Responses to Conspecific Chemical Stimuli in the Terrestrial Snail *Achatina fulica* (Pulmonata: Sigmurethra)[1]

Ronald Chase, Kathleen Pryer, Robert Baker,
and Dale Madison[2]

Department of Biology, McGill University, 1205 McGregor Street, Montreal, Quebec, Canada H3A 1B1

The giant African snail, *Achatina fulica*, followed trails made with the mucus of *A. fulica*, but did not follow those consisting of mucus from *Otala vermiculata*. In olfactometer experiments, *A. fulica* and *Helix aperta* oriented preferentially toward the odor of their own species when both odors were presented simultaneously. Species specificity was less pronounced when the odor of *O. vermiculata* was paired with either of the other two snail odors. Sexually mature *A. fulica* that had been housed individually for 30 days prior to testing followed mucus trails better than did similar snails housed collectively. Immature *A. fulica* did not follow trails better after isolation, but showed a facilitative effect of isolation on conspecific orientation in the olfactometer. Three-week-old snails, maintained in individual containers from the time of hatching, also oriented preferentially toward conspecific odors.

Aplysia, along with some other marine opisthobranch mollusks, is well known as a subject for experiments in neurobiology and behavioral physiology. By contrast, the pulmonate mollusks, although widely used in certain other biological fields, have seen only limited use in neurobiology. This is especially unfortunate in the case of some very large terrestrial pulmonates, which are suitable for such work, and which offer economic and convenient alternatives to the marine mollusks. The nervous system of several large species has already been exploited to some extent for anatomical and physiological work (Chase and Goodman, 1977; Nisbet and Plummer, 1976; Prior and Gelperin, 1977). However, since our

knowledge of the behavior of these animals is relatively poor, the present investigation was undertaken in order to develop *Achatina Fulica* as a subject for studies in behavioral neurobiology.

Recent reports have drawn attention to the importance of chemoreception in the determination of pulmonate behavior. For example, it has been shown that at least some snails (Suzuki, 1968) and slugs (Gelperin, 1975) can learn to associate the odor of a food with the noxious experiences which follow ingestion of that food. They learn to avoid eating the food. Conversely, we reported that *Achatina* can retain for 4 months an orientation preference for food odors that have been positively conditioned (Croll and Chase, 1977). Gelperin (1974) has shown that the slug *Limax maximus* uses olfactory cues to return to a "home" location, and *Helix pomatia* probably homes by the same mechanism (Edelstam and Palmer, 1950). We report in the present paper that terrestrial pulmonates respond to chemical cues of an additional sort, namely, those which derive directly from conspecific animals.

METHODS

General

Three species of snail were used in these experiments. Adult specimens of the giant African snail *Achatina fulica* were obtained either from the field in Hawaii or from a cultured stock. Immature *A. fulica* of known age and lineage were obtained from cultured stock. Specimens of *Otala vermiculata* and *Helix aperta* were purchased through commercial markets. Except where otherwise noted, the animals were maintained in small glass cages (30 × 17 × 20 cm) that were lined with a thin plastic film and filled with about 6 cm of sand. About 8 to 10 adult *A. fulica* occupied a single cage; the occupation rates for other snails varied in proportion to their relative size. Fluorescent room lights were controlled to give a 12:12 light:dark cycle. All experiments were conducted during the regularly cycled hours of light. The cages were watered and supplied with lettuce at regular and frequent intervals so that the majority of animals remained in an active (nonaestivating) state throughout the period of experimentation. Nevertheless, in order to facilitate rapid performances, snails were usually "warmed up" before an experimental trial by placing them in a shallow bath of warm water. When experiments involved the testing of two or more groups of snails, selection from the groups was by either serial alternation or random order.

Open Field Techniques

Snails were placed individually on a piece of construction paper at the center of a drawn circle with a radius of 7.5 cm. An amimal was permitted to travel freely until its head crossed the circle, at which point it was

removed from the paper and the position of crossing was recorded. A screened plastic enclosure (9 × 9 × 15 cm) containing 12 active adult *A. fulica* was placed tangential to the circle, resulting in the geometric relations illustrated in Fig. 2. The initial orientation of the test animal relative to the target box was systematically varied, as was the position of the target box on the circle. The experiments were conducted within a large glass enclosure free of air currents. In preliminary experiments, a box identical in construction to the target box, but containing wet paper, was placed tangential to the circle at a position directly opposite the target. Since snails were not attracted to the control target, it was not subsequently used.

Trail Following Techniques

Mucus trails were made on pieces of black construction paper that lay flat inside a large glass enclosure. A humidifier within the enclosure maintained the relative humidity at approximately 80% and the temperature at about 27°C. These conditions were near-optimal both for promoting snail activity and for preserving the trails in a fresh condition. Immediately following each replicate of an experiment, the paper was removed and the trails were marked with colored pencil for later analysis.

True trails. A snail, arbitrarily selected and designated the blazer, was placed at a central location on the paper and permitted free movement for 5 min. If the blazer produced a mucus trail with a minimum length of 25 cm within the allotted time, a second animal, arbitrarily selected and designated the follower, was placed on the paper at the same initial starting point and with the same initial orientation as the blazer. The follower was given 5 min to travel a minimum distance of 10 cm. Trail lengths were measured as the actual distance traveled, including turns. A replicate was considered complete and suitable for analysis only if all of the foregoing constraints were satisfied.

Smear trails. We observed that trail following was dependent upon the actual amount of mucus in the blazer's trail, which varied considerably. Furthermore, when the mucus content was very low, it dried quickly and became difficult to see for purposes of analysis. In consideration of these factors, subsequent experiments utilized trails produced by the experimenter rubbing the foot of one to three animals over the paper to form a single straight mucus trail at least 30 cm long. All of the experiments that used smear trails involved two groups of snails differing in either recent experience or species identity. Hence, a trail was first formed using one or more animals from the appropriate group, and then a random procedure was used to determine the group from which the follower would be selected. The follower was placed in contact with the origin of the smear trail and was consistently headed in a particular direction, while the compass orientation of the smear trail was systematically varied in differ-

ent replicates within a range of 45°. The follower was given 10 min to
travel a minimum distance of 10 cm.

Olfactometer Techniques

Adult snails were tested individually in Plexiglas olfactometers, as
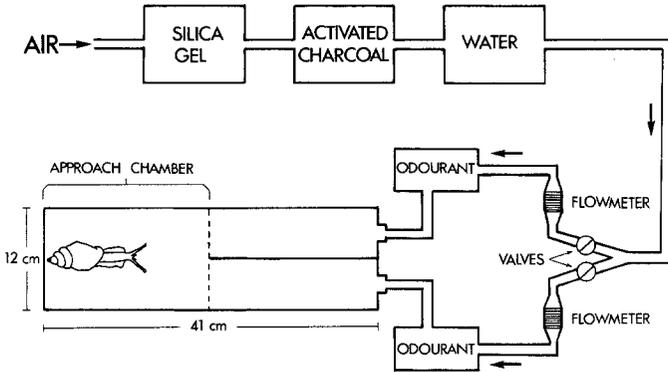illustrated in Fig. 1. They were permitted 20 min to make a choice. To

FIG. 1.   Airflow system and olfactometer used in odor discrimination experiments.

discourage backing out and simultaneously to encourage choice behavior,
a 100-W incandescent lamp was sometimes placed at the open end of the
olfactometer. Airflow through the two sides of the olfactometer was
adjusted until equal, and was at the rate of approximately 0.1 m/sec. Snail
odors were introduced into the olfactometer by inserting into one or both
airstreams a flask containing about 2 cm of water and 10 snails that had
first been rinsed with water in order to remove fecal matter, scraps of
lettuce, and cage sand. When snails were present in only one airstream, a
jar holding a small amount of water was placed in the other.

A variety of measures was adopted to ensure that neither inherent
physical features of the olfactometer nor residues of snail mucus or snail
odor within the olfactometer might bias the choices made by test animals.
One such measure, which was also an expediency, was that we had two
independent airflow systems operating simultaneously. Odors introduced
into the right airstream in one of the systems were introduced into the left
airstream in the other. We used four olfactometers during each experi-
ment. While two were in use, the other two were thoroughly scrubbed
with concentrated detergent (Sparkleen) and then rinsed well with water.
One aspect of the cleaning involved the removal of the approach chamber
(see Fig. 1) so that it could be scrubbed especially well with a sponge. In
reassembling the olfactometers we shuffled the top–bottom, left–right
orientation of the chambers as well as the matching of particular chambers
with particular olfactometers. We also shuffled the assignment of particu-

lar olfactometers to the two airflow systems. Finally, when experiments involved two distinct groups of snails, as most of them did, each airflow system was used to test snails alternately from the two groups. We examined the efficiency of these control procedures by appropriate analyses of our data, and we are confident that no unintended biases were present.

Hatchlings were tested in a smaller, modified version of the apparatus described above. The airflow system was the same, but the choice chamber itself consisted of a molded plastic Y-tube with an inner diameter of 1.0 cm. A hatchling had to travel approximately 4.0 cm in order to express a choice.

Analysis

Open field orientation. The circular distribution of orientation in the open field experiment was analyzed using the Rayleigh test (Batschelet, 1965) and a modification of the Rayleigh test, the *V* test (Batschelet, 1972).

Trail following. All data were reduced to a quantitative measure of trail following, namely, the coincidence index (Townsend, 1974),

$$\frac{L_c}{(L_{b,s} \times L_f)^{\frac{1}{2}}} \, ,$$

where $L_{b,s}$ is the length of the blazer or smear trail, L_f is the total length of the corresponding follower trail, and L_c is the total length of the follower trail which coincides with the blazer or smear trail. Experimental replicates were combined to yield a mean coincidence index.

In experiment 2, a mean control coincidence index was used as an estimate of the amount of trail overlap which would be expected if the followers acted independently of the preexisting trails. Individual control coincidence indexes were determined by the superimposition of two blazer trails. In order to collect a sufficient number of unique blazer trails for this purpose, a set of blazer trails was obtained according to the usual procedures and criteria, but these trails were used only for calculation of the mean control coincidence index; no follower snails were placed on them. To derive the control indexes, pairs of blazer trails were selected at random and one of the trails was copied onto a sheet of transparent plastic so that it could be superimposed over the other. In experiment 2, mean experimental vs mean control coincidence indexes were evaluated by means of a model I single-classification analysis of variance.

In experiments 3 and 4, the data consist of mean coincidence indexes of various experimental groups. For experiment 4, the appropriate pairs of means were tested for significance using a model I single-classification analysis of variance. Experiment 3 required application of the a posteriori procedure, the Student–Newman–Keuls test (Sokal and Rohlf, 1969).

Olfactometer choices. These data were analyzed using the *G* test (Sokal

and Rohlf, 1969) with a correction for continuity due to the relatively small samples. Reported levels of significance for this test, and for the analysis of variance, are one-tailed except in experiment 6. It was predicted that trail following and olfactometer choices would be in the direction of conspecificity, and that isolated animals would perform with greater specificity than socialized animals.

RESULTS

Experiment 1: Open Field Orientation

This was a preliminary experiment, modeled after natural conditions, to determine whether a snail's direction of movement is influenced by local aggregations of conspecifics. The results, illustrated in Fig. 2, show that the presence of other nearby conspecifics significantly affects the spatial distribution of traveling $A.$ $fulica$ (Rayleigh test, $P < 0.001$). It is noteworthy that since the experiment was conducted in still air, the snails exhibited a sensitivity to odor gradients, and anemotaxis was not an element of the response. Because $A.$ $fulica$ moves predominantly in a forward direction when placed in an open field free of known significant odors,

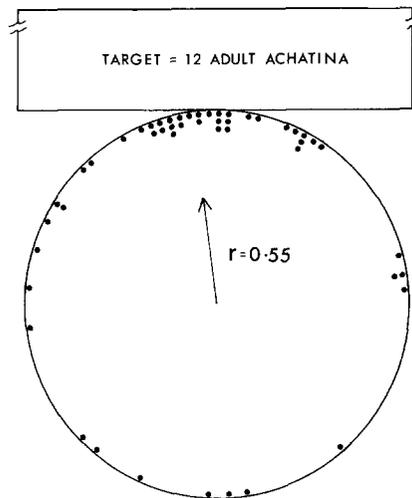

TARGET = 12 ADULT ACHATINA

r=0·55

FIG. 2. Orientation of $A.$ $fulica$ to a conspecific olfactory target in an open field arena. Circle radius equals 7.5 cm; target box to scale. Snails were placed individually in the center of the circle; the point at which each snail intersected the circumference is marked with a dot. Sample size is 49 snails. The arrow points to the mean direction of exits, with r indicating the degree of concentration about the mean (when $r = 1.00$, all exits are at the same location). The deviation of r from zero is significant (Rayleigh test, $P < 0.001$). The clustering of exit points about the predicted direction (the point at which the target box is tangent to the circle) is also significant (V test, $P < 0.0001$). Analysis according to the methods of Batschelet (1965, 1972).

individual performances were particularly striking in the cases where a snail was required to turn 180° in order to reach the target animals. In the absence of an odor stimulus, angles of turning seldom exceed 45°.

Experiment 2: Following the Mucus Trails

In this experiment, adult *A. fulica* were selected at random from the laboratory population and arbitrarily assigned either to blaze a mucus trail (a "true" trail; see Methods) or to follow one. The extent of trail following was evaluated by comparing the mean coincidence index of blazer/follower combinations (the experimental mean, $N = 38$) with the mean coincidence index of superimposed blazer trails (the control mean, $N = 38$). The results were that the experimental mean was 0.49 and the control mean 0.18. Since this difference is significant (ANOVA, $P < 0.001$), it can be concluded that trail following occurs.

Experiment 3: Species Specificity of Mucus Trail Following

While experiment 2 shows that *A. fulica* follows mucus trails made by conspecifics, it leaves open the question as to what features of the trail trigger the behavior. The present experiment was designed to limit the possible answers to that question by determining whether the phenomenon is species specific. Smear trails were made using either *A. fulica* or *O. vermiculata*. The trails made with *O. vermiculata* were about 2.0 cm wide, while those made with *A. fulica* were about 3.0 cm wide. In each instance, the follower species was selected by a coin-flip.

Table 1 shows that *A. fulica* follows trails composed of conspecific mucus better than it does trails made of mucus from *O. vermiculata* (SNK, $P < 0.05$). The ability to distinguish these trails suggests that *A. fulica* is responding to some chemical property of the trail, rather than to its texture. This conclusion is consistent with unpublished observations that *A. fulica* ignores trails that look like snail trails but are made with chicken egg albumen. It is also evident from Table 1 that *A. fulica* follows conspecific

TABLE 1
Species Specificity of Mucus Trail Following

Species identity			
Trail	Follower	Number	Mean coincidence index
A. fulica	*A. fulica*	14	0.491[a]
A. fulica	*O. vermiculata*	14	0.199
O. vermiculata	*A. fulica*	14	0.277
O. vermiculata	*O. vermiculata*	14	0.132

[a] This value is significantly different from each of the other means (SNK, $P < 0.05$), which do not differ among themselves.

trails more than does *O. vermiculata* (SNK, $P < 0.01$). Indeed, the data from *O. vermiculata* indicate that trail following does not occur to any meaningful extent in this species.

Experiment 4: Effect of Social Isolation on Mucus Trail Following in Sexually Mature and Immature Snails

Trail following in *A. fulica* is adaptive probably because it is a mechanism whereby individual snails can locate conspecifics. If the snails do tend to aggregate, at least in pairs, and for whatever advantage, then one might expect that the responses to conspecific cues would be strengthened by a period of social isolation. This experiment tested that hypothesis by comparing the trail following of two groups of *A. fulica:* One group (the social group) was housed with 8–10 animals per 30 × 17 × 20-cm aquarium for 30 days prior to testing, while the other group (the isolate group) was housed with just one animal per 7 × 14 × 19-cm aquarium for the same period of time. The experiment was conducted with smear trails, made in every instance using social animals. After each trail was made, a coin-flip determined whether a social snail or an isolate snail would be selected as follower.

The experiment was performed twice. In the first case, all of the snails were more than 1 year old and were judged sexually mature. In partial confirmation of this judgment, several clutches of eggs were laid by these animals during and immediately after the experiment. The second experiment was conducted using a group of siblings that was 6 months old at the time of testing. We judged these snails as immature because none of them had laid eggs at the time of testing and, during 4.5 years of observation, we have never observed egg-laying in any other animals so young.

Table 2 shows that the mean coincidence index of the mature isolate group was more than double that of the mature social group (ANOVA, $P < 0.01$). This result therefore supports the hypothesis that trail following in *A. fulica* has a social function. Since isolation of the immature animals

TABLE 2
Effect of Social Isolation on Mucus Trail Following
in Sexually Mature and Immature Snails

		Mean coincidence index		
	N	Socials	Isolates	Level of significance
Mature	14	0.30	0.65	$P < 0.01$
Immature	30	0.39	0.39	NS

resulted in no significant effect, the data suggest that sexual mating is the specific social function served by trail following. This interpretation is consistent with the report by Jeppesen (1976) that social isolation promotes sexual activity in *Helix pomatia*. A syllogism is completed with Townsend's finding (1974) that sexually active *Biomphalaria glabrata* are especially responsive to conspecific mucus trails. It should also be noted that the sexual activity of *A. fulica* is greatest during wet weather (Berry and Chan, 1968), a circumstance which favors the preservation of mucus trails.

Description of Trail Following Performances

The above account of trail following needs to be supplemented with a more qualitative description. Particularly significant is the impression one receives while observing the animals that trail following is an all-or-none phenomenon, that is, snails either ignore the mucus altogether or else attempt to follow it. Some snails exhibit frequent lateral oscillations of the head and apparent chemosensory sampling of the substrate with the lip and anterior tentacles, especially in the vicinity of mucus, while other snails show little or none of this behavior. Interesting in this context is the frequency distribution of values of individual coincidence indexes (Fig. 3). The distribution has peaks at the high and low ends, but it is not symmetrical. The solitary peak representing complete trail following
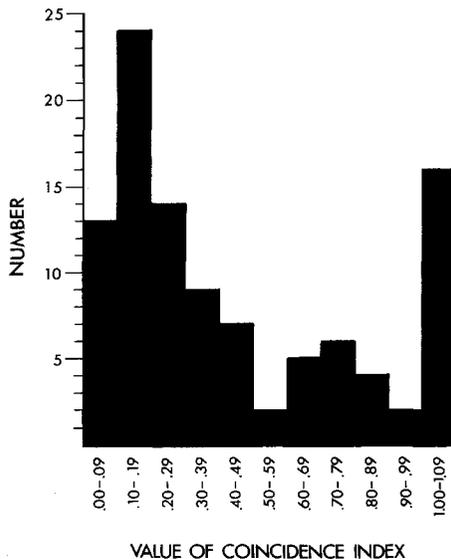

FIG. 3.   Frequency distribution of values of individual coincidence indexes. The sample consists of all replicates from experiments that used smear trails; $N = 102$. Values greater than 1.00 resulted from instances in which a follower snail turned about and traveled twice on a given trail segment.

suggests that occasional follower snails are able to "lock in" to trails, an occurrence which could depend on either the responsiveness of the follower snail or some property of the trail itself.

Experiment 5: Species Recognition by Odor

This experiment tested the hypotheses that (1) terrestrial snails can discriminate species by olfactory cues alone, and that (2) given a choice, snails orient preferentially toward the odor of their own species. Choice behavior was elicited by the use of an olfactometer. The experiment was conducted in three parts, each of which paired two species of snail. In each case the odor of one of the species was carried in the left airstream and the odor of the other species was carried in the right airstream. Adult test subjects were chosen alternately from the two species.

The results, presented in Table 3, show that species discrimination was

TABLE 3
Species Recognition and Choice Behavior in the Olfactometer

		N	Number of choices to conspecifics	Number of choices to other species	Level of significance
(A)	A. fulica	25	20	5	$P < 0.005$
	H. aperta	25	20	5	$P < 0.005$
(B)	H. aperta	25	7	18	$P < 0.05$
	O. vermiculata	25	19	6	$P < 0.025$
(C)	O. vermiculata	25	18	7	$P < 0.05$
	A. fulica	25	14	11	NS

exhibited by and between A. fulica and H. aperta (A), and that each of these species preferred the airstream which contained the odor of conspecifics (G test, $P < 0.005$). However, in Table 3 (B) and (C), where O. vermiculata was paired with H. aperta and A. fulica, orientation preferences were weaker. Also, H. aperta oriented significantly more often toward the odor of O. vermiculata than toward the conspecific odor. These data suggest that either O. vermiculata yields an odor which other snails find attractive, or the odor effectively masks species specific cues, or both.

Experiment 6: Odor Recognition of Siblings

Since the preceding experiment demonstrated that at least under some circumstances snail species are discriminated by odor, we asked next whether sibling relationships were also marked by detectable and behaviorally significant olfactory cues. This experiment was conducted with an olfactometer in a manner similar to the several parts of experiment 5, using two groups of sibling A. fulica. One group was 16 weeks old at the

time of testing, the other 19 weeks old. Each sibling group was hatched out and subsequently maintained in a separate container, but otherwise treated identically. During the experiment, 10 individuals from each sibling group served as sources of the olfactory stimuli, while other individuals were alternately selected from the two groups for testing.

Data from the two sibling groups were pooled because a test for heterogeneity indicated no difference between the samples. There was a total of 72 replicates. The results were that 43 snails chose the olfactometer arm which contained the odor of siblings, while 29 snails chose the arm with the odor of nonsiblings. Since this experiment was motivated by several hypotheses which led to contradictory predictions of the results, the test for significance was two-tailed. By this criterion the difference is not sufficient to demonstrate a significant discrimination of sibling relationships (G test, $P > 0.05$).

Experiment 7: Effect of Isolation on Choice Behavior in the Olfactometer

Like experiment 4, this experiment was directed to the question of whether a snail's recent social experience influences its response to conspecific chemical stimuli. An isolate group and a social group of *A. fulica* were established and treated in the manner described for experiment 4. All of the snails, including the stimulus animals, were 6-month-old siblings considered to be sexually immature (reasons given in description of experiment 4). Tests were conducted in the olfactometer, with the odor of conspecifics presented on one side of the apparatus and the other side simply moisturized.

Table 4 shows that the social group preferred the water side of the

TABLE 4
Effect of Social Isolation on Choice Behavior of Sexually
Immature Snails in the Olfactometer

	N	Number of choices to conspecifics	Number of choices to water only	Level of significance
Socials	30	9	21	$P < 0.05$
				Difference, $P < 0.005$
Isolates	30	22	8	$P < 0.025$

olfactometer and the isolate group preferred the side containing conspecifics. The difference between the group performances was significant (G test, $P < 0.005$), indicating an effect of social experience on response to conspecific olfactory stimuli. The positive result obtained here with immature snails is consistent with that obtained in experiment 4 when adult animals were used to test trail following after social isolation, but it is inconsistent with the negative results which were obtained in experiment

4 when the same population of immature snails was used. This paradox is analyzed in the Discussion.

Experiment 8: Sensitivity of Isolated Hatchlings to Conspecific Odor

The subjects for this experiment were sibling *A. fulica,* 3 weeks old at the time of testing. Eggs from a single clutch were placed in clean 6.0-cm glass petri dishes, one egg to each dish, where the hatchlings were maintained prior to testing. Although the snails contacted their own mucus and were subject to their own volatile chemical products, each individual was completely isolated from other snails. The snails were tested in a Y-tube olfactometer, with the odor of conspecifics presented on one side of the apparatus and the other side simply moisturized. The result was that 29 of 31 animals chose the side of the olfactometer containing the odor of conspecifics (*G* test, $P < 0.001$). Siblings of the isolated snails, hatched and maintained collectively for the same period of time, chose the conspecific side on each of 10 trials. These data show that *A. fulica* responds to conspecific stimuli from an early age, and they suggest that the response is not learned.

DISCUSSION

Surprisingly, to the best of our knowledge, this is the first formal description of mucus trail following in a terrestrial gastropod.[3] Although several authors have reported the phenomenon in aquatic snails (e.g., Townsend, 1974; Wells and Buckley, 1972), apparently comparable studies have not been previously undertaken with terrestrial species. However, the suggestion made by Wells and Buckley (1972) that the phenomenon might be universal among gastropods has not been borne out by the present study. Experiment 3 failed to produce convincing evidence of trail following in *Otala vermiculata.* Furthermore, although *O. vermiculata* oriented more strongly toward the odor of its own species than that of others in the olfactometer experiment (5), the response was not necessarily species specific since *H. aperta* and *A. fulica* also oriented strongly toward the odor of *O. vermiculata.* It is worth noting that *O. vermiculata* is indigenous primarily to the Mediterranean region, where the relatively arid climate would not favor the evolution of trail following behavior because dry air promotes the conservation of mucus while also contributing to the rapid desiccation of trails. Conversely, similar arguments suggest that the semitropical homes of *A. fulica* are especially compatible with trail following.

The species specificity of trail following shown by *A. fulica* (experiment 3) is consistent with the specificity of the same behavior in the freshwater

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[3] *Note added in proof.* The following recent article should be consulted for results similar to our own: Cook, A. (1977). Mucus trail following by the slug *Limax grossui* Lupu. *Anim. Behav.* **25,** 774–781.

pulmonate *Biomphalaria glabrata* (Townsend, 1974) and the opistho-branch *Navanax inermis* (Paine, 1963). It is also clear from the results of experiment 5 that *A. fulica* can distinguish its own purely airborne odors from those of *H. aperta* and that it orients preferentially toward the odor of conspecifics. These results raise the question whether the behavior of *A. fulica* in the olfactometer experiments and in the trail following exper-iments might not represent a single phenomenon. This could be the case if snail mucus were the source of one or more volatile chemicals which are attractive to conspecifics. But it is also possible that mucus may release some volatile chemical stimuli while retaining other less volatile ones. Alternatively, the airborne stimuli might derive from a source other than the trail mucus. In the latter two cases there is an obvious mechanism for the functional differentiation of trail following and orientation to airborne odors. However, even if both behaviors depended on sensitivity to a single chemical substance, the proximal and distal perception of that substance might nevertheless involve different sensory structures, thus implying processing at different loci in the central nervous system and perhaps different functional consequences.

All pulmonates of the order stylommatophora possess two pairs of tentacles. The posterior (eyestalk) tentacles have been strongly impli-cated in the olfactory perception of distant cues (Suzuki, 1968; Gelperin, 1974), and we have found in this laboratory that food-finding behavior of *A. fulica* in the olfactometer is dependent on intact posterior tentacles (Croll, unpublished). However, a role for the anterior tentacles has not been established. They, along with other parts in the head region, are sensitive to chemical stimulation (Schulz, 1938) and frequently appear to sample the substrate. These facts suggest that the anterior tentacles could be specifically involved in contact chemoreception, as might be used, for example, in trail following. Lesion studies should help to clarify this issue.

Another way to consider the relationship between trail following and responses to purely airborne stimuli is to ask if they have the same adaptive significance. A difference is indicated by the discrepant effects of isolation on trail following and olfactometer performance (experiments 4 and 7). Isolation was associated with more trail following in mature *A. fulica* compared to social controls, but had no apparent effect in immature animals. These data imply that trail following is used for finding sexual mates. On the other hand, since the isolation of immature snails was associated with more conspecific choices in the olfactometer, one is led to the uncomfortable conclusion that airborne stimuli (but not trails) contain information of a nonsexual nature which is especially useful to snails which have been recently deprived of conspecific contacts.

Why would snails be interested in the whereabouts of conspecifics except for purposes of mating? One reason is because the presence of numerous conspecifics implies a hospitable habitat. This circumstance

could be used to advantage by snails simply through the mechanism of attraction to conspecific odors. The effect of social isolation on the olfactory choices made by immature snails suggests that the advantages of aggregation are sufficient to endow the conspecific response with a motivational component. Furthermore, since mucus trails are ordinarily laid by single individuals, it is not surprising that trails hold no special attraction for immature animals deprived of the aggregate stimulation implied here. But this still leaves unexplained how the chemosensory properties of mucus trails differ from those of purely airborne stimuli, and by what means snails discriminate that difference.

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