to the typically poor germination of *ade12* spores unattended by other adenine markers. The hybrids of parental mutants × wild type gave only 53 viable spores from 21 asci (viability 63.0 percent) including only a single instance where an *ade12* spore survived. To contend with this explanation for the lack of *ade12* segregants from the backcrosses, seven partial revertants were crossed to a noncomplementing *ade12* allele, *ade12-55*. The diploid hybrids were adenine independent and excreters of hypoxanthine. The dissection of 60 asci gave 9 with two viable spores, 32 with three viable spores, and 19 with all four spores surviving. No more than two adenine-specific auxotrophs were found in an ascus and these were invariably identified as *ade12-55* by complementation tests. Thus, although we are assessing the allelism of several independent events of mutation simultaneously, when the data for any one of them is moderate, we conclude from the total absence of recombinants that these reversions are allelic to the *ade12* locus.

The recovery of allelic partial revertants demonstrates that the enzymatic and regulatory functions associated with the *ade12* locus are mutationally separable, a condition that would not obtain if either property were merely the physiological consequence of a monofunctional mutation. Our results support the hypothesis that this locus encodes a novel type of protein with catalytic and repressor functions.

Note added in proof: A current report by Lomax and Woods (*11*) demonstrates that the prototrophic, hypoxanthine-excreting mutants designated *pur1* (*10*, *11*) are allelic to *ade12*. Such mutants, by single mutation from wild type, are the functional equivalent of our enzyme-restored partial revertants *ade12E*. The finding is consistent with our hypothesis.

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3. In *S. cerevisiae* the *ade1* locus controls phosphoribosyl-aminoimidazole carboxylase; *ade2*, phosphoribosyl-aminoimidazole synthetase; *ade13*, adenylosuccinase. The purine biosynthetic step of *ade8* has not been identified.
4. Media used in this study include: synthetic minimal medium (MM): amino acid-free Difco yeast nitrogen base, 6.7 g/liter, and glucose, 20 g/liter. SC contained the following supplements to MM, in micrograms per milliliter: adenine sulfate, 20; L-histidine HCl, 10; L-leucine, 60; L-lysine HCl, 60; L-tryptophan, 10; uracil, 10. In SAD the adenine was omitted; in SHX, hypoxanthine, 20 μg/ml, was substituted for adenine. YEP: glucose (20 g/liter), peptone (20 g/liter), yeast extract (10 g/liter). The genetic capability to form pigment at all is shown on YMA: glucose, 40 g/liter; yeast extract, 3 g/liter; Bacto-peptone, 5 g/liter; and malt extract, 3 g/liter. The ability to form pigment in the presence of excess adenine is tested on GBHA: Difco yeast nitrogen base (6.7 g/liter), glucose (50 g/liter), and (in micrograms per milliliter) adenine, 75; L-histidine HCl, 5; L-leucine, 60; L-isoleucine, 60; L-lysine HCl, 60; L-tryptophan, 30; uracil, 20; L-arginine HCl, 10; L-methionine, 30; L-aspartic acid, 10; glycine, 10; L-proline, 40; L-serine, 20; and L-phenylalanine, 50.
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10 February 1970; revised 6 April 1970

Homing Behavior, Orientation, and Home Range of Salamanders Tagged with Tantalum-182

Abstract. *Using radioactive tags, we recorded movements of salamanders* (Plethodon jordani) *in their home areas and during homing. Males occupied home areas about three times larger than those of females and made occasional excursions into outlying regions. Homing after 22- to 60-meter displacements was direct and rapid, once initiated. Course headings at 1 meter from release were random; those at 2 meters and more were home-oriented. Males initiated homing movements sooner than females, although both sexes traveled at similar rates. Increased incidence of climbing on vegetation after displacement suggests olfactory mechanisms of orientation. These observations give direct evidence of homing orientation in caudate amphibians.*

Homing ability and size of the home range has been studied in *Plethodon jordani* (*1*) and other species of salamanders, and general course and time estimates of homing have been given (*2*). However, more detailed records of home range and homing movements on substantial percentages of experimental animals are needed before homing success can be attributed to any system(s) of homing orientation. Animals displaced beyond the limits of their home range can theoretically return to the home area by random or patterned movements alone without the operation of homing orientation mechanisms. Although patterned movements can be oriented with respect to the release point, neither patterned nor random movements have any consistent spatial relationship to the position of the home area, the characteristic of the homing orientation system. The lack of continuous tracking devices has greatly limited homing studies in salamanders. By using radioactive tagging methods, we obtained the first direct evidence of continuous homing orientation in salamanders which were displaced outside their normal home areas (*3*).

The study was conducted near Highlands, North Carolina, during August and early September 1969, in areas of mixed hardwood-hemlock forest with mostly rhododendron–mountain laurel understory. Herbaceous cover ranged from sparse to medium dense, and most areas contained a deep layer of fallen leaves and logs. Adult *P. jordani* (*4*) were collected by hand at night (between 2000 and 2330 E.S.T.), usually from burrow entrances. The size of each salamander was measured and the sex was determined; each salamander was marked by toe-clipping and was tagged by the injection of a 3- to 5-mm long, 18-gauge ^{182}Ta wire (20 to 48 μc) into the abdomen. Salamanders thus treated could be located in the habitat at about 2 m distance with a scintillation detector system (*5*). Direct observations were often made under subdued lantern light while the salamanders were on the surface at night. Each tagged salamander was either released at the point of capture (control) or displaced in an opaque container (*6*). Release usually occurred within 20 minutes of capture. Displacements were made in parallel, two salamanders of either sex being displaced in the same or opposite directions with sufficient spatial separation to avoid confusion over identification. Searches were made from two to eight times each night (between 1930 and 0600 E.S.T.) and once during the day

(*7*). Because of the general sensitivity of the salamanders to disturbances on the surface at night, continuous following was only occasionally attempted. Locations of detected animals were marked, and the distance and direction of movement were determined daily. Salamanders in burrows over about 0.5 m in depth sometimes avoided detection unless the scintillation probe was on the surface directly over the animal. For purposes of analysis, climbing behavior was considered to have occurred only if the salamanders were spatially separated from the ground by 0.1 m or more (*8*). Movements by 25 tagged salamanders (all displacements from 22 to 60 m, and controls) are reported here. Displaced salamanders that returned to within 7 m of the point of initial capture were considered to have homed. In the analysis below, rejection of the null hypothesis was based on the .05 level of significance, unless otherwise stated.

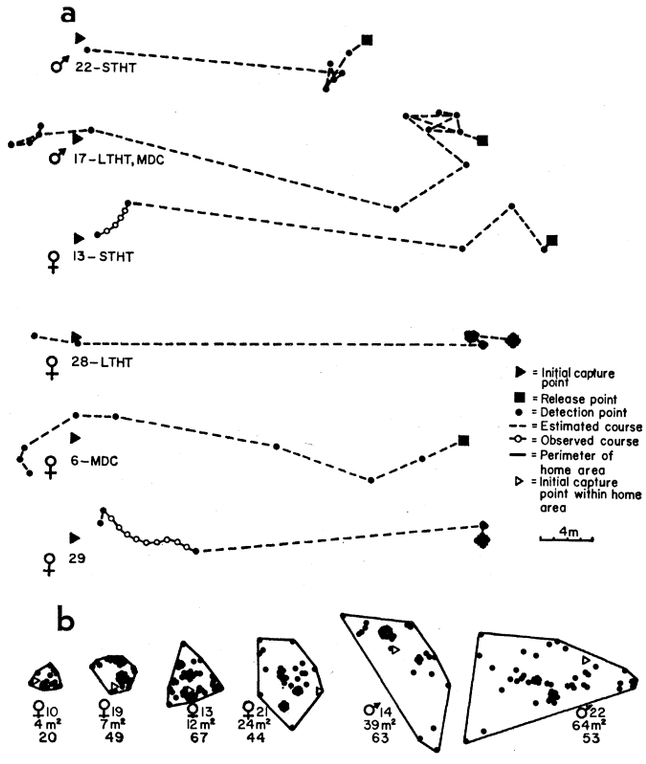
Before one considers the course taken by salamanders returning home, the normal home range must be defined. The significance of the course, as an indicator of the operation of one or more orientation systems, is a function of the position and size of the home area. The initial capture was assumed to be within the normal home range of each animal and was therefore used to reference the home position. Two findings support this assumption: first, the occurrence of the initial points of capture within the six home areas measured (*9*) (Fig. 1); and second, the fact that 23 of the 24 displaced salamanders (96 percent) returned to within a few meters of their initial capture position. The sizes of the six areas measured were similar to previous estimates for a 3-month period (*1*) and were about three times larger for males than for females (Fig. 1). Control male 20 (*10*) was once found 22 m from the initial point of capture. Temporary journeys by males 14 and 22 carried them about 7 m from areas normally frequented. Because of such trips and the larger home ranges, males were probably more familiar with areas nearer their release sites than females were. Nevertheless, the displacement distances were considered sufficient to move salamanders of both sexes into areas beyond those of direct familiarity. Thus, if a substantial percentage of course headings were toward the vicinity of initial capture, this would be considered evidence of homing orientation, and not, for example, orientation within the home area for a preferred burrow or forage area.

Table 1. Homing time and climbing of control and displaced salamanders. DD, distance displaced; DR, direction displaced; TND, total night detections; CN, climbing night (night 1 = release night); DCO, distance of climbed object from point of release R or initial capture C; THT, total homing time; RTT, return trip time.

Subject No., sex	DD (m), DR	TND	CN	DCO (m)	THT (night hours)	RTT (night hours)
10 F	0	11	—	—	—	—
13 F	0	35	—	—	—	—
19 F	0	25	—	—	—	—
21 F	0	23	16	4.0 C	—	—
14 M	0	34	—	—	—	—
20 M	0	3	—	—	—	—
22 M	0	24	—	—	—	—
6 F	28 NW	11	—	—	25.7	7.0
7 F	28 SE	10	1	1.0 R	12.5	4.3
8 F	34 SW	11	—	—	56.4	3.1
9 F	30 E	12	—	—	56.1	3.0
10 F	22 NE	3	1	0.0 R	6.9	1.5
11 F	30 SE	11	1	2.0 R	25.7	4.1
12 F	30 NW	12	2	0.7 R	36.7	3.9
13 F	35 E	9	1	0.7 R	6.8	1.1
19 F	60 SW	8	1 1 1 3	2.3 R 2.7 R 11.0 R 2.0 C	11.6	7.0
21 F	22 SW	12	1	2.0 R	31.1	1.8
26 F	28 E	3	—	—	20.8	1.8
28 F	34 S	14	—	—	83.1	1.8
29 F	30 SE	12	1	0.0 R	27.1	2.7
14 M	30 W	8	1	3.3 R	13.7	5.2
15 M	28 NW	5	—	—	—	—
16 M	28 SE	7	1 3	0.0 R 5.0 C	7.2	2.2
17 M	30 S	12	—	—	42.3	1.7
18 M	26 E	7	—	—	5.8	1.3
22 M	22 SW	12	—	—	3.3	0.8
23 M	30 NW	0	—	—	10.1	10.1
24 M	30 E	5	—	—	16.4	3.2
25 M	30 NE	3	—	—	4.2	4.2
27 M	28 S	7	—	—	25.2	5.2
31 M	30 N	13	—	—	89.9	34.1

With the position and size of the home area defined, we were able to consider the homing courses for evidence of homeward orientation. Although interval checks on positions of displaced salamanders did not give a continuous record of the animals' movements, they did give a consecutive series of positions which could be connected by dashed lines to approximate the course of movement (*11*) (Fig. 1). Two observations support the contention that the estimated courses are good approximations of the actual routes taken. First, the actual course segments of the two salamanders continuously followed (females 13 and 29) would be similar to the approximated courses constructed by connecting the first and last positions for the two continuous records. Second, both the estimated courses and the body axes of the salamanders detected on the surface between the release site and home were generally oriented in the home direction. The estimated positions of the salamanders of both sexes along the courses at selected distances from the release point were assembled (*12*) (Fig. 2). These positions 2 m and greater from release were nonrandom ($P < .01$) and were oriented in the home direction (*13*). Further, there was no difference between the directional orientation of the males and that of the females at each distance from the release point. Since homeward orientation was observed at distances of 2 m and more from the release point, the existence of a homing orientation mechanism is evident.

The abrupt nature of the homing movements further supports the existence of an orientation system. Two time intervals were measured (*14*): the total homing time (THT), which is the interval between release and the estimated arrival time at home, and the return trip time (RTT), which is the best estimate of the time taken to travel over 80 percent of the distance home once directed movement away from the release point was initiated (*15*) (Table 1). For the 20 displaced salamanders analyzed, the median THT was 20.8 night hours; the extremes varied from 3.3 to 83.1 hours (*12*). The median RTT was 1.8 hours with variations from 0.8 to 7.0 hours. Since the RTT values were less than 40 percent of the THT values except for male 25, the THT values were determined mainly



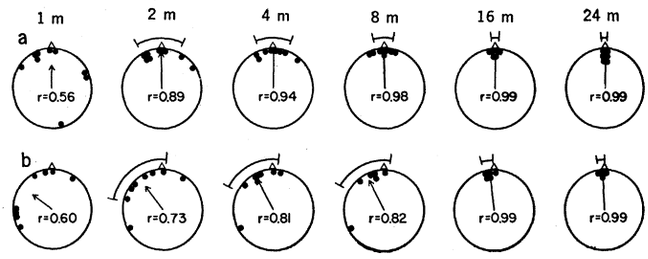


Fig. 1 (left). Size of home range and selected course estimates of radioactively tagged (a) displaced and (b) control salamanders. The size of the home area and the total number of observations are shown below each enclosed home area. The most deviant course MDC, and the courses of the shortest total homing time STHT and of the longest total homing time LTHT, are indicated for each sex. Estimates of the course of animals 19, 23, and 31 were not considered because of incomplete records.

Fig. 2 (above). Estimated positions of (a) displaced female salamanders and (b) displaced male salamanders relative to the points of release and initial capture at selected distances from the release point. The center of each circle represents a composite release point. Nine courses are analyzed for the females. The number of courses analyzed for the males is eight courses at 1, 2, and 4 m, seven courses at 8 m, and six courses at 16 and 24 m. △, Home direction; ●, estimated salamander position; |—|, angular deviation; ↑, mean direction vector (r = length, a measure of dispersion about the mean direction).

by the length of time the salamanders remained close to the point of release and not by the time taken to make the return trip. In comparing the THT and the RTT values of the males and females, we found that the THT values for the males were significantly greater than the values for the females, although the RTT values were not significantly different (*16*). Thus the males initiate the home trip sooner than the females, although both sexes move at a similar rate. Since males have larger home areas than females and thus have direct familiarity with areas near the release site, the earlier initiation of homeward movement by males may be the result of an earlier detection of information associated with the home area.

The behavior of the displaced salamanders, which suggested that olfaction might be involved in the homing orientation system, differed from that of the controls both in climbing frequency and in form of movement. Of the climbing detected, the one instance by control salamanders in 155 night observations was significantly less than the 11 instances by displaced salamanders in 124 detections within 4 m of the release point (*15*). In addition, although only one of the six controls was observed to climb during 155 night detections prior to displacement, five of these six controls climbed during 31 night observations after displacement later in the study. Climbing by displaced salamanders occurred significantly more often on the release night than on all other nights, and occurred within 3.4 m of the release point rather than at any other location (*16*). Since air flow interferences are reduced above low-relief vegetation, litter, and topographic obstructions, climbing could facilitate the detection of home-associated odors.

The movements of the two salamanders (females 13 and 29) which were continuously observed while they returned to their home areas differed in rate and form from the movements of salamanders not engaged in the return trip part of the homing response. Both animals traveled at an increased speed of about 1 m/min, pausing often for typically less than 1 minute (*17*). Sliding movements supplemented the normal crawling form of locomotion. The speed and direction of movement seemed characteristically regular, and course changes were first apparent at the beginning of each phase of locomotion. The head was inclined above the body axis up to about 30 degrees, particularly during pauses. Similar head inclination was characteristic of salamanders resting on vegetation above the ground. These movements may represent frequent sampling of airborne odors that could identify the home area.

We conclude that *P. jordani* possesses a well-developed homing orientation mechanism. The senses involved in this system remain to be conclusively demonstrated for this and other species of salamanders, although evidence for an olfactory (*1*, *18*) or photoreceptive (*19*, *20*) basis, or both, has been reported. A celestial compass mechanism (*20*) is unlikely since *P. jordani* home during the night after nocturnal displacement in opaque containers under a moderately dense forest canopy. Blinded individuals displaced under similar conditions also home (*1*). An olfactory mechanism seems more likely, and it is not difficult to envision such a mechanism operating in terrestrial environments (*21*).

The homing orientation in *P. jordani* is not associated with shorelines (*22*), nor is it allied with seasonal breeding migrations. It is a separate, direction-independent, behavioral response which may well be responsive to different selective pressures although similar senses may be involved.

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3. The movement of an *Ambystoma maculatum* was continuously monitored after it was displaced in daylight 45 m from a breeding pond. It returned directly toward the pond for a distance of 34 m [C. R. Shoop, *Biol. Bull.* **135**, 230 (1968)].
4. *Plethodon jordani* is completely terrestrial (no aquatic larval stage and no breeding migrations), nocturnal, and lungless. It is quite sedentary and restricted to moist environments both because respiration is partly cutaneous and because of the vulnerability of the eggs to desiccation.
5. A Thyac III (Victoreen) scintillation survey meter and a model 489-55 gamma scintillation probe [3.17 by 3.82 cm NaI (Ti) crystal] were used.
6. Seven salamanders (10, 13, 14, 19, 20, 21, 22) served as controls for 1 to 4 weeks. Six were displaced later in the study. Salamander 20 disappeared 1 week after initial capture and thus could not be displaced.
7. Generally checks were made more often soon after the salamanders were released or during evenings when conditions seemed suitable for homing.
8. Data presented here indicate that, occasionally, *P. jordani* climb on tree trunks and other vegetation up to a height of about 2.3 m. Although this behavior has been reported [R. Gordon, J. MacMahon, D. Wake, *Zoologica (New York)* **47**, 9 (1962)], no reason has been given for its occurrence.
9. The method that gives the maximum home range as indicated by isotopes was used to estimate the size of the home area [H. Ambrose III, *Amer. Midland Natur.* **81**, 535 (1969)]. This method makes it possible to include areas of marginal familiarity to the salamander which we wished to include since the salamanders, upon arriving in such areas, could possibly use local landmarks to find the more frequented areas.
10. The size of the home area of this salamander was not determined. It was detected five times within 3 m of the release point during 3 days after release, but was detected only once thereafter 22 m from the release point 6 days after release.
11. Excluding salamanders 15 and 20 which disappeared, we detected salamanders on 588 of 606 attempts. Eight of the failures were for two salamanders which disappeared for 3- and 6-day intervals. The locations of the detection points, therefore, were not biased to include only those in the vicinity of release and home or between these areas.
12. Only those salamanders displaced upon initial capture were used in the course analyses (Fig. 2), thus excluding salamanders 10, 13, 14, 19, 21, and 22. Salamanders 19 and 23 (1 to 24 m) and 31 (8 to 24 m) were omitted from both the course and time analyses because failure to detect them during searches prior to their being detected at home gave unreliable course and time estimates. For the course analysis, any point along the estimated course (dashed line) was considered to be the best estimate of the salamanders' position between the actual (observed) positions.
13. E. Batschelet, *Amer. Inst. Biol. Sci. Monogr. 1* (1965). The Rayleigh, Stephens, and F analyses were used, when appropriate. All courses were examined for possible influence due to distance and direction of displacement. In addition, the observer's position at release, the position of a nearby creek, and the direction uphill and downhill to the release point were studied for their possible effects. In no case were there any noticeable effects on the homing courses.
14. Since *P. jordani* move on the forest litter only after dark, all movement times were considered in terms of cumulative dark hours (1930 to 0600 E.S.T.).
15. For example, male 18 released at 2220 hours, was detected 4.5 m from the release point at 0250 hours and 2 m from the initial capture site at 0530 hours on the same night. The best estimate of his arrival at home is 0410 hours, the midpoint of the interval prior to his being detected at home. Thus the THT was from 2220 to 0410 hours, a time of 5.8 hours. The RTT is 1.3 hours, one half the duration of the period from 0250 to 0530 hours.
16. S. Siegel, *Nonparametric Statistics* (McGraw-Hill, New York, 1956), pp. 116–127 (Mann-Whitney U test, timing analysis); *ibid.*, pp. 42–47 (chi-square one-sample test, climbing analyses).
17. Without the pause components, then, the salamanders displaced 30 m could have made the return trip in 30 minutes.
18. D. Grant, O. Anderson, V. Twitty, *Science* **160**, 1354 (1968); V. Twitty, *Of Scientists and Salamanders* (Freeman, San Francisco, 1966).
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21. D. Ferguson and H. Landreth, *Behaviour* **26**, 7 (1966). The necessity of wind and its flow in the one direction favorable for information transmission was thought to be relatively inefficient. Wind directions recorded in this study (in the woods) varied by as much as 180 degrees nightly. These variations along with the low wind speeds (typically from 0.1 to 0.8 m/sec) would support the operation of a short-range olfactory-based orientation system. Such a system operates in various animal groups; see, for example, E. O. Wilson, W. F. Blair, G. Tembrock, in *Animal Communication*, T. A. Sebeok, Ed. (Indiana Univ. Press, Bloomington, 1968); M. Jacobson, *Insect Sex Attractants* (Interscience), New York, 1965).
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23. We thank Mrs. M. Madison for her assistance throughout the study, and Dr. T. Howell for many courtesies at the Highlands Biological Station. Supported by NSF grant GB2496 to Highlands Biological Station, by NIH predoctoral fellowship GM 44846 to D.M.M., and by AEC research support agreement AT (30-1) 3554 to C.R.S. Work by D.M.M. was done in partial fulfillment of the requirements for the Ph.D. degree.

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3 February 1970; revised 23 April 1970 ■

Amphetamine: Differentiation by d and l Isomers of Behavior Involving Brain Norepinephrine or Dopamine

Abstract. d-*Amphetamine is markedly more potent an inhibitor of catecholamine uptake by norepinephrine neurons in the brain than is* l-*amphetamine, whereas the two isomers are equally active in inhibiting catecholamine uptake by the dopamine neurons of the corpus striatum. In behavioral studies,* d-*amphetamine is ten times as potent as* l-*amphetamine in enhancing locomotor activity, while it is only twice as potent in eliciting a compulsive gnawing syndrome. This suggests that the locomotor stimulation induced by amphetamine involves central norepinephrine, while dopamine neurons play an important role in the induced compulsive gnawing behavior. Assessment of differential actions of* d- *and* l-*amphetamine may be an efficient method to differentiate behaviors involving norepinephrine or dopamine in the brain.*

The behavioral effects of many drugs are thought to involve the catecholamines norepinephrine or dopamine in the central nervous system. Investigators have had only limited success in ascertaining whether particular effects are attributable to interactions with norepinephrine or dopamine, or both (*1*). By comparing and contrasting the biochemical and behavioral actions of *d*- and *l*-amphetamine, we have developed a method for the differentiation of behaviors mediated by norepinephrine or dopamine.

Amphetamine produces several types of behavioral effects in animals. It enhances locomotor activity, an action which may be a model for the central stimulant effects of amphetamine in man, and it provokes a compulsive gnawing sydrome. Both of these actions are thought to involve dopamine or norepinephrine, or both. Some studies implicate the corpus striatum, an area which contains the bulk of brain dopamine, in mediating the compulsive gnawing syndrome (*2*). Although indirect evidence suggests that norepinephrine tracts are important in effecting the enhancement of locomotor activity by amphetamine (*3*), some workers have favored a preponderant role for dopamine in eliciting this behavior (*4*).

Brain dopamine and norepinephrine are stored in distinct neuronal tracts (*5*). The corpus striatum contains very high concentrations of dopamine and low concentrations of norepinephrine, while in most other brain regions norepinephrine is the predominant catecholamine. In nonstriatal brain regions, *d*-amphetamine is ten times as potent as *l*-amphetamine in inhibiting catecholamine uptake by synaptosomes (pinched off nerve endings), while in the corpus striatum the two amphetamine isomers are equally active (*6*). This uptake system is thought to reflect reuptake of catecholamine released at synapses