A previous account has established that the newt Taricha rivularis returns to the home segment of breeding stream after displacement for major distances.\(^1\) Of the questions raised by this finding, the present paper deals with two. One concerns the route taken by the homing animals, principally whether it is terrestrial or aquatic; the other pertains to the timing of the homing journey, with primary reference to its initiation and completion. These and other aspects of our studies on newt homing have been touched upon in other publications,\(^1-3\) especially in a book on salamander biology,\(^4\) but in this and a series of papers to follow, our findings will be presented in more detailed, definitive form.

Aerial photographs and descriptions of the study area in the coastal mountains of Sonoma County have already been published;\(^1, 4\) the streams and topography of the area are further shown in Figure 1. Pepperwood Creek, especially the portion ("experimental stretch") designated by the numbered segments or "stations," is the stream within which our most intensive homing studies have been based, but reference will also be made to important evidence on the course and timing of homing from interstream displacements.

**Intrastream Displacements.**—Of the numerous displacements that have been made within the experimental stretch, three lend themselves most directly to clarification of the questions at hand. Figure 2, although published elsewhere,\(^4\) is reproduced here because it serves so well to introduce these questions and also bears materially on their answers. The histogram shows the locations of stream recaptures of animals displaced for a straight-line distance of approximately 1 mile. (On recapture the animals were given a toe marking to avoid recording the same animals again on subsequent encounters.)

One will note the virtual absence of any animals in the long stretch of stream intervening between the home area and the release site. Most of the animals were recaptured in the home segment of stream, and almost all of the remainder were at or near the release site. *Rivularis* is aquatic only during the breeding period, and annually throughout this season we patrol the entire experimental stretch regularly and intensively. We can thus be sure that animals recaptured in the home segment of stream during the later years following displacement have not re-entered the stream at points en route home, either to use it as a homing pathway or perhaps for any navigational cues it might afford them in resuming their terrestrial homeward migration. Otherwise, we would have encountered them at intermediate sites between the displacement and home areas.

However, the design of this experiment leaves unanswered certain crucial questions. First, recording of the locations of recaptures was not begun until the next breeding season, one year following displacement; accordingly, the histogram gives no indication whether, or for what distances, the animals may have executed a homeward migration in the stream channel during the remainder of the same breed-
Fig. 1.—Topographic map (100-ft contour intervals) of experimental area, Sonoma County, showing the streams, Pepperwood, Jim, and Danfield creeks, used for the intra- and interstream displacements of adult _rivularia_. The "experimental stretch" of Pepperwood Creek is marked off into 58 segments or "stations," each approximately 50 yards in length, and identified by numerals painted on boulders or trees along the streamside.

ing season in which they were displaced. Second, all members of the series were given an identical marking (foot amputation) which makes it impossible to follow the history of individual animals and thereby determine, for example, whether any of the newts recorded near the release site on the histogram subsequently homed after having accepted this foreign location for 1 or more years. For these reasons, as well as others less directly relevant to the subjects of the present account, we
The principal homeward exodus from the release area begins as the animals leave the water at the end of the breeding season. Of a total of 106 members of the series captured in land traps (wire-mesh fences that funnel migrating animals into escape-proof cages) situated near the release site, 68 were taken during this period, 36 during the following fall and winter after the onset of rains, and 2 after the new breeding season began. In the meantime, many members had arrived at the home segment, and Figure 3B shows how radically the distribution of the animals in the stream has changed from the preceding year. A few animals re-entered at or near the release site, but the great majority were found in the home segment. The number actually completing the return during the first year was greater than the histogram shows, since not all animals enter the water for breeding each year whether they are in the home area or in a foreign one; also, some inevitably escape detection in our stream patrols. Six members of the series caught in a land trap near station 9 before or during the 1964 breeding season were not subsequently performed two new series of displacements within the experimental stretch, marking all animals individually by coded toe clipping (for coding formula see ref. 4). Following release, the sites of recapture were recorded for all members of the series encountered in our stream patrols during the remainder of the breeding season.

The majority of any group of displaced animals, presumably because of the disturbance resulting from handling, transportation, and marking, tend to leave the stream and seek to hide on land. Undetermined but usually substantial numbers of them, varying apparently with the severity of the surgical trauma, soon return to the water, where they may remain for the rest of the breeding season. When these animals are encountered, we have no way of distinguishing them from others that may not have left the stream at all following displacement; hence, we do not know whether the location in the stream where we find a recently displaced animal has been reached by strictly aquatic movements or by re-entry into the stream after terrestrial excursions along the streamside.

In any event, recaptures in both of the series show that any homing movements in the stream channel are of limited extent and accordingly can account for only a minor portion of the total homing excursion. This is evident in Figure 3A, showing recaptures during the remainder of the same breeding season of animals displaced downstream, as indicated by the bracket and arrow. The recaptures, both in numbers and maximum distances traveled, are indeed greater in the upstream direction, but it is clear that homeward movements in the stream leave the animals far short of their objective. Many of the members of this series were recaptured two or more times before the breeding season ended; in the histogram such animals are entered only once, at the locations of capture furthest upstream or downstream from station 46, the release site.

FIG. 2.—Histogram showing recaptures of animals collected from stations 1–8, inclusive, and displaced downstream to station 54. (Each station is approximately 50 yards long, but because of the winding course of the experimental stretch the straight-line distance between stations 1 and 54 is only 1 mile.)
found in the stream during that season. Since this was the only land trap present in 1964 adjacent to the home segment of stream, and was situated at its extreme upper limit, one may be sure that there were other animals present in the home area that went undetected.

An interesting manifestation of the homing “drive” is that trap captures of animals displaced during the breeding season continue decidedly later into the spring than do those of native residents of the local population, even though the peril of desiccation increases greatly with the seasonal cessation or marked decline in rainfall. This was evident in the present series, but closer attention was given it in other series displaced subsequently. For example, after trap captures had virtually ceased at the close of the 1966 breeding season and the onset of dry weather, inspection of the traps on May 7 following a light rain of 0.3 in, a few days earlier netted a total of 51 animals displaced in March, and 17 nondisplaced ones. On May 12, after an intervening rain of only 0.05 in., 79 displaced animals and 8 nondisplaced ones were found in the traps. During the winter and early spring, the captures of resident animals greatly exceed those of displaced ones, since displaced animals represent only a small minority of the total population. A closely related manifestation of the homing drive is the tendency of displaced animals to emerge from underground hiding earlier after the resumption of rain the following autumn.

An overwhelming majority of the animals found in the first trap patrol in autumn, 1965, were members of a series displaced the preceding spring. For example, of 18 animals found in two traps near the release site, 16 were members of this series. A much fuller documentation of the “restlessness” that prolongs the movements of displaced animals in the spring and triggers them earlier the following autumn will be given in a later paper, but the pertinence of the phenomenon to the timing of the homing migration calls for at least passing reference in the present paper.

Returning to the series represented in Figure 3, captures in land traps situated different distances uphill from the release site show that the homeward terrestrial pathway seemingly parallels the stream at only modest distances from it. Fifty, 37, and 13 members of the series were captured in traps located 45, 100, and 240 yards, respectively, uphill from the south shore of the stream. No captures were made in traps located higher uphill above this stream segment near the crest of the mountain ridge separating Pepperwood and Jim creeks. Only a small percentage of the animals migrate along the lightly wooded northern side of the stream, as shown by the capture of only five members of the series on this side of the stream.

Sixty-one members of the series were captured in the home segment of stream the first year following displacement (Fig. 3B). The two remaining histograms (C, D) show the mounting accumulation of animals in the home area in the second and third years, and the corresponding reduction and eventually virtual cessation of captures near the release site. Ninety-four new captures were made in the home area during the 1965 breeding season and 33 in 1966; in constructing the histograms these new captures were added to those entered for the preceding season or seasons. Additional captures may be anticipated for 1967 and subsequent years.

Implicit in the fact that the number of animals present at or near the release site decreases during the years following displacement is the conclusion that animals may execute delayed homing, after having accepted the foreign site for substantial periods of time. Of the animals recorded at the release site (Fig. 3B) 1 year follow-
ing displacement there, four were subsequently recaptured in the home segment of the stream. Further reference to delayed homing will be made later in relation to series displaced for greater distances.

Figure 4 shows the results in the second series, similar to the one just described, except that the displacement was in the opposite or upstream direction. The histograms speak for themselves, and since the results are so closely comparable to those of the preceding series, little further comment is required. It should be explained, however, that the presence of only two land traps in the general vicinity of the displacement site, instead of several as in the preceding series, does not permit us to deal profitably with some of the issues discussed above, such as the time of initiation and the course of the terrestrial homing migration. However, all available information supports the conclusions drawn from that series.

**Speed of the Homing Migration.**—The displacements mentioned thus far were made during the spring breeding season. The dry weather that ensues shortly thereafter and prevails until autumn precludes migration, and this long period of the year (as well as arid periods that are not uncommon even during autumn and winter) cannot be included in any assessment of the time consumed by the homing
journey when newts are recaptured in the home segment of the stream the following breeding season. It is accordingly pertinent to mention a series in which animals were displaced after the autumn rains began and were recaptured in the period intervening before the end of the spring breeding season. The animals were taken in land traps near stations 1 and 9 during trap patrols made from November through March, and released near the streamside at station 20. Of 49 animals subsequently captured in the home area, 2 were taken within less than 1 month following displacement, 27 during the second month, and 20 during the succeeding 40 days. These data, of course, represent in most cases the maximum times required for the homing returns, since the intervals between successive trap patrols were usually about 10 days, and also because many of the animals undoubtedly arrived in the home area considerably in advance of their entry into the traps or their detection in the stream after beginning of the breeding season. There is one indisputable record, however, of an animal that was captured in the land trap at station 9 one day following its displacement from there to station 20, a distance of about 1/4 mile.

**Interstream Displacements.**—From Pepperwood Creek to Danfield Creek: Seven hundred and forty-seven *rivularis* were displaced in 1961 from the lower portion of the experimental stretch of Pepperwood Creek to upper Danfield Creek (*arrow*, Fig. 1), a straight-line distance of 1.5 miles and possibly twice this distance overland, across the mountainous terrain separating the two streams. Three hundred and ninety-three of these animals have been recaptured subsequently in Pepperwood Creek, the great majority of them in the segment from which they were originally collected. Of particular relevance in the present connection are 17 instances of delayed homing following residence at the release site for 1 or more years. Eight of the animals returned to Pepperwood Creek after remaining a full year at the release site, eight after 2 years there, and one after 3 years in the alien locality. This shows that *rivularis* can retain memory of the home stream, and the ability to relocate it, after prolonged periods of separation from it. However, 10 members of the series were recorded in Danfield Creek during the 1966 breeding season, 5 years after being transferred there, and it is possible that these may have developed a permanent identification with the new stream. There is good evidence that the homing animals in this series cross the mountain ridges separating the two streams, instead of following Danfield Creek or its shores downstream to the confluence with Pepperwood Creek and thence upstream to their home segment. However, this conclusion about the course of homing following interstream displacements can best be documented in the series whose description follows.

From Danfield Creek to Jim Creek.—In 1963, 730 males were displaced from a 0.4-mile segment of upper Danfield Creek to a point deep in the canyon of upper Jim Creek (*arrow*, Figs. 1 and 5), an overland distance of approximately 5 miles. Of especial interest, in addition to the remarkable fact of successful returns over this major distance, is information concerning the course and timing of homing gained from captures along the homeward route, in land traps, and in the intervening Pepperwood Creek. The locations of the traps, and the captures made in them and in the experimental stretch, and in the home segment of Danfield Creek, are shown in Figure 5.

The displacements were made during March 1963, and no captures were made in the traps until after rains began the following autumn. In November and Decem-
Fig. 5.—Recaptures of animals en route home after displacement from upper Danfield Creek (portion indicated by broken line to upper Jim Creek (arrow). (A) Captures in traps on the ridge separating Jim and Pepperwood creeks; (B) in the traps along the experimental stretch of Pepperwood Creek or in the stream itself; and (C) in the home segment of Danfield Creek. The numbers of dual or triple captures of the same animals at these three locations are summarized in the lower left-hand corner. Locations of the land traps are indicated by lines, along the experimental stretch and on the ridge between the experimental stretch and Jim Creek.

Ber, animals began to be intercepted in the traps on the ridge (location A in Fig. 5) between Jim and Pepperwood creeks, and before spring a total of 48 was captured here. Following the first captures in the ridge traps, captures began in the traps along the experimental stretch, and during the winter and spring, 60 members of the series were caught in them and in the stream itself (location B). During the same spring, 28 captures were made in the home segment of Danfield Creek (location C). The following year, the number of captures in the ridge traps decreased to 12, and none at all was made the following year, thus confirming that the majority of displaced animals tend to initiate the homing journey the first year following displacement. During these second and third years new captures in and along the experimental stretch totaled 70 and 10, respectively, and in the home segment of Danfield Creek, 106 and 47. Of the 181 animals thus far recovered in the latter location, 49 had been previously captured on their way home, either at locations A or B, or at both.

The number of these double or triple captures, shown in the lower left corner of Figure 5, actually exceeded our expectations. The traps are so widely spaced, and accordingly screen the homeward route so incompletely, that only a small minority of animals moving in this general direction would presumably be captured; the probability that a given animal would be intercepted at more than one point along the route is even much lower. Clearly, then, the animals in this series followed a fairly direct overland route in returning home, not the more circuitous passage down or along Jim Creek from the release point and then eventually up Danfield Creek. This inference is supported by the fact that no members of the series have been found in the lower part of Jim Creek, in Pepperwood Creek below the experimental stretch, or in the long portion of Danfield Creek below the home segment of this stream.

Because of the difficult access to it, the release site in the steep-walled canyon of upper Jim Creek is seldom visited, and accordingly we have only fragmentary data
concerning the number of animals that may have remained there. However, since the homing animals must ford Pepperwood Creek en route to Danfield Creek, our intensive patrols of the experimental stretch have afforded an opportunity to observe any disposition of the animals to accept this foreign stream as a new home. During the 1966 breeding season, 28 members of the series were found in the stretch, or in the land traps along its course, that had been captured there earlier in 1964 or in 1965, or in both. This number will probably decrease during the next few years through resumption of the homeward migration, but, as suggested earlier for the series displaced from Pepperwood to Danfield creeks, it is possible that in some instances a permanent identification may be developed with the experimental stretch.

Since weather conditions permit newt migration only during limited portions of the year, the completion of the homing journey by some members of the series within the first year after displacement gives some measure of the rate at which these rather sluggish animals can traverse major distances over very rugged terrain. As mentioned earlier, our methods permit us to ascertain only the maximal intervals between departure from the release site and arrival at the home area, and accordingly we shall not attempt to present a general analysis of our data on rates of movement by members of the present series. However, to cite examples that are not atypical, we may mention two animals captured in Danfield Creek within 1 month after being recorded in the experimental stretch of Pepperwood Creek.

Summary.—Adult rivularis displaced from their native stream segments to foreign ones make the homing journey on land, either parallel to the stream after intrastream displacements or directly overland across intervening mountain ridges after transfer to foreign streams. The majority initiate their return during the same spring in which they are displaced, but substantial numbers remain near the release site until the beginning of rain the following autumn. A small percentage homes successfully after remaining at the release site for as long as 3 years, and a few probably adopt the foreign site permanently.

In spite of the perils of desiccation, displaced animals continue their migrations into late spring, after native residents of the local population have taken shelter underground. They also emerge from underground hiding earlier after the resumption of rain the following autumn.

Recaptures at the home site continue to mount for 4 or 5 years, but several members of a series displaced for 5 miles completed the return trip within 1 year. Specific examples are cited in which animals have homed for a distance of about 1/4 mile in 1 day and 2 1/4 miles in less than 1 month.

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2 Twitty, V. C., Science, 130, 1735 (1959).
4 Twitty, V. C., Of Scientists and Salamanders (San Francisco: W. H. Freeman and Co., in press).