Natural History and Behavior of *Nordus fungicola* (Sharp) (Coleoptera: Staphylinidae)

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ABSTRACT Details on the natural history and behavior of *Nordus fungicola* (Sharp) in Barro Colorado Island, Panama are presented. These beetles have bright coloration and wave their abdomen conspicuously. They feed on small drosophilid flies or fly larvae, and the typical grooming behavior after feeding is described. Beetles interacted aggressively with ants of the genus *Ectatomma,* and a preliminary experiment shows that beetles may use chemical secretions for defense. Male–male and male–female interactions, and copulatory courtship are described. Males were not observed guarding females after mating. Females are not receptive after copulation.

KEY WORDS behavior, copulatory courtship, Staphylinidae, *Nordus fungicola*

Nordus fungicola (SHARP) BELONGS to the rove beetle family Staphylinidae (Staphylininae: Staphylinini: Xanthopygina), which consists of >46,200 described species (Newton et al. 2001) and represents one of the most dramatic radiations in the history of life. Despite the fact that staphylinids are abundant and surely ecologically important in many microhabitats (Ashe 1998), very little is known about their behavior and ecology. Knowledge on the behavior and natural history of the Xanthopygina is so limited that for many of the genera (e.g., *Elmas* and *Allostenopsis*) we do not even know the habitat in which they occur. A few seminal studies suggest that their great diversity is accompanied by a diverse array of complex behavioral patterns, often mediated by chemical communication or secretions from complex and highly specialized gland systems (Peschke 1987, Alcock and Forsyth 1988, Forsyth and Alcock 1990a,b, Alcock 1991, Peschke et al. 1996, Betz 1999).

The genus *Nordus* has a neotropical distribution and currently includes 36 species. *N. fungicola* is ideal for studying the natural history and behavior of a rove beetle. It is abundant in certain localities (e.g., Barro Colorado Island, Panama) and can be easily found in the lowland tropical rainforests of southern Costa Rica and Panama, because it is a diurnal beetle that is commonly visible on top of rotting fruits and mushrooms.

Adults of *N. fungicola* (Fig. 1) are easily recognized by their striking colors. The head, pronotum, and elytra are brilliant golden-red, and the abdomen is shining black with patches of whitish pubescence and a bright yellow apex. These relatively large (up to 1.5 cm in length) staphylinids fly vigorously around rotting fruitfalls and fungi during the day, frequently landing on the surrounding vegetation where they engage in a variety of behavioral interactions with conspecifics and others. The aim of this paper is to provide data about the natural history and behavior of these beetles.

Materials and Methods

Field observations were made on Barro Colorado Island (BCI), Panama, from 8 June to 12 August 2000 and from 5 July to 13 July 2001 between 0900 and 1800 h. Analysis of feeding, mating behavior, and other interactions was based on field observation, videotape recordings (Sony Hi8, Tokyo, Japan), and photographic slides. Ten adults were kept in a metal cage (30 by 30 by 30 cm) in a shaded area of the laboratory clearing for observations during the night.

Beetles interact with ants of the genus *Ectatomma* (Formicidae) on rotting fruits in the forest. To test the role of chemical secretions on the ant–beetle interactions, 82 beetles were collected and killed by freezing (−15°C). Twenty-nine beetles were kept in n-hexane for 6 h to remove nonpolar hydrocarbons from their external cuticle and afterward were placed in an oven for 12 h to remove the n-hexane. I presented treated beetles (hexane extraction, presumably without nonpolar hydrocarbons) and frozen but untreated beetles (presumably still containing nonpolar hydrocarbons) to ants of the genus *Ectatomma* as food by placing them in the pathway between the ant colony and the rotting fruits of *Gustavia superba* Berg (Lecythidaceae). The pathways were new every day and were established by the ants before the beginning

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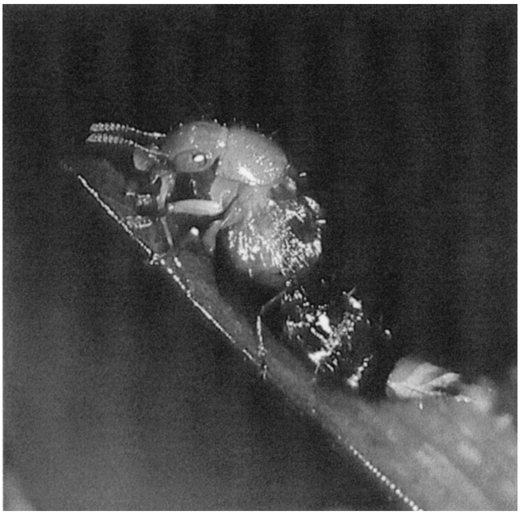

Fig. 1. *N. fungicola* on leaves in Barro Colorado Island, Panama. Reprinted from Chatzimanolis 2000, with permission from the Journal of the Kansas Entomological Society.

of the trials. Only one beetle was presented at a time, the ant involved in the interaction was removed from the colony after the trial, and not >10 beetles were presented per colony.

Results

General. Adult beetles flew vigorously around rotting fruits on the forest floor (palm or *G. superba*) or fungi. On landing on the substrate, they always ($N = 590$) raised their abdomens over their backs (Fig. 2) and waved them antero-posteriorly four or five times, followed by a slower side to side movement, and prominently displayed the brilliant yellow apex of the abdomen. All other species of staphylinid beetles observed in the field waved the abdomen up and down only; they were never observed to wave their abdomen in a left-right motion. Forsyth and Alcock (1990a) reported that *Leistotrophus versicolor* (Gravenhorst) moves the abdomen from side to side but did not mention an up-and-down movement. When disturbed by sudden movement and perhaps loud noises, *N. fungicola* flew away and landed on the surrounding vegetation, usually within a meter of their previous place. Sometimes ($N = 40$) when individuals of *N. fungicola* were on vegetation surrounding rotting fruits and fungi, they performed a 360° turn lasting 1 min, periodically waving their abdomen.

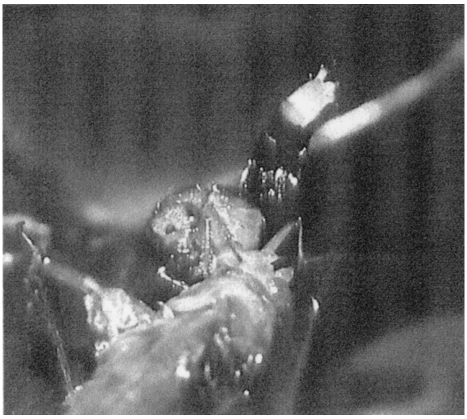

Fig. 2. *N. fungicola* waving its abdomen.

Individuals of *N. fungicola* used mostly the middle and hind legs for walking, and when standing, the front legs almost never touched the substrate. The front legs were used for grooming and feeding (described below).

Approximately 10 *N. fungicola* were kept in a metal cage for a period of 2 wk. The captured adults were not active at night; at this time they remained motionless on the walls of the metal cage while being grouped together within a radius of 3 cm.

Both sexes have a pair of apicolateral tergal glands beneath abdominal segment VIII that were everted when the beetle waved its abdomen and were visible with the aid of a 200-mm telephoto lens. Secretions from these glands were bright yellow, had a piquant smell, and left a brownish stain on human skin, which suggests the presence of quinones (Peschke and Metzler 1982). Also, when the beetles were under stress, they secreted a brownish fluid from the mouth. More detailed results of the chemical analyses of both chemical secretions will be presented elsewhere.

Grooming. Grooming behavior always took place immediately after food intake and also occurred at other intervals. The front legs (especially the setae on the protarsi and the protibiae) were used to clean the mouthparts and the head in a circular motion, starting behind the head and ending at the mouthparts. The protarsi of both males and females are greatly enlarged, and effective grooming might be a function of these enlarged tarsi. The head turned right and left to facilitate the movement of the front legs. The middle legs were used to clean the hind legs and to brush off the elytra and the first abdominal segments, while the hind legs were used to clean the rest of the abdomen. When cleaning the abdomen, the beetles curved the last abdominal segments downward to reach the more apical segments. Also, the hind and fore legs were rubbed against each other. The hind wings were folded beneath the elytra with the help of the upwardly bent abdomen.

Feeding. Adult beetles of both sexes stalked and attacked drosophilid flies ($N = 196$) on a variety of substrates. Most commonly, the substrate was rotting fruits of palm or rotting fruits of *G. superba*, but the beetles also exhibited this behavior on mushrooms ($N = 5$), monkey feces ($N = 2$), and on fruit piles of banana and watermelon created by the observer either in the laboratory or in the field. *N. fungicola* slowly approached the drosophilid flies with small "steps" until one-half a centimeter away, and then quickly attacked by extending the front legs, mandibles, head, and thorax toward the fly. The final strike was given usually with the enlarged protarsi and more rarely

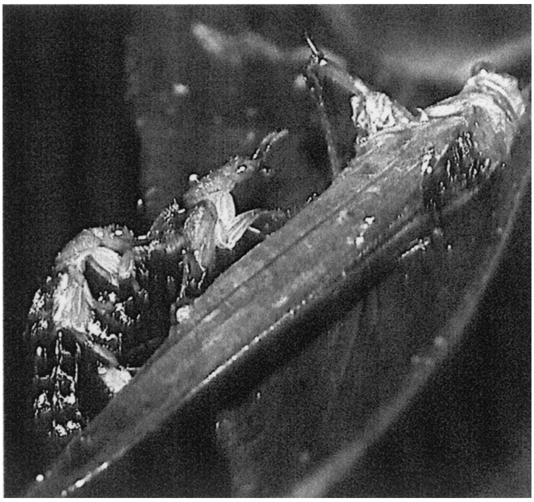

Fig. 3. Mating almost always occurs near sources of food.

Fig. 4. Touching the tips of the abdomen is a typical male–male interaction.

with the mandibles. The beetle manipulated the captured fly with its front legs and mandibles and chewed and sucked its body. Many beetles in the family Staphylinidae, like most predaceous terrestrial arthropods (Cohen 1995), feed by extraoral digestion. Adults were observed eating three to four drosophilid flies in sequence, and if undisturbed afterward, remained at the site for ≈15–20 min without any apparent activity. Beetles never tried to attack and seemed to avoid interactions with flies larger than or equal in size to the common house fly (*Musca domestica* L.).

Adults attacked other fly larvae, especially the larvae of *Ptecticus nigrifrons* Enderlein (Stratiomyidae) in *G. superba* fruits ($N = 18$) (Chatzimanolis 2000). They also used their mandibles to cut open rotting mushrooms ($N = 5$) to extract fly larvae. The larvae of *N. fungicola* similarly fed on fly immatures in *G. superba* fruits (unpublished data). Adults were also observed eating dead, rotting moths ($N = 2$) and similarly decomposed crickets ($N = 3$).

Mating. In total, 15 mating events were observed, 4 of which were recorded with a camcorder. Mating was observed only near sources of food and in particular on *G. superba* fruits ($N = 11$), on leaves near a dead cricket ($N = 3$) (Fig. 3), and on monkey feces ($N = 1$). On three occasions, a large aggregation of beetles was observed on rotting *G. superba* fruits. I sampled the beetles from three of these aggregations and found that there was a male biased sex ratio (9:1, 10:1, and 11:1, respectively). In these cases, males did not defend a specific territory on the fruits and kept moving constantly.

In these aggregations, males were not aggressive to each other and were never observed fighting with their mandibles. When one male encountered another, they faced each other and approached until they were approximately a half-centimeter apart. They turned rapidly, almost 90°, repeatedly touching each other with the apices of their abdomens (Fig. 4) for less than 2 s ($N = 57$).

When a female landed on the substrate, the closest male attempted to mate with her. Females sometimes ($N = 10$) avoided copulation by rapidly waving their abdomens when the male tried to mount them. There was no apparent courtship before copulation except that males slowly approached females from behind and touched their antennae to the female abdomen for 1 s before attempting to mount.

The following description of copulatory courtship was the same for all mating events observed. Beetles mated in a parallel position, with the male on top of the female, for ≈69.5 ± 1.2 s. During the first phase of copulation, both middle legs of the male simultaneously tapped the last abdominal segments of the female slowly and both front legs simultaneously tapped the first segments of her abdomen. The male jerked his body forward and dorsally at periodic intervals. All the above movements were relatively slow. After ≈30–40 s (time varied in different mating events), the male started jerking his body more rapidly and tapped on the female's body more quickly; this marked the initiation of the second phase. In both phases the frequency of tapping with the front legs was about twice the frequency of tapping with the middle legs. This general pattern of copulatory courtship, consisting of two distinct phases, is similar to that described for *Megalopus armatus* Lacordaire (Coleoptera: Chrysomelidae) (Eberhard and Marin 1996) and in a very general way to that of other insects and arachnids (Eberhard 1991, 1994).

In four different mating events, another male tried to displace the male that was mating and attach himself to the female by curving his body and attempting to replace the copulating male's genitalia with his own. These attempts were unsuccessful.

After mating, the pair usually ($N = 13/15$) repeatedly touched each other with the tips of their abdomens and separated a few seconds later. Females did not try to mate again with the same or another individual for as long as observations were possible. Females left the fruit pile after a few minutes and ovi-

Table 1. Acceptance of beetles with and without nonpolar hydrocarbons

	Beetles rejected as food	Beetles accepted as food
Nonpolar hydrocarbons absent	1[a]	28
Nonpolar hydrocarbons present	12	31

[a] Fisher's exact test ($P = 0.01$).

posited in a different fruit pile, away from the fruit pile of the mating event.

A unique phenomenon present in these beetles is the large aggregations of males (although rarely observed; only three times in a period of 12 wk) on rotting fruits of *G. superba.* This system cannot really be defined as leks, because females can use the fly larvae in the fruits as a food resource and because it is not clear if there is differential mating success among males, but rather is a scramble competition system, probably without aggression, that may arise because of the high density of rival males on fruits.

Interactions with Other Insect Species. When another insect approached, the beetles generally started oscillating their antennae in a vertical plane (0 to 45°) at an increased rate. They also waved their abdomens faster for a period of a few seconds.

Adults of *N. fungicola* were extremely aggressive (i.e., attacked with their mandibles) when interacting with adults of a related xanthopygine, *Xenopygus analis* (Erichson) ($N = 7$) and other staphylinids ($N = 4$). These beetles share the same habitat (i.e., rotting fruits) with *N. fungicola* but are rarely seen because they tend to be under or inside the substrate. The aggressive behaviors were observed in those rare instances when they appeared on the surface of the substrate. Beetles did not interact with dung beetles ($N = 20$) or cockroaches ($N = 3$) that were also present on rotting fruits.

Both *N. fungicola* and ants of the genus *Ectatomma* fed while on rotting *G. superba* fruits. Ants fed on the actual fruit, whereas the beetles fed on flies and fly larvae that were on or in the fruits. The beetles and ants only interacted if they were less than 1 cm apart. If an ant approached a beetle, the beetle would immediately turn its abdomen toward the ant and rapidly wave it back and forth multiple times ($N = 32$). In the vast majority of instances ($N = 25$ of 32; 78.1%) the ant left immediately.

To test whether chemical substances are involved in the interaction, a preliminary experiment was made in which beetles with and without nonpolar hydrocarbons on their bodies were offered to the ants as a source of food (see Materials and Methods). The results are shown in Table 1. These results demonstrate that ants more often rejected beetles that had nonpolar hydrocarbons on their bodies (Fisher exact test, $P = 0.01$) than beetles lacking nonpolar hydrocarbons.

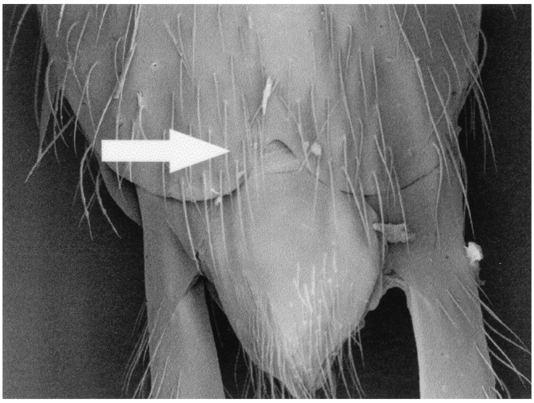

Fig. 5. The last abdominal sterna of *N. fungicola.* The white arrow points on the "v" shape modification of the eighth sternum.

Discussion

Betz (1999) described the grooming behavior for various *Stenus* (Coleoptera: Staphylinidae) species, and Valentine (1973) described the general patterns of grooming behavior in Coleoptera. Betz (1999) mentioned that the main role of the self-grooming behavior was to spread pygidial secretions over the entire body, which could act as fungicides, antimicrobics, or even make the beetles unpalatable to predators. This may be the case in *Nordus* as well, because the grooming behavior in *Nordus* is almost identical to that described by Betz (1999) for *Stenus.*

Recently, Betz and Mumm (2001) published data on the predatory legs of *Philonthus marginatus* (O. Müller) (Staphylinidae). He described the functional morphology of the legs and especially how they are used to capture prey. *N. fungicola* appears to have similar front legs (with greatly expanded tarsi, see Fig. 1), and observations in the field suggest that the same mechanisms that operate in *Philonthus* are present in *N. fungicola.*

Nordus, along with *Elmas* and *Allostenopsis,* are the only genera in the subtribe Xanthopygina (total of 37 genera) with relatively big eyes (in proportion with the rest of the head). Among these genera, *Nordus* has proportionally the biggest eyes, and these could be a strong aid in the pursuit of prey. However, I was not able to tell if the beetle oriented its longitudinal body axis with the prey, so it is not clear if there was a visual alignment with the prey stimulus.

Males of all species of the genus *Nordus* have well-developed secondary sexual characters that are absent from most other genera in the subtribe Xanthopygina. These secondary sexual characters are extreme modifications of the apical margins of the seventh and eighth abdominal sterna (Fig. 5). These structures are displayed when male beetles wave their abdomens, physically contact other individuals in male–male interactions, and in postmating male–female interactions. Eberhard and Marin (1996) argued that a first step in determining the function of a sexually dimorphic character is to see if it is used in male–male or male–female interactions. He stated that if the structure is displayed in male–female interactions in a way that would increase the female's perception of it, then this structure is likely to have a role in sexual selection by female choice. If, however, the structure is used in male–male combat in a way that will increase their mating success, then it is likely to have a role in sexual selection by male combat. In this case, however, these sexually dimorphic structures do not seem to be used in any of the above instances.

Male–male interactions appeared not to be aggressive and to not affect male mating success. There is, however, the hypothesis that males interact with chemical secretions and thus their behavior might be aggressive. The male–female interaction, besides mating, is only postcopulatory, because before copulation, the male sexual characters do not come into contact with the females. One can argue that males display their secondary sexual characters to females by waving their abdomens, but these structures are relatively small and it is doubtful that females can actually see them from a distance of a few centimeters. Also, it is not clear if the male's secondary sexual structures contact the female's abdomen during copulation and if they have any role during copulation.

Males of *N. fungicola* do not guard females after mating as do males of the related staphylinids *Ontholestes cingulatus* (Gravenhorst) (Alcock 1991), *L. versicolor* (Alcock and Forsyth 1988), and genus *Eumicrota* (Ashe 1987). Females of all of the above species except *N. fungicola* are receptive immediately after mating, and so the benefit to males of guarding females immediately after copulation is high. *N. fungicola* females, however, are not receptive after mating and also do not oviposit at the mating site (like *L. versicolor*), and thus, there is no need for males to be involved in such a high-cost behavior as mate-guarding.

An interesting aspect of the biology of *N. fungicola* is chemical communication. The preliminary experiment presented here suggests the use of secretions for chemical defense in interspecific interactions. A factor not taken into consideration here is the waving of the abdomen (the bright yellow tip could a strong visual signal) and the influence it could have in combination with the chemical secretion in repelling the ants. Further experimental manipulation is needed to determine if the behavior exhibited by the ants is caused only by the release of chemical substances by *N. fungicola* or by a combination of the chemical and visual signals. It is not clear, however, if there is chemical communication in intraspecific interactions, either between males or between males and females.

This study establishes the ground plan for the behavioral interactions of *N. fungicola,* although much more work must be done in all the several aspects of the behavior described above. It is yet unknown if all species of *Nordus* exhibit similar behaviors. Although some of the behavioral aspects (for example grooming or mating behavior) described above are expected to be similar in other genera of the subtribe, other aspects like the chemical interactions or the peculiar waving of the abdomen of *Nordus* may be unique for xanthopygines or even staphylinids. The phylogenetic position of *Nordus* is still enigmatic within the Xanthopygina, and for that reason, it is difficult to place the above behavioral observations in a phylogenetic context. The absence of other behavioral observations in Xanthopygina makes it difficult to place the above behavioral observations even in a taxonomic context.

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