Newts: Sun-Compass Orientation

Abstract. *Rough-skinned newts, captured from breeding ponds, oriented on courses that would have intersected the familiar shorelines at right angles, when released in a circular arena on land under the sun or moon. Pondward migrants oriented similarly. Reorientation failed under complete cloud cover and after 7 days of darkness in an environmental chamber, but persisted in newts whose eyes were excised and in those displaced more than 27 kilometers in darkness. Both normal and blind animals compensated for displacement in sunshine. Preliminary evidence suggests that alternative light receptors in blinded animals may be associated with the optic tectum. No evidence of olfactory guidance was observed.*

Several anuran amphibians employ a sun-compass mechanism for guidance in activities associated with the home shore (*1*) and in migratory movements (*2*). The toad *Bufo woodhousei fowleri* can learn an escape route relative to a light cue, and the directional choice can be altered by manipulation of the daily light-dark regime (*3*). Terrestrial salamanders migrate long distances to particular breeding sites (*4, 5*).

Although these movements appear to be guided (*6*), the mechanism involved is in doubt. The ability of the newt *Taricha rivularis* to home after extirpation of the eyes led Twitty to conclude that olfactory cues were used in orientation (*7*). In laboratory experiments *T. granulosa* used a sun-compass mechanism to determine direction of a goal, but olfactory cues appeared to confirm the goal's identity (*8*).

We now report field studies in which rough-skinned newts, *T. granulosa*, oriented by the sun during the breeding season. Newts from breeding ponds, when tested on land with only celestial cues visible, moved in directions that would have returned them to water at the home shore. *Taricha granulosa*, captured en route to a breeding site, maintained the same compass course when released 27.6 km away, presumably beyond the reach of familiar odors; they failed to select an expected compass course under cloudy skies or after 7 days in darkness. Under the sun, surgically blinded newts moved in the expected direction as well as did normal animals.

Our experimental animals came from a population of *T. granulosa* breeding in fish ponds (*9*); a test site was established nearby (*10*). Their directional choices were tested in a circular arena (13.4 m in diameter; walls, 1.98 m) constructed of black plastic (No. 55 Griffolyn) nailed to posts (5 by 10 cm) driven into the ground. They were released in the center of the arena and recovered from drop-traps (4-liter cans sunk to ground level) located at 15° intervals around the wall. The ground inside the arena was bare, and the walls obscured all landscape; the arena has been described (*2*). Although most newts were tested on the day of capture, some late afternoon collections were held overnight.

Altogether 1001 newts were captured with a dip net along straight segments of shore at the breeding ponds and placed in black plastic bags, pending release in sunshine. Equal numbers were taken from the four shores representing the four basic compass points. Newts from a north shore went southward (Fig. 1a), those from a south shore went northward (Fig. 1b), those from an east shore went westward (Fig. 1c), and those from a west shore went eastward (Fig. 1d). The mean angle of the scores, computed vectorially (*11*) (Fig. 1, a–d), is within 44° of the expected direction; the newts generally moved in directions that would have taken them to water at the home shore, not toward the ponds. The test arena was about 0.4 km from the breeding ponds, presumably within range of olfactory cues.

More newts (172) were taken from the water along the same four shores

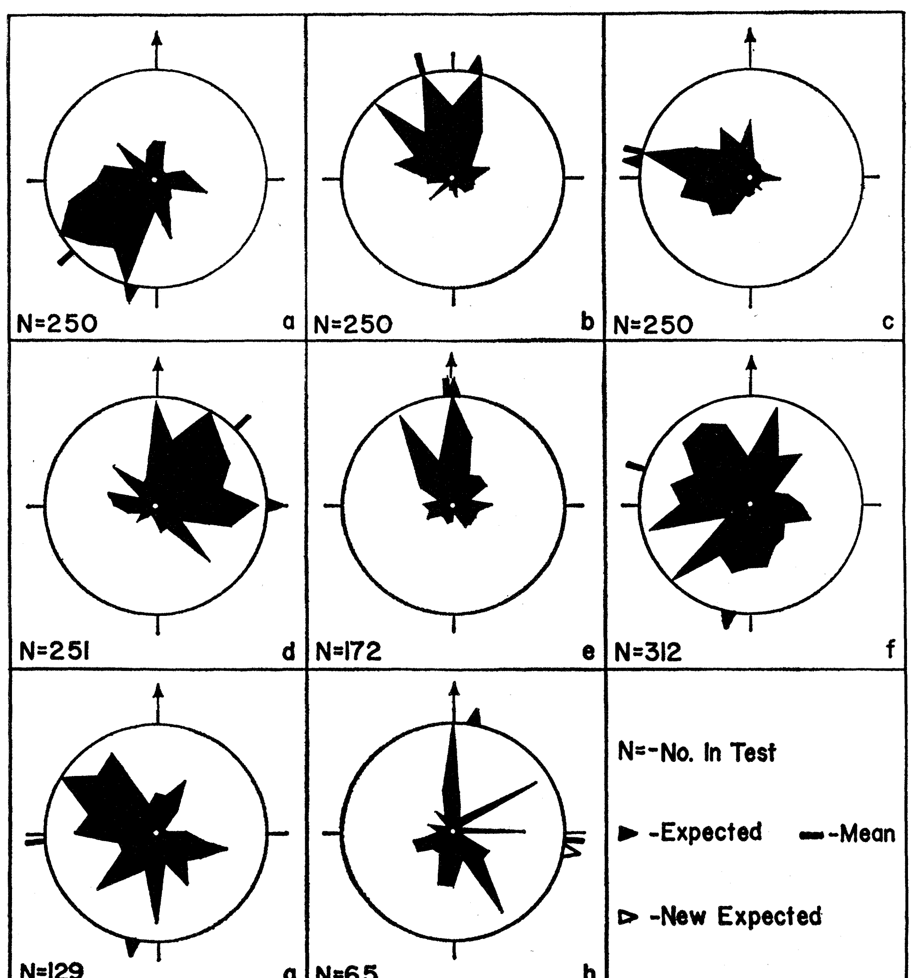

Fig. 1. Responses in the test arena of newts captured in breeding ponds. Animals were from shores having water located southward (a), northward (b), westward (c), eastward (d). Newts were tested in moonlight (e), under cloudy skies (f), after 7 days in constant darkness (g), and after 7 days in darkness followed by 7 days in a 12-hour: 12 hour light-dark regime initiated 6 hours after sunrise (h). The largest number of newts caught in a single trap is represented by the radius; the number in each of the other 23 traps is a radial line of proportional length in the appropriate direction; connection of distal points on the 24 radii encompasses the shaded area. When the data in all diagrams were analyzed statistically with the Rayleigh test, a hypothesis of random distribution was rejected (*P*, .01) in all instances but (f) and (g). Arrows point northward.

Table 1. Recaptures of marked newts in a series of parallel drift fences after 229-m displacement from the breeding ponds. Individuals trapped at the first fence were considered on course; those trapped only at a subsequent fence were termed off course.

Condition of displacement	Number of newts moved		Newts recaptured					
			On course			Off course		
			Number		Percentage	Number		Percentage
	♂	♀	♂	♀		♂	♀	
In black bag	142	206	23	41	18.4	3	8	3.2
Under cloud	112	94	32	28	29.1	8	14	10.7
In sunshine, normal	138	123	28	18	17.6	0	0	0.0
In sunshine, blinded	43	87	3	13	12.3	0	0	0.0
Totals								
	435	510	86	100	19.7	11	22	3.5

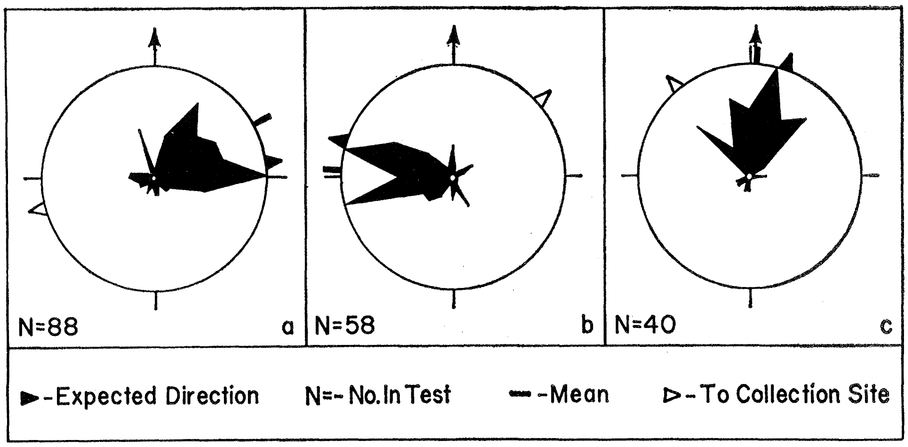

Fig. 2. Scores by newts transported long distances from the collection site to the test arena; they were captured in a breeding pond 27.68 km westward (a), on land as they approached a pond 6 km northeastward (b), or in a drift fence at a site 27.6 km northwestward (c). When all data were analyzed with the Rayleigh test, a hypothesis of randomness was rejected (*P*, 0.1). Arrows point northward.

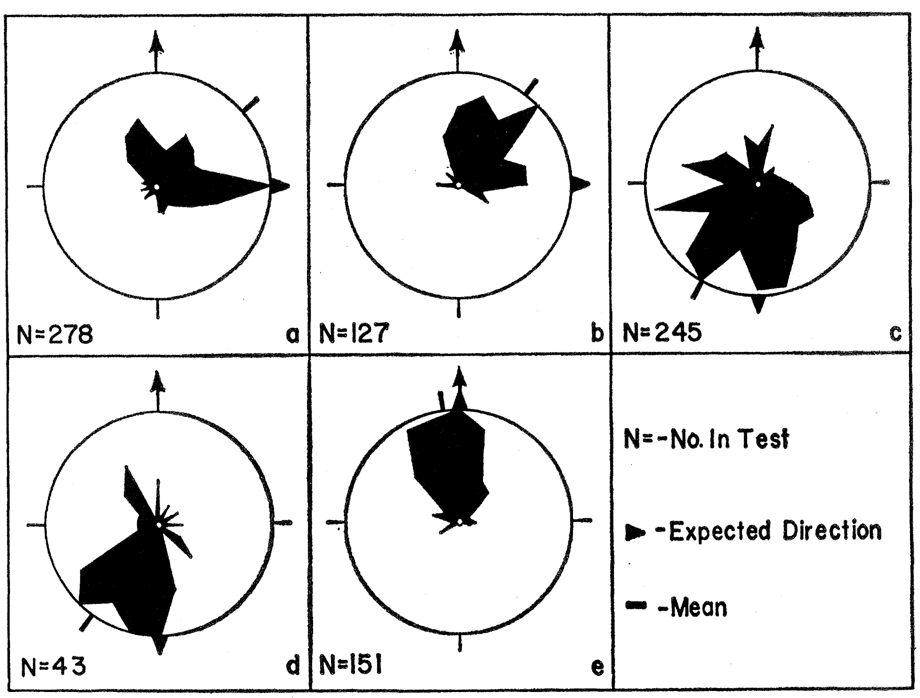

Fig. 3. Response of newts displaced 183 m on a compass course in sunshine before testing: westward displacement of normal (a) and blinded newts (b); northward displacement of normal (c) and blinded animals (d); blinded newts displaced southward (e). Random distribution was rejected (Rayleigh test) in all tests (*P*, .01). *Expected direction*: direction opposite the displacement. Arrows point northward.

and treated similarly, except that they were released at night in five tests in moonlight. When all the diagrams of these results are rotated so that the directions toward water coincide (Fig. 1e), the directional choices are toward water relative to the home shore, and the mean angle of the scores is within 2° of the expected direction.

Several groups of *T. granulosa* from the north shores of these ponds were handled in the manner described, but were released under cloudy skies lacking celestial cues. These 312 newts tested moved in random directions (Fig. 1f); they responded slowly, often remaining stationary for more than 1 hour. Animals released during showers of hail or snow, however, left the center of the pen faster in an apparent search for cover.

Animals must know local time in order to use the sun as a compass, and prolonged darkness should affect this sense of time. A group of 129 newts, captured along a north shore, were placed in an environmental chamber in total darkness at 20° to 21°C for 7 days before being taken to the test pen in black plastic bags and released in sunshine; their directional choices were random rather than toward water at the home shore (Fig. 1g). More newts (65) were kept similarly in darkness for 7 days before being exposed for 1 week to a light-dark regime equivalent to outdoors but initiated 6 hours after sunrise each day. At the home shore these newts would have had to move northward to find water, but, if their time sense had been altered by 6 hours, they would have moved eastward. The directional choices in these tests were scattered, but many went either northward or eastward (Fig. 1h). Although there was marked difference in the responses in comparison with those of newts tested after 7 days in darkness, the expected shift of directional choices was incomplete.

Taricha granulosa were captured in a small pond located 27.68 km west by air of the test arena, brought there immediately in black bags, and released in sunshine; they were caught along a straight shore having water to the east. Their directional choices (Fig. 2a) were eastward, with a mean angle of scores within 18° of this direction, and opposite the direction of the nearest ponds. The results were similar to those with animals that were captured near the test site, where familiar odors were likely (Fig. 2).

Although the preceding evidence establishes that newts can use celestial cues to associate land-water positions, it does not show that migrating animals use the mechanism. A large migration of *T. granulosa* approaching a breeding pond was fortuitously encountered, and their directional response was tested in the arena. A group of 58 females was captured by hand, within 9 m of the water, on a straight segment of shore; in black bags they were taken to the test arena to be released the following day. Most of their directional choices corresponded to the direction traveled before capture; they were not toward the pond (Fig. 2b). Forty more newts were captured by drift fences and traps as they approached a pond 27.60 km by air from the test site; their directional choices in the test arena corresponded to the course they had been traveling when trapped (Fig. 2c).

The following experiments tested the awareness of *T. granulosa* to displacements imposed upon them. Altogether 278 newts were captured from various shores, placed in light-tight containers, and taken to the arena. Before testing, the animals were placed in a clear plastic container, walked on a straight course (east to west) for 183 m, returned to the light-tight containers, and taken to the center of the arena for release. Most of them moved in a direction opposite the displacement (Fig. 3a). Animals from a shore having water in a direction opposite the direction of displacement scored with greater accuracy. Newts (127) from a west shore were treated similarly except that both eyes were excised and they were held for 24 hours before displacement in sunshine; all were held and transported in light-tight plastic bags. Their directions were generally eastward, in a direction opposite the displacement (Fig. 3b). The directional choices of these newts were away from the ponds, and their performance compared favorably with the precision of normal animals in the expected direction. This finding reduces the probability that olfactory cues were used, and suggests that blind newts can ascertain the sun's position (Fig. 3).

Normal (Fig. 3c) and blinded animals (Fig. 3d) were used to repeat the last two series of tests; they were displaced northward for 183 m in bright sunshine. The scoring patterns in both series were generally in the expected direction—opposite the displacement. A final group of 151 newts, from a south shore, were blinded and displaced 183 m southward before testing; the results show a precise northward pattern (Fig. 3e). A blinded newt usually held its head high and positioned it in different directions as it moved; although these animals moved back and forth on a chosen course, they ultimately reached the wall in the expected direction.

The movements of *T. granulosa* in their habitat were compared with movements in the test arena by translocating them from the breeding pond and releasing them behind a system of drift fences. A series of three plastic drift fences (55 m long, 61 cm high), with drop-traps, was arranged with one fence 23 m from the ponds and with the others parallel and at 91-m intervals; each fence was centered on a line extending westward from the ponds. The 945 newts were individually marked, translocated 228 m from the ponds, over the center of each fence, and released; the spatial relations were optimal for use of olfactory cues. Table 1 shows the recaptures of normal animals moved in sunshine, in light-tight containers, and under cloudy skies, as well as the recaptures of blinded newts (eyes excised) translocated in sunshine. The positions of recaptured animals were noted, and each newt was released on the opposite (pondward) side of the fence. During these experiments the weather became dry and warm, interrupting natural breeding migrations. The percentages of recaptures were not significantly different among the four groups, but the numbers of newts recaptured off course (those that missed the first fence) correlate with the nature of the translocation. All normal or blinded newts moved in sunshine were captured on a direct line heading for the ponds. Although the distance to the first fence was only 23 m, newts transported in black bags and under cloudy skies were often captured initially at the second or third fence. Two newts transported and released under cloud cover were recaptured in a drift fence 0.4 km eastward and at right angles to the system of fences. The *T. granulosa* denied celestial cues during displacement may have used random movements in attempting to locate familiar areas (Table 1).

The responses of *T. granulosa* thus indicate that a course is determined relative to celestial cues. Awareness of newts to translocation in sunshine suggests that a sun compass may function in local movements and in migrations; their directional choices were affected under cloudy skies, after exposure to darkness for long periods, and after subjection to altered light regimes, but not by excision of both eyes. Observations did not indicate that blinded newts relied on olfactory or other cues, but did suggest awareness of the sun's position. *Taricha granulosa* appear to obtain information with vitiated visual sensory equipment and do not abandon the sense for another. We made no attempt to determine the site of reception—such as exposed nerves in the socket, or skin receptors. Twitty (*4, 7*) witnessed homing by blinded *T. rivularis*, but he did not test a hypothesis of light reception without eyes (*12*).

Our newts relied on a sun-compass mechanism in the absence of other cues, but presumably the same animals use all available cues for orientation in their natural habitat. The sun is a dominant feature in the environment, and many amphibians can use it for direction finding (*1–3*). We postulate that a sun compass is a basic mechanism in orientation of amphibians.

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12. Preliminary laboratory investigations provide some insight into the nature of light reception in blind newts. Using techniques and apparatus described (*8*), we trained 24 newts to move in a particular direction under an artificial "sun." Equal numbers of the trained newts were subjected to surgery to produce experimental groups that were blind, blind with severed olfactory tracts, and blind with destroyed optic tecta. On testing, directional training relative to the light cue persisted in the blind, blind anosmic, and sighted anosmic animals, but not in the blind group lacking optic tecta. Newts with eyes excised were alert, demonstrated responsiveness to light cues by head motions and attitudes, and exhibited deliberate directional choices. Those lacking optic tecta showed no evidence of visual stimulation.
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