# Behavioral Repertory of Adult *Cylas formicarius* (Fabricius) (Coleoptera: Brentidae)

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## Abstract

Adult female and male sweetpotato weevils, *Cylas formicarius* (Fabricius), have repertories of at least 19 and 21 behavior patterns, respectively. These are described and named, including eight self-grooming patterns. Consistent with the species' slight sexual dimorphism, few behavior patterns are peculiar to one sex. The sequence of self-grooming movements is analyzed for each sex. Comparative assays of vagility and overall activity do not show any difference between the sexes.

*Cylas* Latreille is a paleotropical genus of about 25 known species that form a distinctive group within the superfamily of weevils (Coleoptera: Curculionoidea) and are currently placed in the family Brentidae (Wolfe 1991; Thompson 1992). The sweetpotato weevil, *Cylas formicarius* (Fabricius), feeds and breeds on *Ipomoea* spp. and other Convolvulaceae (Austin 1991). Worldwide, it is the foremost pest of sweetpotato, *Ipomoea batatas* (L.). Because of its economic importance, *C. formicarius* has been the subject of much research, including several basic bionomic studies (Sutherland 1986 and references therein). Some of these (*e.g.*, Gonzales 1925) include occasional comment on behavior.

Adult *C. formicarius* are slender, smooth, and hard-bodied (Fig. 1). Sexual dimorphism is slight and appears limited to the antennae, eyes, and wings (Starr *et al.* 1997). The antennae are similar in structure, but much longer in males. Males likewise have substantially larger eyes. Differences in wing size are slight, though statistically significant. Both sexes fly and appear to be more active at night, with males reportedly more vagile than females (Christian 1938; Howard 1982; Proshold 1983). Aside from this, no secondary sexual behavioral differences have been noted, as far as we know.

Valentine (1973) reviewed grooming behavior in beetles, identifying 17 behavior patterns. Our purpose here is to provide a behavioral catalog of adult *C. formicarius*, with a discussion of sexual diethism.

## Material and Methods

All weevils were of the "elegantulus" color form, drawn from a laboratory culture at the University of Georgia, USA. As a safeguard against any genetic adaptation to laboratory conditions, wild-caught insects from southern Florida were added periodically to the culture. Voucher specimens are deposited in the University of Georgia's Museum of Natural History (UGCA) and the personal collection of G. William Wolfe.

Except where noted, all observations were made under red light to simulate night. We observed females and males in a variety of situations. In each of these, we began with a period of qualitative observation in order to form a preliminary catalog. This was followed by at least one longer period, in which we counted occurrences (acts) of different behavior patterns and refined our descriptions of these. The following are the situations employed, in which "segregated" means that each chamber contained only same-sex

**Fig. 1.** Male *Cylas formicarius* in the rearing-up posture. Body length = 6 mm, including proboscis. Photograph by Melvyn Yeo.

individuals, while "integrated" means that each chamber contained individuals of both sexes. A "bare" chamber is one with a filter-paper floor and a drop of water. Numbers in brackets are summed recorded acts by females and males, respectively, in the given treatment, for a total of 1,984 female acts and 2,168 male acts.

1. Segregated in a bare chamber (510, 519).
2. Segregated with sweetpotato after fasting one day (491, 533).
3. Integrated with sweetpotato after fasting one day (501, 585).
4. Integrated with potted sweetpotato plant under dim white light (245, 274).
5. Segregated in olfactometer chamber with sweetpotato leaf odor flow (237, 257).

Outside of these five situations, we supplemented the qualitative-descriptive treatment of some uncommon patterns, with emphasis on sexual behavior and oviposition.

Our observations were in an area in which *C. formicarius* is not found in the wild. The necessary quarantine conditions prevented any significant observations or assays of flight or flight-related behavior.

After noting presumed self-grooming patterns in the course of compiling the behavioral catalog, we observed segregated groups of 2-3-week-old weevils in bare, white-lit chambers with attention only to bouts of grooming, *i.e.*, sequences of grooming acts uninterrupted by non-grooming behavior. This treatment served to refine our description of these behavior patterns and our estimations of their relative frequency. Because we watched several individuals at once, we were not always sure that the first grooming motion noted was in fact the first of the bout. Where grooming was apparently disturbed by another individual, the bout was disregarded in computing bout lengths and terminal patterns.

To compare the overall activity level between sexes, we performed two replicates of the following assay. Five females and five males were isolated in standard plastic Petri dishes (inner diameter 94 mm and height 13 mm) and allowed to equilibrate for 30 minutes. At 5-minute intervals in the succeeding 60 minutes, each individual was scored as either immobile (0) or active (*i.e.*, in motion, 1), resulting in a cumulative score between zero and 12 for each of 10 females and 10 males.

To compare vagility between sexes, we performed eight replicates of the following assay. Five females and five males were segregated in standard plastic Petri dishes and allowed to equilibrate for several minutes, after which the lids were removed and the sequence in which individuals first touched the outside substrate after climbing from the dish was recorded for five minutes. Effectively, this amounted to a series of eight races, each with a different group of females and males, counting only the sequence in which sexed individuals finished the race.

Hypothesis testing was performed using Chi-squared or Mann–Whitney tests where appropriate. Alpha was set at 0.05.

## RESULTS

**I. Behavioral Catalog.** For convenience, behavior patterns are grouped according to supposed function. Numbers in brackets after each behavior name indicate the summed number of acts observed in females and males, respectively, in observation periods that did not focus on a particular class of behavior; they do not include data from Table 1. For example, we recorded 872 acts of walking by females and 845 by males. Where a particular pattern commonly occurs in rhythmic repetition (*e.g.*, steps in walking or the two types of palpation), we treat an uninterrupted bout as a single act. We characterize a posture as "sustained" if it typically lasts more than one second, while a "brief" posture is more than momentary but typically no more than a second. Except where indicated, each pattern is found in apparently identical form in both sexes.

## MOBILITY/SENSATION

Walk (872, 845): Sweetpotato weevils walk in a form of the double-tripod gait characteristic of many insects (Gillott 1980). We observed no other

**Table 1.** Recorded numbers of self-grooming acts/patterns in female and male *Cylas formicarius*. Further explanation in text. Rub substrate was observed outside of a recording period.

| Behavioral pattern | Females | Males | Total |
|---|---|---|---|
| Rub antenna | 29 | 20 | 49 |
| Rub head | 105 | 33 | 138 |
| Rub elytron (leg 2) | 50 | 16 | 66 |
| Rub elytron (leg 3) | 9 | 1 | 10 |
| Rub legs 1–2 | 144 | 61 | 205 |
| Rub legs 2–3 | 58 | 21 | 79 |
| Rub legs 3 | 19 | 3 | 22 |
| Rub substrate (snout) | 0 | 0 | 0 |
| **Total** | **414** | **155** | **569** |

gait. For purposes of counting acts, we treated an individual as walking only while it was not palpating (see below) for at least one second.

Drop (0, 1): The weevil falls on its side and remains motionless, with the legs moderately flexed and the antennae tucked in close to the body, directed posteriorly. We noted it only once in our observation periods, but it is a common response by both sexes to physical disturbance by the experimenter and thus easy to induce.

Self-right (0, 1): This is the pattern of rising out of the dropped posture. The following description is based on responses of 31 females and 31 males that were induced to drop. Typically, the weevil starts by stretching and waving the antennae and then the mid- and hindlegs on the upper side of the body. On a flat surface, this is without effect, as neither leg reaches the substrate, nor does it roll the body into a new position. The underlying foreleg is then swept around past the head and beneath the body to grasp the substrate with the tarsus. That foreleg then flexes to begin rolling the body up onto its venter, as the other legs follow in a similar stretching-grasping-flexing motion. The overlying legs are then used to grasp the substrate as the weevil rises to a standing position. From the sweeping of the underlying foreleg, this is a fluid and apparently stereotyped set of motions that quickly rights the insect.

Palpate (antennae) (396, 379): The weevil, either in motion or stationary, taps the substrate or another individual with the terminal club of one or (usually) both antennae.

Palpate (snout) (190, 116): The weevil, either in motion or stationary, taps the substrate with the tip of the snout. We could not see which mouthparts make contact.

Bite (31, 8): The tip of the snout is pressed against the substrate and held there briefly, with the terminal club of the antennae usually flat against the substrate. We assumed, but could not be certain, that

the mandibles are brought into play. We observed biting most commonly with respect to sweetpotato roots, but also stems. In bare-chamber situations, the weevils occasionally bit the underlying filter paper.

Bore (chew) (75, 67): The insect assumes a sustained posture similar to biting, with the snout penetrating successively deeper into the substrate. In the transition from biting to chewing boring, the antennae are lifted off the substrate and gradually directed posteriorly, sometimes above the head, not tucked close below the body as in dropping. The orientation of the snout to the substrate varies from approximately perpendicular to acutely forward at about 30°. In our observations, the substrate was always a sweetpotato root or stem. Boring may result in a hole little broader than the snout, in which case penetration is at most to the level of the eyes. However, where it produces a wider hole, the weevil may insert its entire head and prothorax.

Bore (push) (15, 5): The weevil assumes a posture similar to chewing boring, with the obvious differences that the substrate is soil and the weevil enters completely into it. This pattern has something more of a pushing-shaking aspect, but our main reason for distinguishing it is that we assume there is no use of the mouthparts in boring into soil.

Rest (94, 28): The body lies immobile against the substrate, with the legs moderately drawn in and the antennae extended posteriorly, although not tucked in close under the body. This is not simply a cessation of walking. Individuals sometimes enter the at-rest posture upon contact with another.

Rear up (59, 110): The insect stands with the body strongly lifted away from the substrate anteriorly, so that the head is raised at an angle of roughly 45°, usually with the antennae waving (Fig. 1). All feet remain on the substrate, although the forelegs may be fully extended. The posture may be held for several seconds. Males sometimes assume this posture upon being mounted by another male.

## SELF-GROOMING

Square-bracketed numbers identify Valentine's (1973) description of the behavior pattern.

Rub antenna (56, 67) [6]: The head is lowered to rest at least the tip of the terminal antennal club against the substrate. The corresponding protarsus is then rubbed distally over the club and sometimes the entire antenna. Males show a greater tendency than females to lay most or all of the antenna against the substrate.

Rub head (42, 22) [7]: A foreleg is raised and rubbed anteriorly over the head or the prothorax and head, after which the tarsus is commonly drawn through the mouthparts in a continuous motion. Depending on whether the leg passes a) above and/or to the side or b) below the head, there appear to be

two distinct patterns, which we can characterize as <u>rub head above</u> and <u>rub head below</u>. However, these movements are executed quickly and are often difficult to distinguish. We treat them together for all quantitive purposes.

<u>Rub elytron (leg2)</u> (16, 13) [8]: One or both midlegs are raised and rubbed along the corresponding elytron posteriorly.

<u>Rub elytron (leg3)</u> (3, 5) [9]: With the hind end of the body tilted upwards, one or both hindlegs are raised and rubbed along the corresponding elytron posteriorly.

<u>Rub legs 1–2</u> (74, 94) [14]: With the body tilted to one side, the fore- and midlegs of the other side are raised and rubbed across each other distally in alternation.

<u>Rub legs 2–3</u> (30, 54) [15]: With the body tilted to one side, the mid- and hindlegs of the other side are raised and rubbed across each other distally in alternation.

<u>Rub legs 3</u> (14, 20) [16]: The weevil stands on its fore- and midlegs, with the posterior end of the body somewhat elevated, and rubs the hindlegs across each other distally in alternation as they extend posteriorly. This sometimes follows fluidly from rubbing elytra with the hindlegs.

<u>Rub substrate (snout)</u> (0, 5): The head is lowered and the snout is rubbed against the substrate, as if in an attempt to scrape away a sticky substance.

## SEXUAL

<u>Mount</u> (0, 130): The weevil climbs onto another from the rear and grasps her/him on the sides with his legs. He palpates the other's head but not her/his antennae with his antennae. Initially, the fore- and/ or midlegs often tap or rub the other's corresponding thoracic terga. A mount together with aedeagal probing (see next) can last several minutes.

In our interpretation, this is exclusively a male behavior pattern, as are mount-inspecting and dismounting. On occasion, we observed females climbing onto the backs of other individuals, but with no distinct front-to-front orientation or palpation of the head, apparently treating the other simply as part of the substrate. We treat this and other un-differentiated climbing motions as forms of walking.

<u>Probe (aedeagus)</u> (-, 104): A mounting weevil slides back to bring the tip of his abdomen close to the tip of the other's abdomen and extends his aedeagus to probe the other's anal-genital region. This is necessarily exclusively a male pattern.

<u>Mount-inspect</u> (0, 2): The mounting weevil rotates his body to face the other's posterior end and palpates the other's anal-genital region with his antennae. This may be followed by a re-mount and renewed probing.

<u>Dismount</u> (0, 92): The mounting weevil rotates his body to one side and walks to the side or rear of the other. In some cases, the weevil dismounts without first probing. In our observations, he rarely climbs down over the other's head and never backs down. Although we observed no behavior that we interpret as an attempt to scrape away a mounting male, males sometimes are more or less shaken off and fall without an orderly dismount. We do not count these incidents as dismounts.

## OVIPOSITION

<u>Probe (abdomen tip)</u> (7, 0): While stationary or walking slowly, the weevil repeatedly touches the tip of the abdomen to the substrate. This is presumably exclusively a female pattern.

<u>Lay egg</u> (10, -): With the tip of her abdomen over a bored hole in the substrate, the weevil tilts posteriorly to apply the tip of her abdomen to the hole, usually for a sustained period. This is a distinct, humped posture, unlike that of resting. She may lean away from the hole and back toward it several times, as if adjusting her position. The position of the antennae is variable. Although the actual deposition of an egg is hidden from view, in all cases where this posture was sustained for many seconds we subsequently found an egg in the hole. We also observed apparently incomplete acts of this pattern, in which the weevil briefly moved back into the laying posture and then withdrew and simply walked away. This is necessarily exclusively a female pattern.

<u>Lay-inspect</u> (0, -): The weevil withdraws her abdomen from the oviposition hole, turns around, and palpates the hole with her antennae for some seconds, often or always applying her snout to the hole (Starr *et al.* 2016). This is necessarily exclusively a female pattern. We did not observe this and the next behavior pattern while enumerating acts but during other times.

<u>Apply oviposition plug</u> (0, -): With her mouth-parts, the weevil puts macerated plant tissue in the hole above the egg, forming a plug (Starr *et al.* 2016).

**II. Self-grooming Sequences.** In only 21 of 167 recorded uninterrupted grooming bouts of females were we certain of having observed the first act. However, the length-frequency distribution (in bouts) of these 21 is sufficiently similar to that of the remaining 146 to suggest that most observed bouts are complete in both females and males. Grooming bouts are usually very short (no more than a few seconds) (Fig. 2), with no significant difference between the sexes in mean length (Mann-Whitney $Z = 1.73$, $P = 0.08$).

The frequencies of patterns observed in periods devoted to observations of self-grooming are shown in Table 1. No significant sexual difference is shown in the relative frequency of the different behavior patterns ($X^2 = 9.9$, $P > 0.10$).
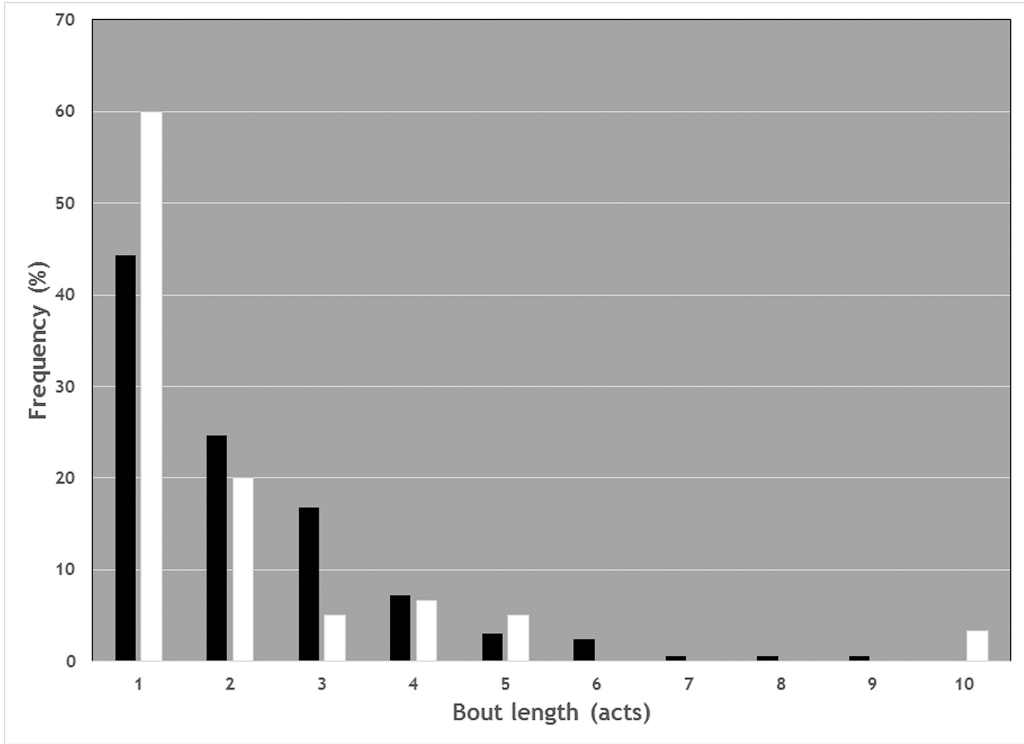
**Fig. 2.** Length-frequency distribution of self-grooming bouts in *Cylas formicarius*. Black bars: 167 bouts in females. Grey bars: 60 bouts in males. Further explanation in text.

The observed and expected frequencies of within-bout transitions between different grooming patterns are shown in Tables 2–3. There is a highly significant departure from randomness in both females ($X^2 > 210$, $P < 0.001$) and males ($X^2 > 79$, $P < 0.001$).

Table 4 shows the observed and expected frequencies with which different patterns appear at the end of grooming bouts. Here, too, there is a significant departure from randomness in both females ($X^2 = 17.6$, $P < 0.01$) and males ($X^2 = 14.9$, $P < 0.05$).

**III. Comparative Overall Activity and Vagility.** The activity assay produced the following scores in ascending order for each sex:

Females 0, 0, 0, 1, 8, 8, 9, 9, 11, and 12,

Males 0, 0, 0, 0, 0, 1, 3, 7, 8, and 11.

Although females appear on average more active than males, a significant difference is not shown (Kruskal-Wallis rank sum test, $P > 0.10$).

The following is the sequence in which sexed individuals finished each vagility trial, with those that remained in the dish at the end of the 5-minute test in square brackets:

1. ♀♀♂♂♀♂[♀♀♂♂]
2. ♀♂♂♀♀♀♂♂[♀♂♂]
3. ♀♂♂♀♂♀♂♀♀[♂♂]
4. ♀♂♂♂♂♀♀♀[♀♂]
5. ♂♂♀♂♀♀♀♀[♂♂]
6. ♀♂♂♂♂♀♀[♀♀♂]
7. ♀♀♀♂♂♂♀♀[♂♂]
8. ♀♂♂♂♀♀♂[♀♀♂]

Treating non-finishers as tied within a trial and summing the ranks of same-sex individuals (*e.g.*, in the first trial females have a sum of 25 and males a sum of 30), no significant sexual difference is found between average rank sums ($X^2 = 3.6$, 7 df, $P > 0.10$). Under these conditions, the minimum and maximum possible sums are 15 and 40, respectively. The largest difference found (trial no. 7) was between 21 for females and 34 for males.

**DISCUSSION**

Under the study conditions, the numbers of observed acts per behavior pattern do not provide a strong index of relative prominence in the life of the

**Table 2.** Observed and expected (from Table 1) transitions between behavior patterns within 181 self-grooming bouts of female *Cylas formicarius*. In each cell, the expected value is below the observed value. **A** = rub antenna; **H** = rub head; **E(2)**= rub elytron (leg 2); **E(3)**= rub elytron (leg 3); **L12** = rub legs 1–2; **L23** = rub legs 2–3; **L3** = rub legs 3. Because repetitive motions of the same pattern are treated as a single act, no pattern follows itself. Asterisks indicate transitions whose expected value is much higher than the observed value. Further explanation in text.

| Following Preceding | A | H | E(2) | E(3) | L12 | L23 | L3 |
|---|---|---|---|---|---|---|---|
| A | | 12* | 1 | 0 | 4 | 0 | 0 |
| | | 3.2 | 2.3 | 0.4 | 6.5 | 3.7 | 0.9 |
| H | 2 | | 0 | 0 | 61* | 1 | 0 |
| | 4.6 | | 10.0 | 1.5 | 28.1 | 15.8 | 3.9 |
| E(2) | 0 | 0 | | 2 | 1 | 19* | 2 |
| | 1.6 | 4.9 | | 0.6 | 10.0 | 5.6 | 1.4 |
| E(3) | 1 | 1 | 0 | | 0 | 2 | 5* |
| | 0.6 | 1.6 | 1.2 | | 3.3 | 1.9 | 0.5 |
| L12 | 5 | 22 | 14 | 0 | | 17 | 0 |
| | 5.4 | 16.2 | 11.7 | 1.8 | | 18.4 | 0 |
| L23 | 3 | 1 | 10* | 2 | 5 | | 3 |
| | 1.8 | 5.4 | 3.9 | 0.6 | 10.9 | | 1.5 |
| L3 | 1 | 0 | 1 | 0 | 2 | 2 | |
| | 0.4 | 1.1 | 0.8 | 0.1 | 2.2 | 1.3 | |

sweetpotato weevil. As discussed below, they are more useful as a guide to sexual diethism. Nonetheless, the data provide some fair hypotheses of which patterns are most frequent and which are least frequent under natural conditions. As expected, both sexes walked, palpated features of the substrate, and self-groomed a great deal in all laboratory situations. It is likewise not surprising that sexual

**Table 3.** Observed and expected (from Table 1) transitions between behavior patterns within 66 self-grooming bouts of male *Cylas formicarius*. In each cell, the expected value is below the observed value. **A** = rub antenna; **H** = rub head; **E(2)**= rub elytron (leg 2); **E(3)**= rub elytron (leg 3); **L12** = rub legs 1–2; **L23** = rub legs 2–3; **L3** = rub legs 3. The rare "rub substrate (snout)" is omitted. Because repetitive motions of the same pattern are treated as a single act, no pattern follows itself. Asterisks indicate transitions whose expected value is much higher than the observed value. Further explanation in text.

| Following Preceding | A | H | E(2) | E(3) | L12 | L23 | L3 |
|---|---|---|---|---|---|---|---|
| A | | 9* | 0 | 0 | 6 | 0 | 0 |
| | | 3.5 | 2.9 | 0 | 4.8 | 3.3 | 0.4 |
| H | 1 | | 0 | 0 | 16* | 1 | 0 |
| | 1.2 | | 4.3 | 0 | 7.0 | 4.9 | 0.9 |
| E(2) | 0 | 0 | | 0 | 0 | 9* | 1 |
| | 0.7 | 2.7 | | 0 | 3.7 | 2.6 | 0.3 |
| E(3) | 0 | 0 | 0 | | 0 | 0 | 1 |
| | 0.1 | 0.2 | 0.2 | | 0.3 | 0.2 | 0.0 |
| L12 | 3 | 6* | 4 | 0 | | 4 | 0 |
| | 1.3 | 5.4 | 4.4 | 0 | | 5.0 | 0.6 |
| L23 | 0 | 2 | 9* | 0 | 1 | | 0 |
| | 0.8 | 3.4 | 2.8 | 0 | 4.6 | | 0.4 |
| L3 | 0 | 0 | 1 | 0 | 0 | 2 | |
| | 0.2 | 0.7 | 0.6 | 0 | 0.9 | 0.7 | |

**Table 4.** Observed and expected (from Table 1) frequencies of different behavior patterns as the last pattern in self-grooming bouts of adult *Cylas formicarius*. The rare "rub substrate (snout)" is omitted. In each cell, the expected value is under the observed value. Further explanation in text.

| Behavior pattern | Females | Males |
|---|---|---|
| Rub antenna | 12 | 3 |
| | 12.2 | 7.7 |
| Rub head | 23 | 7 |
| | 44.1 | 12.8 |
| Rub elytron (leg 2) | 17 | 5 |
| | 21.0 | 6.2 |
| Rub elytron (leg 3) | 0 | 0 |
| | 3.8 | 0.4 |
| Rub legs 1–2 | 74 | 37 |
| | 60.5 | 23.6 |
| Rub legs 2–3 | 30 | 8 |
| | 24.4 | 8.1 |
| Rub legs 3 | 11 | 0 |
| | 8.0 | 1.2 |
| **Total** | **167** | **60** |

and reproductive behavior patterns were highly context-restricted.

Given its context and form, dropping is clearly a form of thanatosis. The narrow, deep abdomen and its smooth, relatively high dorsal curve are evidently responsible for the fact that a dropped insect on a level surface lies on its side, rather than on its back. This in turn evidently accounts for the peculiar form of self-righting, unlike any of those described by Chao (1985).

Bore-pushing seems almost certainly to function in reaching roots or buried stems of food plants, presumably in response to odor. However, there is no indication that it is a sophisticated or specialized response. *Cylas formicarius* does not seem especially well suited to burrowing in even loose soil. Furthermore, among its known host plants, *I. batatas* — with which it has been in contact only in recent historical times — is unusual in having a large, attractive storage root (Austin 1991).

We interpret rearing up as primarily a way to more effectively sample airborne odors, with the possible secondary function of facilitating the removal of unwelcome mounting males. Although we observed rearing up only by males in this context, we hypothesize that unreceptive females behave in the same way.

Rubbing the head presumably functions mainly in cleaning the eyes.

Although we observed only males rubbing the snout against the substrate, we assume that it is also part of the female repertory and identical in form.

It is noteworthy that among putative self-grooming patterns we never observed the rubbing together of the two forelegs or the two midlegs, each of which is prominent in wasps of the genus *Polistes* Latreille (Hymenoptera: Vespidae) (C. Starr, unpublished data).

The specifically sexual behavior patterns described were found with certainty only in males. It is not surprising, for example, that males were often seen mounting and probing both females and other males, while no female was seen to do either. If females have patterns specifically associated with courtship or receptivity, these were too uncommon or subtle to claim or attention.

With the possible exception of rearing up, we observed no behavior that seemed specifically directed toward dislodging a mounting male. Indeed, even males being mounted appeared to ignore the other male, and we have often seen such pairs of males moving about for extended periods. There is thus no evident way to detect a mounted female's state of receptivity to the male.

Palpating another individual's antennae with one's own antennae would seem to be an exceptionally sure way to sex her/him. It is thus noteworthy that mounting males were often observed to palpate the other's head but not her/his antennae. We hypothesize that mating attempts most commonly occur when the other insect is boring-chewing. In this situation, she/he will commonly be conveniently immobile for an extended time, but with the antennae relatively inaccessible for inspection. We presume that a male can sex the other individual by palpating the eyes. Consistent with this hypothesis is the observation that males sometimes make orderly dismounts without either aedeagal probing or antennal palpation of the other's anal-genital area.

As noted above, no significant difference is shown between the sexes in the frequencies of different grooming patterns. If any such difference exists, it is likely based on a higher rate of antennal rubbing in males, which accounts for about half of the total Chi-squared value for Table 1. This expectation is consistent with the greater length of the antennae in males.

We expected to find a consistent pattern in the sequence of grooming motions, indicative of a very restricted set of pathways by which dirt is removed from the body. However, we do not detect any such clear, unitary pattern in the data on transitions within grooming bouts (Tables 2–4). In females, three consistent partial pathways are apparent (Table 2):

1. rub antenna → rub head → rub legs 1–2
2. rub elytron (leg 2) ↔ rub legs 2–3
3. rub elytron (leg 3) → rub legs 3.

The first two are also prominent in males, but the data are too few to remark on the third transition (Table 3). Taking these together with data on terminal patterns (Table 4), we tentatively suggest that each of these three "partial" pathways is, in fact, complete in itself, so that a given bout serves to remove dirt either a) from the anterior end of the body via the fore- and midlegs, b) from the posterior end via the mid- and hindlegs, or c) from the posterior end via the hindlegs. Even if this hypothesis is correct, the overall pattern in *C. formicarius* is strikingly different from that found in the fly *Calliphora vicina* Robineau-Desvoidy (Dawkins and Dawkins 1976) and three species of social wasps (C. K. Starr, unpublished data), in which distinct sets of motions are associated with the anterior and posterior ends of the body, with little within-bout association of the two.

The failure to find sexual differences in overall activity or vagility must be regarded as a limited finding, as flight is largely excluded from our assays. It is, therefore, not in direct contradiction to earlier findings of greater activity/vagility in males.

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