Journal of Chemical Ecology, Vol. 8, No. 1, 1982

TRAIL-FOLLOWING RESPONSES OF THE ARGENTINE ANT, *Iridomyrmex humilis* (MAYR), TO A SYNTHETIC TRAIL PHEROMONE COMPONENT AND ANALOGS

S.E. VAN VORHIS KEY and T.C. BAKER

Department of Entomology
Division of Toxicology and Physiology
University of California
Riverside, California 92521

(Received December 1, 1980; revised April 3, 1981)

Abstract—Behavioral evidence indicates that (*Z*)-9-hexadecenal (*Z*9-16:ALD) is a trail pheromone component of *Iridomyrmex humilis,* and that the true trail pheromone may be multicomponent. Trail-following responses of *I. humilis* workers to several concentrations of synthetic *Z*9-16:ALD, a constituent of the Pavan's gland, were found to be comparable to responses to gaster extract trails containing ca. 100 times less *Z*9-16:ALD. Of the five aldehyde analogs tested, only (*Z*)-7-hexadecenal (*Z*7-16:ALD) elicited significant trail-following. However, following responses to several *Z*9-16:ALD–*Z*7-16:ALD combinations were lower than responses to *Z*9-16:ALD alone. Trails on filter paper of biologically relevant concentrations of *Z*9-16: ALD lose activity within 2 hr in the laboratory. The release rate of *Z*9-16:ALD measured from filter paper trails was 0.25 ± 0.10 pg/cm-sec. This was used to estimate the trail-following threshold for this compound of Argentine ant workers.

Key Words—Argentine ant, *Iridomyrmex humilis,* Hymenoptera, Formicidae, trail-following, structure-activity, (*Z*)-9-hexadecenal, threshold, trail emission rate, synthetic trail longevity, bioassay.

INTRODUCTION

The failure of attempts to biologically control many honeydew secreting pests, particulary in citrus, can be traced to the presence of Argentine ants, *Iridomyrmex humilis* (Mayr), which interfere with the activites of natural predators and parasites (DeBach et al., 1951a, b). At present, since the removal of chlordane from the market, economical control of this ant cannot be

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obtained with conventional insecticides currently sold in this country, but detailed quantitative analysis of its behavior, particularly pertaining to the retrieval of food, may lead to the development of an alternative control scheme such as an effective bait program. Laboratory attempts to enhance bait pick-up in other species by incorporation of synthetic trail pheromones have been successful. However, field tests indicate that further research is needed for pheromones to be useful in ant control (Robinson and Cherrett, 1973, 1975; Cross et al., 1979).

Recently, (*Z*)-9-hexadecenal (*Z*9-16:ALD) was isolated and identified from ventral gland extracts of *Iridomyrmex humilis* ants, and implicated as a component of the trail pheromone complex by its aggregative and attractive qualities (Cavill et al., 1979, 1980). However, because of insufficient information concerning the assay procedure and because trail-following activity was not reported, conclusions about the behavioral importance of this compound could not be made.

This report is a quantitative analysis of the trail-following activity elicited by *Z*9-16:ALD and several analogs. In addition, measurement of the *Z*9-16:ALD release rate from trails on filter paper, and the duration of biological activity are presented.

METHODS AND MATERIALS

Chemicals. Tetradecanal (14:ALD), (*Z*)-9-tetradecenal (*Z*9-14:ALD), hexadecanal (16:ALD), (*Z*)-11-hexadecenal (*Z*11-16:ALD), (*Z*)-7-hexadecenal (*Z*7-16:ALD), and *Z*9-16:ALD were obtained from the Controlled Release Division of Albany International Corporation. Purity of these compounds was determined by gas–liquid chromatography, using 10% XF-1150 (50% cyanoethyl, methyl silicone) on Chromosorb W, AW DMCS, 100/120 mesh (2.5 m × 2 mm). The 14:ALD was greater than 99.9%, the *Z*9-14:ALD, *Z*7-16:ALD, and *Z*11-16:ALD greater than 98%, the *Z*9-16:ALD greater than 97%, and the 16:ALD greater than 95% free of other volatile impurities.

Biosassay. Laboratory rearing of the Argentine ant, *I. humilis*, has been described previously (Van Vorhis Key et al., 1981). Colonies were provided with new food sources in enclosed dishes immediately prior to bioassay periods. Once recruitment had been initiated through the tubing leading from the nest to the food source; individual unfed ants which had been recruited and were traveling towards the food source but had not yet arrived were redirected and introduced onto the experimental trail directly from the natural trail inside the tubing. Thus disturbance to the ants was minimal.

The techniques for application of trails, making gaster extracts, and bioassay were described previously (Van Vorhis Key et al., 1981). Briefly,

circular trails (50.7 cm circumference, 2 mm wide), were applied to filter paper disks (Whatman No. 1, 24 cm diam), and housed under a glass plate held 3 mm above the disk by a spacer ring. For 2 min after introduction of a single recruited worker ant onto the trail, observations were made of the duration and continuity of trail-following and, when appropriate, the rate of locomotion. Trail-following continuity [following duration (sec)/approaches] was calculated by dividing the time each ant spent within 15 mm of the center of the trail by the number of times it entered this area (approaches).

Dose–Response to Z9–16:ALD. Trail-following by recruited worker ants was measured on Z9–16:ALD trails of 0.01, 0.1, 1.0, 10. 100, and 1000 ng/50.7 cm trails. For comparison, solvent trails and gaster extract trails of an optimum concentration, 0.1 ant equiv/50.7 cm (Van Vorhis Key et al., 1981), were included. Each trail was used twice, and treatments were presented in a randomized complete block design. Trail-following continuity was calculated for 20 ants per treatment and was then compared among treatments using Duncan's new multiple range test on transformed data ($\log_{10}$).

In addition, for uninterrupted trail-following, the time required to travel a 90° arc of the circular trail was recorded for three 90° sections as soon as possible after introduction of the ant to the trail. From this, an average speed of locomotion was calculated for each concentration. Comparisons of rates of locomotion were made using Duncan's new multiple range test.

Longevity of Z9–16:ALD Trails. Trails of Z9–16:ALD, applied at 10 ng/50.7 cm or 1000 ng/50.7 cm to filter paper disks were aged in a fume hood (ca. 23.5° C; air velocity 5 mm above the paper surface = 0.15–0.3 m/sec), for 1, 2, 4, or 6 hr. New trails of each concentration and new and 1-hr-old solvent controls were also included in a randomized complete block design ($N = 15$). Ants were assayed as previously described; a recruited, unfed ant was introduced directly onto each trail as it reached its experimental age. The ants' trail-following responses were recorded and calculations of trail-following continuity made. Analysis was made using Duncan's new multiple range test on transformed data ($\log_{10}$).

Air Extraction of Synthetic Trails. Linear sections (2.54 cm) of new Z9–16:ALD trails, applied to filter paper disks at 1000 ng/50.7 cm were extracted under a nitrogen stream flowing at 30 ml/min, and volatiles were collected in a glass wool plug positioned downwind from the trail section (Baker et al., 1981). Recovery efficiency of this system for aldehydes, acetates, and alcohols was 90–100%. After 2 hr of collection, the glass wool was eluted with ca. 1.5 ml CS_2, and the eluant condensed by steam bath distillation after addition of 30 ng of the internal standard, *E*11–16:Ac. Gas–liquid chromatography was then performed using the XF-1150 column described above. Release rates of Z9–16:ALD were calculated by a peak height × retention time comparison with the internal standard for 5 trail segments extracted individually.

Analog Activity. Trail-following responses to 14:ALD, 16:ALD, Z9-14:ALD, Z7-16:ALD, Z9-16:ALD, and Z11-16:ALD were compared using trails of 10 ng/50.7 cm. Treatments were presented in a randomized complete block design, and each trail was used twice. Ants were introduced as previously described, and the trail-following continuity of 20 ants was measured. Velocity was calculated for ants responding to Z7-16:ALD and Z9-16:ALD ($N = 10$).

Z7-16:ALD + Z9-16:ALD Mixtures. Because of the significant activity of Z7-16:ALD, mixtures of Z9-16:ALD and Z7-16:ALD were tested to see if trail-following response could be increased. A series of ratios—10:0, 9:1, 5:5, 1:9, and 0:10 Z9-16:ALD–Z7-16:ALD—was applied totaling 10 ng of material/50.7 cm trail. The scoring distance from the trail center was reduced from 15 mm to 5 mm to increase the discriminatory power of the assay. Treatments were presented in a randomized, complete block design of 25 replicates per treatment. Trail-following continuity was compared using Duncan's new multiple range test on transformed data ($\log_{10}$).

RESULTS

Dose-Response to Z9-16:ALD. All Z9-16:ALD trail concentrations greater than 0.01 ng/50.7 cm, as well as 0.1 ant equiv gaster extract trails, elicited significantly greater trail-following continuity than solvent controls ($P < 0.05$; Figure 1). The 10, 100, and 1000 ng/trail treatments elicited responses not significantly different from each other nor from gaster extract, but greater than all lower concentrations ($P < 0.05$). The highest average responses (to 100 ng and 1000 ng trails) were 90 sec/approach, ca. 75% of the maximum possible 120 sec/approach, whereas suboptimal Z9-16:ALD concentrations (0.01–1.0 ng) elicited only 17–29% of the maximum. Response to solvent trails was minimal (4%). Displacement of trail-following away from 1000 ng trails of Z9-16:ALD was also observed, similar to that described for high concentrations of gaster extract (Van Vorhis Key et al., 1981). Ants trail-followed parallel to, but several mm away from, the center of these most concentrated trails.

Speed of locomotion, measured as time required to travel a 90° arc of trail, was concentration-dependent (Figure 2). Ants orienting along gaster extract trails and 100- and 1000-ng Z9-16:ALD trails traveled significantly faster (3.04, 2.93, and 2.61 cm/sec, respectively) than ants orienting along trails of 0.01 ng (1.89 cm/sec) ($P < 0.05$). The number of ants demonstrating uninterrupted trail-following for three 90° sections was also concentration-dependent, ranging from 3 (0.01 ng/trail) to 16 (1000 ng/trail).

Synthetic Trail Longevity. Trail-following to 10-ng Z9-16:ALD trails aged under laboratory conditions disappeared within 1 hr (Figure 3).

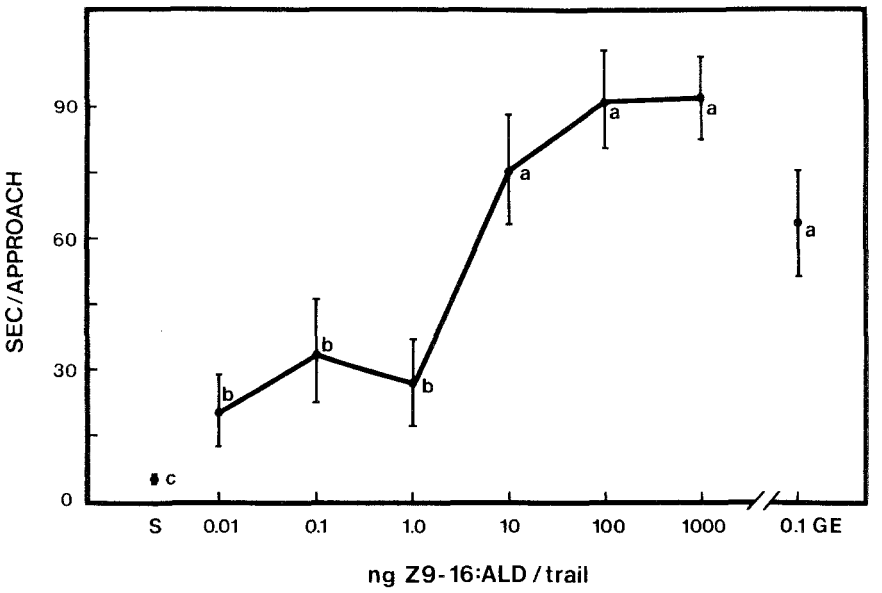

FIG. 1. Trail-following responses of ants to synthetic Z9-16:ALD trails ranging in concentration from 0.01 ng/50.7 cm to 1000 ng/50.7 cm, measured as the trail-following continuity (see text). S = solvent control; GE = gaster extract trail (0.1 ant equiv/50.7 cm); $N = 20$. Brackets around means denote standard errors. Means having no letters in common are significantly different (Duncan's new multiple range test, $P < 0.05$).

Following to 1000-ng trails aged 0–2 hr was significantly greater than to solvent controls. No significant decline occurred for 1000-ng trails during the 1st hour. Responses to 1000-ng trails aged 4 hr or more were not significantly different from responses to solvent controls.

Release Rate of Z9-16:ALD Trails. The mean emission rate from filter paper of 1000 ng Z9-16:ALD trails over the first 2 hr after application was 0.25 pg/cm/sec (± 0.10 SD; $N = 5$). The nitrogen flow rate of 30 ml/min in our apparatus produced a linear velocity of ca. 1 cm/sec, approximately 30 times slower than over the surface of trails being aged in the fume hood for behavioral assays. The low velocity in the apparatus was meant to approximate that which might be found at trail surfaces in the field or in our near static bioassay environment, not the trail aging conditions in our fume hood.

Analogs of Z9-16:ALD. Among the analogs of Z9-16:ALD tested, only Z7-16:ALD elicited significant trail-following activity. Trail-following continuity in response to Z7-16:ALD was similar to that to Z9-16:ALD ($P < 0.05$; Figure 4). Also, the mean speed of locomotion of ants following trails of Z9-16:ALD (1.84 ± 0.76 SD cm/sec) was not significantly different from that of ants following Z7-16:ALD trails (1.37 ± 0.57 SD cm/sec).

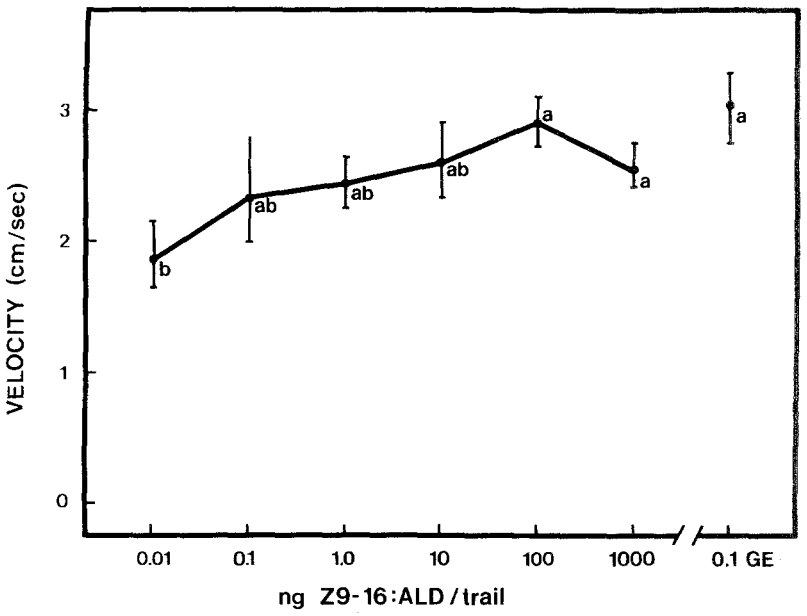

FIG. 2. Velocity of ants following trails of Z9–16:ALD ranging in concentrations from 0.01 ng/50.7 cm to 1000 ng/50.7 cm. GE = gaster extract trail (0.1 ant equiv/50.7 cm). Brackets around means denote standard errors. Means having no letters in common are significantly different (Duncan's new multiple range test, $P < 0.05$; $N = 3, 6, 7, 13, 15, 16$, and 14 for 0.01, .0.1, 1.0, 10, 100, and 1000 ng, and 0.1 gaster equiv trails, respectively.

Z9–16:ALD + Z7–16:ALD Mixtures. Trail-following continuity of ants following 2-component mixtures of Z9–16:ALD and Z7–16:ALD is illustrated in Figure 5. Addition of more than 10% of Z7–16:ALD to Z9–16:ALD significantly reduced trail-following compared to treatments containing 90% or more of Z9–16:ALD. Trails made from a 50:50 mixture elicited some trail-following response, but significantly less than all other treatments ($P < 0.05$). In contrast to the initial experiment where Z9–16:ALD and Z7–16:ALD trails were equally active, in this experiment Z9–16:ALD elicited more continuous trail-following than Z7–16:ALD. This apparent discrepancy in bioassay results probably can be attributed to the more rigorous criteria used to assess trail-following; to be scored as trail-following, ants had to remain within 5 mm of the center of the trail instead of within 15 mm as previously required.

DISCUSSION

For recruited workers of *I. humilis*, 10-, 100-, and 1000-ng trails of Z9–16:ALD elicited strong trail-following that was quantitatively similar to

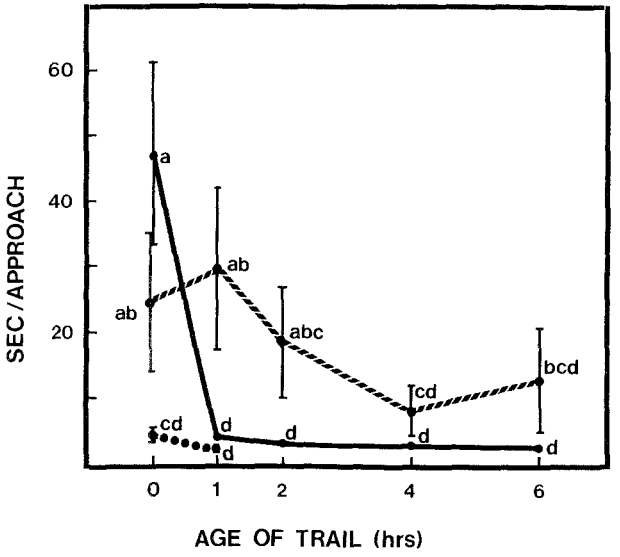

FIG. 3. Activity loss of aging trails of 10 ng Z9-16:ALD/50.7 cm, solid line, and 1000 ng Z9-16:ALD/50.7 cm, dashed line, measured as trail-following continuity (sec/approach). Solvent controls are represented by the dotted line. Activity was assessed for new trails and for trails which had been aged for 1, 2, 4, or 6 hr after application. Brackets around means denote standard errors. Means having no letters in common are significantly different according to Duncan's new multiple range test ($P < 0.05$; $N = 15$).

that elicited by 0.1 ant equiv whole gaster extract trails. More than 50% of the ants trail-followed during the entire test period without deviating from the trail. For all Z9-16:ALD concentrations of 0.1 ng/50.7 cm or more, the linear speed of trail-following ants was not significantly different from that of ants following an optimum concentration of gaster extract.

Cavill et al. (1979) reported a lower response (measured as attraction/aggregation in a multichoice olfactometer) to synthetic Z9-16:ALD than to Z9-16:ALD extracted from ants, and suggested that the concentrations used and/or the activity of minor components in the gaster extract may account for this difference.

Cavill et al. (1980) reported that 370 ventral glands of *I. humilis* workers contained ca. 300 ng of Z9-16:ALD. From this we calculate that the concentration of Z9-16:ALD in optimum (0.1 ant equiv) gaster extract trails is 1.6 pg/cm (0.081 ng/50.7 cm). However, to elicit equivalent trail-following response, trails of synthetic Z9-16:ALD must be $\geqslant$200 pg/cm (10 ng Z9-16:ALD/50.7 cm)—over 100 times more concentrated. This strongly indicates that minor components play a role in the trail pheromone system of *Iridomyrmex humilis*, although high concentrations of Z9-16:ALD alone elicit intense trail-following by recruited workers.

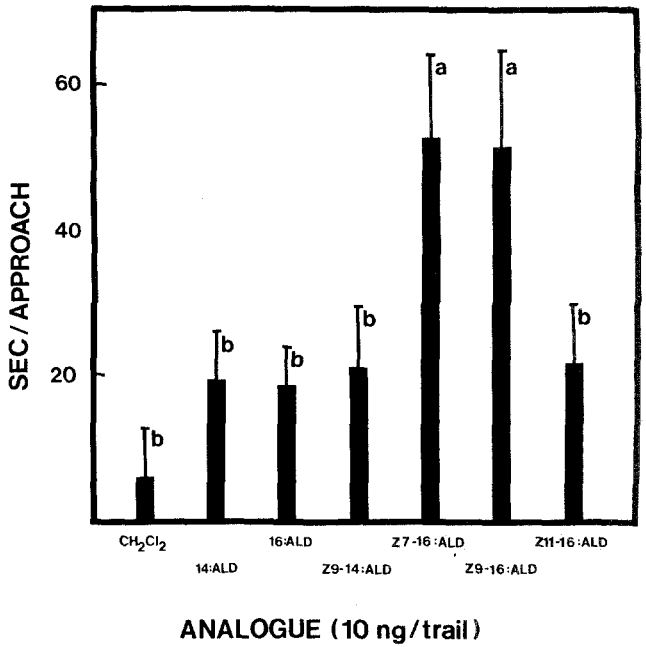

FIG. 4. Trail following responses to 10-ng trails of synthetic analogs of Z9–16:ALD and solvent controls (CH_2Cl_2). Activity is expressed as trail-following continuity (sec/approach). Brackets above means denote standard errors. Means having no letters in common are significantly different (Duncan's new multiple range test, $P < 0.05$; $N = 20$).

Structure–activity studies of trail pheromones in ants have been minimal, as chemical identifications of ant trail pheromones are few (Parry and Morgan, 1979). The structure–activity relationships of several analogs of the trail pheromone of *Atta texana* were elucidated by Sonnet and Moser (1972, 1973), and Caputo et al. (1979). Enantiomeric specificity has been found for alarm pheromone reception by *Atta texana* and *Atta cephalotes* (Riley et al., 1974) and by *Pogonomyrmex barbatus* (Benthuysen and Blum, 1974), and only compounds of similar size and geometry to 4-methyl-3-heptanone, the natural alarm pheromone, were found to be active in eliciting alarm in *Pogonomyrmex badius* (Blum et al., 1971).

Our analysis of the trail-following elicited by several aldehydes related to Z9–16:ALD revealed that Z7–16:ALD is highly active while Z11–16:ALD is not. This indicates discrimination between selected double-bond positions by the ants. Furthermore, the lack of response to Z9–14:ALD indicates sensitivity to changes either in chain length or distance from the double bond to the end of the chain (Gaston et al., 1972; Priesner et al., 1975; Roelofs and

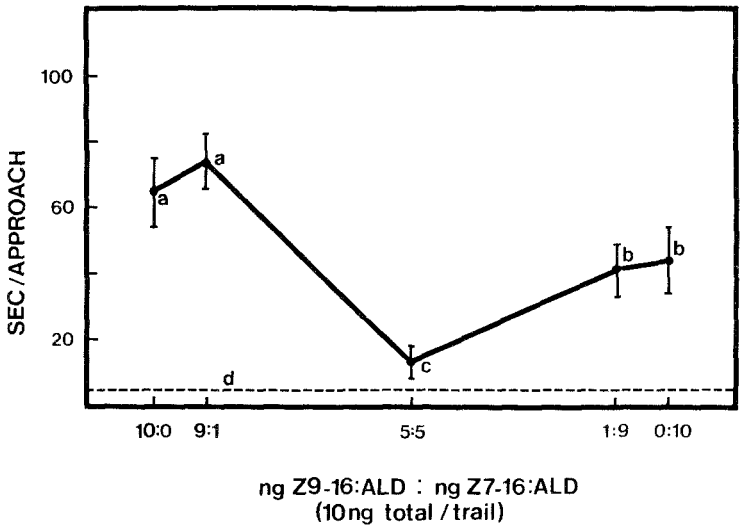

FIG. 5. Trail-following continuity of ants following 10 ng/50.7 cm trails of mixtures of Z9–16:ALD and Z7–16:ALD. Response to solvent controls is indicated by the dashed line. Brackets around means denote standard errors. Means having no letters in common are significantly different according to Duncan's new multiple range test ($P < 0.05$, $N = 25$).

Comeau, 1971). It would be interesting to test (*E*)-9-hexadecenal to determine whether *I. humilis* can discriminate between geometric isomers, but we were unable to obtain any.

Because Z7–16:ALD has not been found in *I. humilis* extracts, yet elicits significant trail-following, it may be mimicking the sensory input of Z9–16:ALD. Alternatively, since chemical and behavioral characterization of the trail pheromone of *Iridomyrmex humilis* is far from complete, Z7–16:ALD may be present in the deposited trail in an as yet undetermined ratio to Z9–16:ALD, although the ratios we tested did not significantly increase, and usually decreased, trail-following. The lower response to the 5-ng Z9–16:ALD–5-ng Z7–16:ALD mixture cannot presently be explained.

Our data concerning the longevity of synthetic Z9–16:ALD trails demonstrate that activity loss is rapid. In contrast, we found in a previous study (Van Vorhis Key et al., 1981), that 0.1 ant equiv crude gaster extract trails elicited significant trail-following for up to 8 hr. Cuticular waxes and other less volatile components of these crude extracts may be responsible for extending the normal lifetime of a trail, and other as yet unrecognized volatile active components may also help increase longevity.

The Z9–16:ALD from 1000-ng trails is emitted at 0.25 pg/cm/sec in the low (ca. 1 cm/sec) N_2 velocity of our collection device, a rate probably similar

to that in the "static-air" bioassay environment. This low rate is somewhat surprising in that only ca. 18% of the aldehyde will have been emitted during the first 4 hr, yet trail-following activity drops to near zero during that time. The higher wind velocity to which aging trails were subjected in the laboratory hood between tests might have accelerated evaporation of material compared to that in the collection device. Additionally, some aldehyde may have oxidized during the aging period, resulting in decomposition products such as acids, which might act antagonistically to reduce trail-following response to the remaining Z9–16:ALD.

Under the conditions of our assay procedure, the lowest concentration of pheromone causing at least 50% of the ants to follow a trail without interruption during the 2-min assay was emitted by 10-ng Z9–16:ALD trails and was designated as the threshold (Howard et al., 1976). We were able to collect and quantify emissions from 1000-, not 10-ng, trails in our apparatus. However, if we use this higher rate, an ant trail-following at its mean velocity of 2.61 cm/sec would encounter in 1 sec of following approximately 0.25 pg/cm/sec/2.61 cm = 9.6×10^{-14} g/sec (2.3×10^{8} molecules/sec). This then is a conservative estimate of the Z9–16:ALD trail-following threshold for *I. humilis*. The actual threshold is undoubtedly lower, since the above-threshold 10-ng trails should emit at lower rates than the 1000-ng trails we measured. Moreover, lateral and vertical diffusion of the molecules makes it likely that an ant's small receptor surface would sample only a small fraction of the emitted trail. Although ants may encounter large concentrations by antennal contact with the applied 10-ng trail, we have shown that trail volatiles alone elicit following and that contact is unnecessary (Van Vorhis Key et al., 1981). Similarly, ants trail follow several mm out from the edges of a 1000-ng Z9–16:ALD trail.

Barlin et al. (1976) reported that *Solenopsis richteri* ants which had no access to food for 3 days could follow 10 fg/cm of trail pheromone, while the trail-following threshold of fed ants was ca. 80 fg/cm. Tumlinson et al. (1972) reported that *Atta texana* workers can detect 80 fg/cm of their trail pheromone. Other such calculations have been made by Riley et al. (1974) for *Atta cephalotes,* Ritter et al. (1977) for *Monomorium pharaonis* (L.), and Cross et al. (1979) for *Atta sexdens rubropilosa* Forel. Ours, however, is the first study to estimate the threshold from volatilized, rather than deposited, trail pheromone concentrations.

Further chemical characterization of the trail pheromone of *I. humilis* and investigations of trail-following responses to other possible trail components (Cavill et al., 1980) are needed. Z9–16:ALD certainly must be considered a component of this species' trail-following system due to the intense following it evokes, and an assessment of its value to Argentine ant control programs is necessary.

Acknowledgments—The authors thank Lyle Gaston for the use of his laboratory and GLC, Richard S. Vetter for preparing the figures, Craig F. Kennedy for applying the 510 trails we assayed, Iain Weatherston of the Controlled Release Division of Albany International for kindly supplying the synthetic aldehydes used for these studies, and L.P.S. Kuenen and P.L. Phelan for helpful discussion.

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