors to be perceptive for quinones and the existence of quinone receptors in other clades of the Scarabaeidae,

the exploitation of a novel resource using quinones as odorous cues was probably only a small evolutionary step for the *Onthophagus* species.

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