HERPETOLOGICA

VOL. 23 June 30, 1967 NO. 2

MOVEMENTS AND ORIENTATION OF THE TAILED FROG, *ASCAPHUS TRUEI*[1]

HOBART F. LANDRETH AND DENZEL E. FERGUSON

Certain anuran amphibians use celestial cues in orientation. Ferguson (1963) found that the southern cricket frog, *Acris gryllus*, employs a sun compass. The same species uses the mechanism to maintain a compass course (Y-axis) that bisects the home shore at right angles (Ferguson, Landreth, and Turnipseed, 1965). The toad, *Bufo fowleri*, (Ferguson and Landreth, 1966) and the upland chorus frog, *Pseudacris triseriata*, (Landreth and Ferguson, 1966) exhibit Y-axis orientation at the breeding pond. Sun orientation depends on the animal's ability to derive a directional course from the azimuthal curve of a celestial reference and local time. Ferguson, Landreth, and McKeown (1967) have shown that northern cricket frogs, *Acris crepitans*, use a sun compass and possess a sense of time apparently cued by the light-dark regime.

The life history of the tailed frog, *Ascaphus truei*, was studied by Gaige (1920), Noble (1927), and Noble and Putnam (1931). A morphological and ecological study of the species was conducted by Metter (1964). Although this unique frog has been the focus of several investigations, its movements and orientational mechanism are unknown.

The purposes of a study of *Ascaphus truei* were (1) to determine the extent of movements; (2) to determine the mechanism of orientation; and (3) to compare the orientational mechanism with that of other anurans.

Ascaphus truei inhabits cold, swift, mountain streams and has a life history and ecology that are unique among American anurans. The species is voiceless and lacks a tympanum. All amphibians known to depend on celestial cues are pond breeders that usually form large breeding aggregations and voice characteristic calls. The adaptive refinements shown in the orientational mechanisms of these species suggest a basic mechanism rather than a recently derived characteristic. The primitive status of *A. truei* with its specialized life history and peculiar habitat provides an opportunity to test the validity of this assumption.

[1]This research was supported by grant GB 3991 from the National Science Foundation.

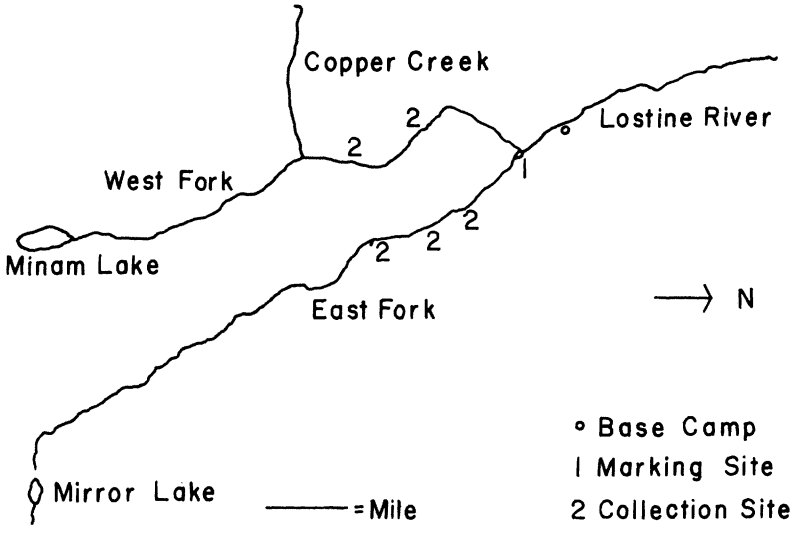

FIG. 1.—Study area on the Lostine River, Wallowa-Whitman National Forest, Oregon.

METHODS

An 11-week field study was conducted in the Wallowa-Whitman National Forest and Eagle Cap Wilderness Area of eastern Oregon. A base camp was set up on the Lostine River, 17.5 miles south of Lostine, Oregon (Fig. 1). The river flows north and is formed by the junction of two smaller streams, the East and West Fork, about 0.75 mile south of the base camp. All specimens tested or marked were collected from the Lostine River, its forks, or tributaries of the forks.

The forks of the river are each about 7 miles long and originate in different lake basins separated by a high mountain ridge. Each stream flows through an open glaciated valley. About 2.5 miles above their junction, the streams cascade swiftly through narrow canyons containing a dense coniferous cover (e.g., *Abies, Picea, Pinus*). Although specimens were collected from the entire length of each fork, most frogs were found in the 2-mile segments above the confluence.

The movements of toe-clipped *A. truei* were determined in home streams. This study involved 17 collections made between June 15 and August 25 from a small stream (540′ long, 3.5′ average width, 5–32″ deep, elevation 5675′). During the spring this stream is an auxiliary channel of the East Fork and carries excess water from snow runoff. The stream originates as an overflow from a waterfall on the East Fork and flows northeast (9% grade) and empties into the Lostine River 40 yards below the junction of the two

main river forks. A spring joins the study stream 100 yards downstream from its origin. The upper 130 yards of the study stream was marked off into 10-yard reference segments. The tree canopy over the stream was moderately dense and the banks supported a heavy growth of shrubs. All frogs were collected by hand during the day, usually from under rocks in the stream or from crevices along the banks, marked, and released in the same stream. Movements were determined by recaptures of these marked frogs.

For field tests of orientation, frogs were captured by hand during the day from under rocks at various locations on the two major forks of the Lostine River. Most collection sites were rocky deltas where smaller streams emptied into larger channels or potholes in auxiliary channels formed by high water. Frogs were transported to the test sites in light-tight, black plastic bags sewed from two layers of #55 Griffolyn. In certain experiments frogs were placed in heavy, clear plastic bags, moved a specific distance on a compass course, placed in the light-tight plastic bags, and taken to the test sites. One or two inches of water were placed in each black plastic bag containing frogs, and the bags were carried to camp in a heavy canvas backpack. At camp, bags of frogs were held in a portable ice chest at 10 C to 15 C until tested.

Some tests were conducted in an aquatic test pen on a gravel bar beside the Lostine River (elevation 5500′) near camp. This pen was a portable wading pool (8′ diameter, 20″ high), placed on leveled ground, and filled with 10 inches of water. Frogs were placed in a floating release device anchored at the center of the pool by a cord tied to a small piece of iron. This release mechanism sank slowly, leaving the frogs free to make directional choices and swim or crawl to the side of the pool. The release container was a clear plastic ice-cream carton (6.5″ diameter, 4.75″ deep) weighted with 0.5 inch of plaster of Paris at the bottom to keep it upright. A false bottom of screen held the frogs above the plaster and holes near the bottom of the container admitted water at a rate that sank the device in 2.5 minutes. Once the release device was afloat, the two observers moved away from the pool in opposite directions to respective points where each could see half of the pool. Several preliminary tests established that directional choices of frogs were unaffected by the position of the observers. A directional choice was recorded for each frog at the point where it touched the wall of the pool.

A similar wading pool was used for terrestrial tests. This pen was positioned on a level platform in an open meadow (0.5 mile east of camp). Frogs were released in the center of this pen from a 0.25-inch mesh hardware cloth cage (9″ diameter, 4″ high). The animals were placed in the cage, the observers moved back in position to score the test, and after 1.5 minutes the frogs were

released. The bottomless release device was lifted with a long pole to free the frogs.

Climatological data were recorded each day at the base camp. Summaries of these data are: (1) Total precipitation (funnel rain and snow gauge, Science Associates Co., Model 508) for the period was 1.48 inches with 1.03 inches during the last 11 days of June. (2) The relative humidity (recording hygrothermograph, Belfort Instrument Co., Model 2065) fluctuated daily between 90% to 100% (2 a.m. to 8 a.m.) and 10% to 40% (2 p.m. to 6 p.m.). There was a striking inverse relationship between air temperature and relative humidity. (3) The air temperature (maximum-minimum thermometer, Taylor Co.) reached a high of 86 F (August 3) and a low of 28 F (June 24, 25, and August 21) with a mean of 55.2 F for the 11 weeks. (4) The mean water temperature of the Lostine River at a one-foot depth (maximum-minimum thermometer, Taylor Co.) was 46.8 F with a high of 58 F and a low of 34 F. Water temperatures (quick reading thermometer, Schultheis Corp., Model 96723) where *A. truei* were collected ranged from 42.8 F to 64.8 F with most specimens taken from water between 50.0 F and 53.6 F. (5) Barometric pressures and elevations were recorded with an altitude barometer (Taylor Co., Model 2075 F).

A cage was constructed on a straight segment of relatively open shore to determine the ability of tailed frogs to orient to an unfamiliar shore. This pen (6′ long, 4.5′ wide, 2′ high) was constructed of 0.25-inch hardware cloth nailed to posts (2″ × 4″) driven into the ground. A strip of hardware cloth along the inside top edge of the pen formed a barrier to escaping frogs.

Experiments and Results

Marking and Moving Experiments

From June 15 to August 19, 1966 marking and moving experiments were conducted in which *A. truei* were captured, marked, and either replaced at the collection site or moved to another site in the same stream. The frogs were moved in clear plastic bags or in light-tight, black plastic bags. A total of 248 frogs was moved and 37.5% (93) were recaptured. Of the recaptures, 63 were recaptured once, 23 twice, 5 three times, and 2 four times. Table 1 shows the number of male and female frogs moved, recaptured, and percent recaptured relative to the manner and direction of displacement before release. The highest percentage of recaptures (42.6%) involved frogs moved in clear plastic bags. The next highest percentage of recapture (33.3%) was of frogs replaced in the stream at the collection site; the lowest recapture percentage (30.5%) was of frogs moved in black plastic bags. Little difference was observed between frogs displaced downstream in view

TABLE 1.—Recapture of marked *Ascaphus truei* in relation to method and nature of displacement.

	Method of displacement								
	Black plastic bag			Clear plastic bag			Total		
	Female	Male	Total	Female	Male	Total	Female	Male	Total
Upstream									
Number	13	20	33	33	30	63	46	50	96
Recapture	3	9	12	20	20	40	23	29	52
% Recapture	23.1	45.0	36.4	60.6	66.7	63.5	50.0	58.0	54.2
Downstream									
Number	14	12	26	35	31	66	49	43	92
Recapture	4	2	6	7	8	15	11	10	21
% Recapture	28.6	16.7	23.1	20.0	25.8	22.7	22.4	23.2	22.8
Total displaced									
Number	27	32	59	68	61	129	95	93	188
Recapture	7	11	18	27	28	55	34	39	73
% Recapture	25.9	34.4	30.5	39.7	45.9	42.6	35.8	41.9	38.8
No displacement									
Number	—	—	—	—	—	—	25	35	60
Recapture	—	—	—	—	—	—	8	12	20
% Recapture	—	—	—	—	—	—	32.0	34.3	33.3

of the surroundings and those displaced in light-tight bags, but a higher percentage of frogs moved upstream in clear plastic bags was recaptured. Only two individuals (3.4%) displaced in black bags returned to the collection site; both were moved upstream. Of the specimens moved in clear plastic bags, nine (14.3%) returned to the collection site after an upstream displacement and six (9.1%) returned after being removed downstream. The frogs moved in black bags had a greater probability of being recaptured since they were displaced during the first 2 weeks of the study. The stream above the spring stopped flowing by August 12, but water remained in small potholes.

A size difference was noted between *A. truei* collected in the mainstream of the Lostine River and those found in the small stream where the marking and moving experiments were conducted. The frogs of the small stream were smaller, and all frogs collected appeared to be smaller than those found by Metter (1964). Snout-vent lengths of *A. truei* from the river were as follows: 75 males (Range = 22.1 mm—36.2 mm, $\bar{X} = 30.3$ mm, S.E. = ± 0.04 mm); 78 females (Range = 22.3 mm—45.1 mm, $\bar{X} = 30.9$ mm, S.E. = ± 0.05 mm). Sizes of frogs from the tributary were: 84 males (Range = 22.0 mm—34.2 mm, $\bar{X} = 26.3$ mm, S.E. = ± 0.04 mm); 79 females (Range = 22.2 mm—36.2 mm, $\bar{X} = 26.3$ mm, S.E. = ± 0.04 mm).

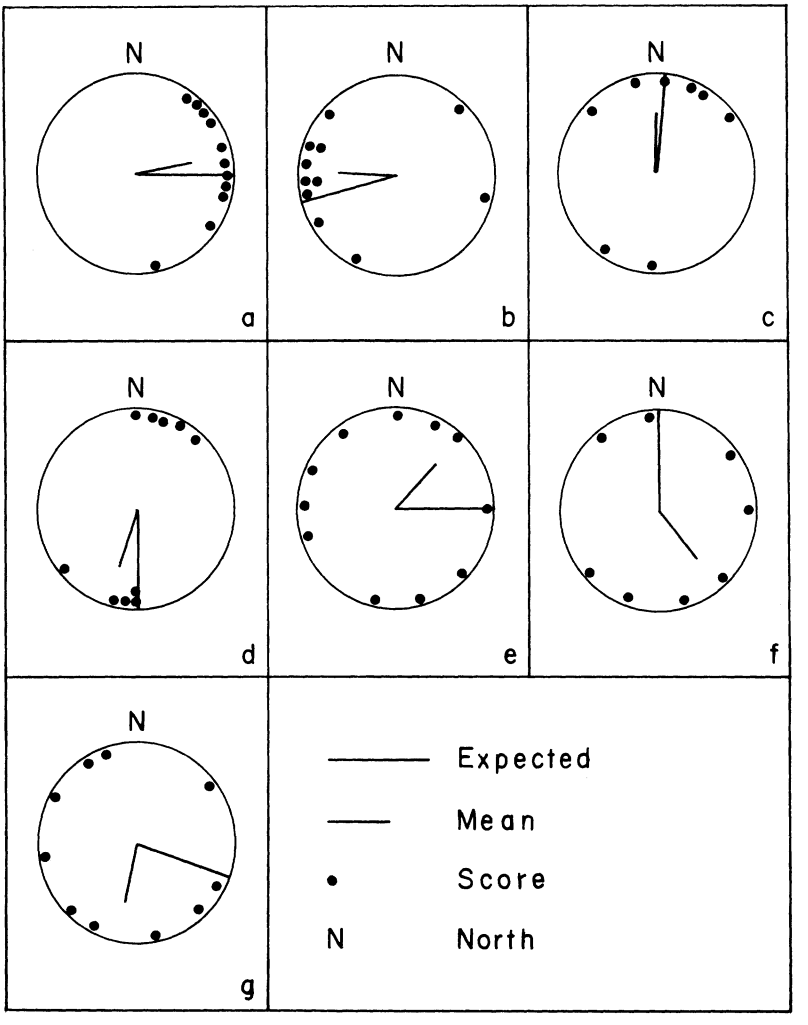

FIG. 2.—Daytime directional responses of tailed frogs in an aquatic test pen when celestial cues were visible (a, b, c, & d) and without celestial cues (e, f, & g). Frogs brought to the test arena in lightproof bags from a) east shore; b) west shore; c) north shore; d) south shore; e) tested under complete cloud cover; f) after sunset; g) before sunrise.

TESTS OF DIRECTIONAL RESPONSES

The use of celestial cues for orientation to a shoreline by tailed frogs was examined in four aquatic tests between August 14–23, 1966. Four groups of frogs were collected from four shores facing in different directions. The specimens were placed in black plastic bags containing water, moved 2.0 to 2.5 miles to camp, held over-

night, and tested the following morning. The directional choices of 11 frogs taken from an east shore are shown in Fig. 2-a. All 11 scores are in a direction that would have taken the individuals to shore. The direction perpendicular to shore (read facing land and with east as 0°) was 0° and the mean angle was 11° with an angular deviation of 36.2°. All angular measurements are made with 0° located at the east and the mean angle computed vectorially (Batschelet, 1965). Of the 11 frogs taken from a west shore (perpendicular 195°) and tested in the aquatic arena, nine scores were toward land and two frogs scored toward water (Fig. 2-b). The mean angle was 176° with an angular deviation of 53.1°. The scores of frogs from a north shore (Fig. 2-c) show six toward land and two toward water. The perpendicular to the shore was 85°, the mean angle was 87°, and the angular deviation was 61.7°. The frogs from the south shore (perpendicular 270°) scored in a bimodal pattern on their release in the aquatic arena with six scores toward land and five in the opposite direction (Fig. 2-d). These scores were grouped at 30° intervals and processed vectorially. The mean angle was 252° and the angular deviation was 17.7°.

The scores of these four aquatic tests were pooled so that the home direction was toward the east (perpendicular 0°). Of the 41 scores, 32 were in a direction toward land and nine were in the opposite direction. The mean angle was 359° with an angular deviation of 59.5°. When these data were analyzed statistically for randomness with the Rayleigh test, the hypothesis of random distribution is rejected at the 1% significance level [$Z = 8.5511 > Zp$ ($p = 1\%$) $= 4.6052$].

A series of three control tests was conducted when celestial cues were not available. On August 22, 1966 at 4:50 p.m. an aquatic test was conducted using the above procedures under complete cloud cover with frogs from an east shore (perpendicular 0°). The 11 scores appear randomly distributed (Fig. 2-e), *i.e.*, six individuals went toward land and five scored away from land with a mean angle of 49° and an angular deviation of 77.7°. A test was conducted in the aquatic arena on August 13, 1966 at 8:30 p.m. with the sun below the canyon wall, a uniformly lighted sky, but no moon or stars. The eight frogs scored at random with three scores toward land and five away (Fig. 2-f). The shore perpendicular was 90° and the mean angle was 310° with an angular deviation of 76.4°. A third test was conducted before sunrise on August 10, 1966 at 5:55 a.m. The 10 frogs were taken from an east shore (perpendicular 12°), placed in a clear plastic bag, walked 95 yards on a compass course of 70° west of north, placed in a black plastic bag, and tested. Under an evenly illuminated sky and no moon or stars, the frogs scored at random with a mean angle of 259° and an angular deviation of 32.4° (Fig. 2-g).

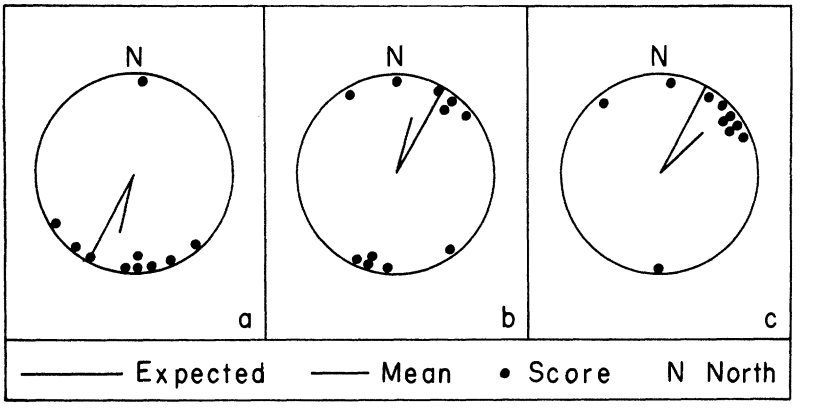

FIG. 3.—Directional responses of *A. truei* that were caged on an unfamiliar shore for 5 days. a) Terrestrial test; b) Aquatic test; c) Aquatic test of frogs removed from the cage and displaced in view of their surroundings.

The scores of these last three tests were pooled so that the two perpendiculars and the homeward direction coincided at east. The 20 scores appear randomly distributed and have a mean angle of 334° with an angular deviation of 76.9°. When the Rayleigh test is applied to test randomness one may accept the hypothesis of a random distribution at the 5% significance level [$Z = .2895 < Zp\ (p = 5\%) = 2.9957$].

Three tests were conducted that demonstrate the ability of *A. truei* to relate the position of a new shoreline to celestial cues. Frogs were captured from various shores and placed in a large wire pen for 5 days prior to testing. The pen had a gravel bottom and several large rocks were placed along the straight shore (perpendicular 62°) so that the activities of the animals would be directed between land and open water. A group of 10 frogs was removed from the pen, brought to the test site in a black plastic bag and tested on July 27, 1966 at 2:10 p.m. In a terrestrial test, nine frogs scored in a direction that would have taken them to water and one scored in the opposite direction (Fig. 3-a). The mean angle was 256° with an angular deviation of 45.8°. On August 4, 1966 at 10:45 a.m. an aquatic test was conducted with 11 frogs from the same pen treated as in the preceding test (Fig. 3-b). Six scores were toward land and five scores were toward water. This was a symmetrical, bimodal distribution with a mean angle (75°) and an angular deviation (26.6°) that were computed after the scores had been grouped at 30° intervals. A third group of frogs was taken from the pen, placed in a dry, clear plastic bag, and walked 90 yards on a compass course 15° east of north. The animals were then placed in a black plastic bag and taken to the aquatic

test site. When released, 9 of 10 frogs swam to the segment of the test arena that corresponded to land in the training pen (Fig. 3-c). The mean angle was 44° with an angular deviation of 43.6°.

The scores of the last three tests were pooled so that the expected homeward directions coincided at east (0°). The mean angle of these pooled scores was 355° with an angular deviation of 59.5°. We reject the hypothesis of a random distribution on the basis of the Rayleigh test at the 1% significance level [$Z = 6.5487 > Zp$ $(p = 1\%) = 4.6052$].

Various aspects of the orientational mechanism, especially the relationship between the positions of land and water, were illustrated by several tests. A group of eight *A. truei* (5 males and 3 females) was found in a small isolated pothole (8″ long, 7″ wide, and 2″ deep) 40 yards from the main river. These frogs were placed in a dry, clear plastic bag, carried 97 yards on a compass course 30° west of north, placed in a black plastic bag, and taken to the terrestrial test site. The results of this test (Fig. 4-a) show that six of eight scores were in a direction opposite the displacement direction. The mean angle was 307° (home, 300°) with an angular deviation of 51.9°.

Independence of response was tested on August 24, 1966, when two groups of frogs from opposing shorelines were released simultaneously in the terrestrial arena. The scores of five frogs from an east shore (perpendicular 0°) and five frogs, marked with a thread around the groin, from a west shore (perpendicular 195°) are shown in Fig. 4-b. The scores of each group were toward water relative to the respective shores. The mean angle of the group from the east shore was 171° (water, 180°) with an angular deviation of 45.8° and the mean angle of the group from the west shore was 20° (water, 15°) with an angular deviation of 38.9°. These scores were pooled so that the direction to water for each shore coincided at east (0°). The mean angle of these pooled data was 7° with an angular deviation of 39.7°. The hypothesis of a random distribution is rejected at the 1% significance level when the Rayleigh test is applied [$Z = 5.2473 > Zp$ $(p = 1\%) = 4.2504$].

Frogs were subjected to displacements under various conditions to determine their response. A group of 10 frogs from an east shore was placed in a black plastic bag and moved 2.5 miles to camp. There the animals were placed in a clear plastic bag containing 2 inches of water and walked due west for 100 yards. They were then placed in a black plastic bag, taken immediately to the aquatic test arena, and tested. Fig. 4-c shows the results of the release with eight scores in the general direction walked, one opposite this direction, and one to the north. The mean angle of these scores was 180° with an angular deviation of 51.3°. The hypothesis of random distribution is rejected at the 5% significance level when

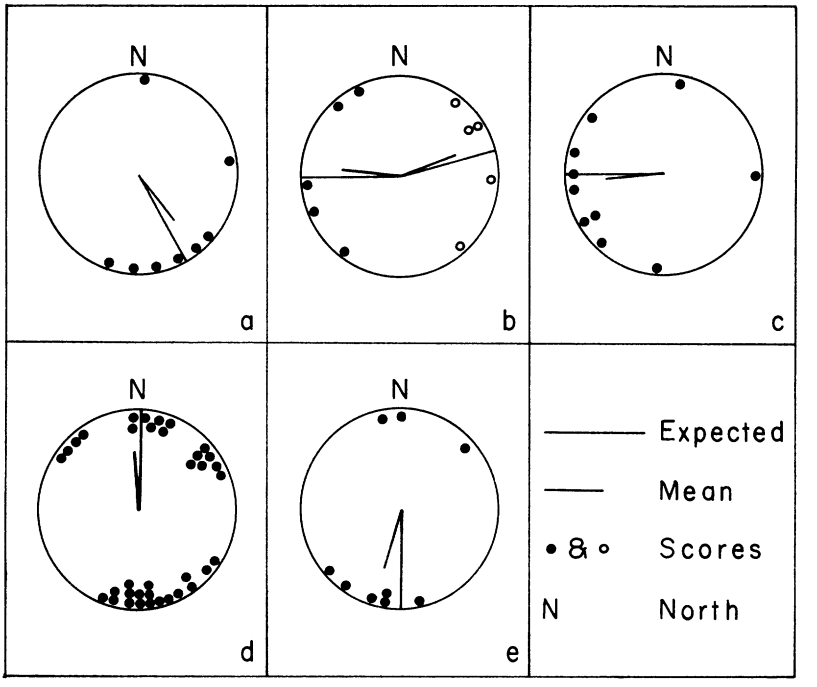

FIG. 4.—Directional responses of *A. truei* in the terrestrial arena. a) Taken from a small pothole, displaced in a dry, clear plastic bag; b) Simultaneous test of frogs from two opposing shores. Aquatic tests of c) frogs moved 2.5 miles in darkness, then displaced in view of the surroundings in water; d) four groups of frogs displaced in a dry, clear plastic bag near the collection site; e) frogs floated downstream in a cage.

the Rayleigh test is applied [$Z = 3.6073 > Zp\ (p = 5\%) = 2.9187$].

A series of four tests was conducted with frogs from an east shore (perpendicular 0°). These animals were placed in black plastic bags, moved 220 yards, placed in dry, clear plastic bags, walked 98 yards on a course 70° west of north, and placed in black plastic bags to be taken to the aquatic test site. The results of these tests (Fig. 4-d) show a marked bimodal, symmetrical pattern with 18 scores in the north half of the arena and 18 scores in the south half. When these scores are grouped at 30° intervals the mean angle is 91° with an angular deviation of 27.8°. This corresponds more closely with the streamflow (90°) than either the shore perpendicular (0°) or the displacement direction (150°).

A group of nine frogs was collected on the same shore as the last four groups and placed in a cage (11″ long, 8″ wide, 4″ high) made of 0.25-inch hardware cloth, and mounted on a piece of rigid polystyrene foam (11″ long, 8″ wide, 1.5″ high). This floating cage was placed in the mainstream of the East Fork at the collection

site and floated downstream. A heavy cord controlled the craft as it was allowed to float 88 yards on a compass course due north at a moderate rate of speed. The frogs were removed from the cage, placed in a black plastic bag, and taken to the aquatic test site. The results of the release of these frogs are shown in Fig. 4-e. Of the nine scores, six are opposite the floated direction and three are in the direction of the aquatic displacement. These scores were grouped at 30° intervals since it was a bimodal distribution and the mean angle (71°) and angular deviation (19.9°) computed.

General Observations

Frogs released in the aquatic arena usually stayed in the release device until it sank and then chose a direction. They either swam to the side of the pool or dived to the bottom and crawled to the side. Frogs usually traveled in a straight line after choosing a direction but moved laterally when they reached the wall of the pool. Splashing the water or passing a shadow over the frogs did not divert them from a chosen course, but caused them to stop momentarily. A sensitivity to water temperature near 20 C caused frogs to struggle to the surface, expose their snouts for several seconds, and then retreat to the bottom. Some individuals dived to the bottom and remained on their backs after several of these trips to the surface. These frogs recovered from the torpid state in cool water.

In terrestrial tests the animals oriented on their directional course while in the release device. They crawled or, rarely, hopped to the wall. Some tried to climb the plastic wall, showing considerable agility, and would have reached the top had they not been removed.

Frogs were found on land at night, but were also seen on land during the day. On August 18, 1966 at 3:30 p.m. two females were seen under a rock 20 ft. from a small stream and a male was captured moving toward the same stream 30 ft. from water. Several frogs were taken from small, isolated potholes that had not contained frogs earlier. An escaped frog was found dead three weeks later, 150 yards from the point of escape. It could have reached water by moving 40 yards downhill.

Discussion

Our experiments indicate that visual cues function in part in the orientational mechanism of the tailed frog. More marked animals returned to the "home" segment of the stream over longer distances when moved in view of the surroundings than did those moved in light-tight containers. No frogs returned when displaced downstream in darkness. This refutes possible use of olfactory or geotactic cues since these mechanisms should function best after a downstream displacement. However, since we carried the ani-

mals to the release point, they were denied rheotactic cues (*i.e.*, streamflow) which are important in the natural habitat. Presumably, auditory cues are of no value to a voiceless species possessing only rudimentary auditory structures.

Frogs moved 3 miles oriented relative to land and water in both terrestrial and static aquatic tests only when the sun was visible. This eliminated the use of familiar landmarks for orientation and demonstrated an ability to employ celestial cues. Holding frogs overnight in light-tight containers did not appear to affect their ability to orient on a compass course perpendicular to the home shore (Y-axis). Thus, *Ascaphus truei* exhibits the Y-axis type orientational mechanism examined in several other species of anurans (Ferguson *et al.*, 1965; Ferguson and Landreth, 1966; Landreth and Ferguson, 1966).

In general, the directional choices of frogs released in the test arenas reflected an awareness to displacements in view of visual cues. Specimens moved from the home shore in view of their surroundings scored in the aquatic test arena in a direction that would be toward land at the home site. In terrestrial tests the scores were in a direction that was toward water at the home shore. The frogs responded differently, however, when moved from the home shore in black bags containing water and then placed in clear plastic bags and moved again. When the second movement was in water and the test conducted in the aquatic arena, the frogs scored on the displacement compass course. If the second displacement was in a dry plastic bag the scores of the frogs were in a direction corresponding to the course of the stream at the home shore. Frogs placed in a cage and floated downstream in view of their surroundings also chose directions correlated to the streamflow when released in the aquatic test arena.

Metter (1964) marked 75 adult *A. truei* in the Blue Mountains of Washington, but recovered only two marked animals in a year and a half. The recaptured frogs were within a short distance of where they were released. Metter thought that frogs moved upstream in the small creeks for protection during the summer since fewer frogs were seen then, but he was unable to prove this with marked animals. The *A. truei* he studied on the Palouse River in Idaho seemed to stay in the mainstream. In our study the frogs appeared to move downstream in the small creeks to the river. Breeding may be facilitated when frogs aggregate in locations along the mainstream of the river. The smaller creeks often become dry during the summer, after the snow runoff.

The plasticity of the orientational mechanism of *Ascaphus* is surely adaptive in their mountain stream habitat. Lateral excursions from the stream can be conducted under the direction of celestial cues. The flexibility of the mechanism is important be-

cause displacement, whether voluntary or not, of organisms living in swift streams could be disastrous if they oriented in water only on the Y-axis.

It is likely that this frog, as any other animal, uses all or any available cues for orientational purposes in its natural habitat. Our study indicates that *A. truei* possesses an orientational mechanism encompassing both rheotactic and celestial cues.

The presence of a Y-axis mechanism in *Ascaphus* suggests that it is a primitive anuran characteristic. The mechanism exhibits certain adaptive refinements, yet shows the basic features evident in other species. The fact that *Ascaphus truei* retains Y-axis orientation suggests that the mechanism may occur in all modern amphibians.

Literature Cited

Batschelet, Edward. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. AIBS Monogr., Washington, D. C.

Ferguson, D. E. 1963. Orientation in three species of anuran amphibians. Ergebn. Biol. 26:128–134.

Ferguson, D. E., H. F. Landreth, and M. R. Turnipseed. 1965. Astronomical orientation of the Southern cricket frog, *Acris gryllus*. Copeia, 1965:58–66.

Ferguson, D. E., and H. F. Landreth. 1966. Celestial orientation of Fowler's toad, *Bufo fowleri*. Behaviour, 26:105–123.

Ferguson, D. E., H. F. Landreth, and J. P. McKeown. 1967. Sun compass orientation of the Northern cricket frog, *Acris crepitans*. Animal Behaviour, 15:45–53.

Gaige, H. T. 1920. Observations upon the habits of *Ascaphus truei* Stejneger. Occ. Papers Univ. Mich. Mus. Zool., 84:1–9.

Landreth, H. F., and D. E. Ferguson. 1966. Evidence of sun-compass orientation in the chorus frog, *Pseudacris triseriata*. Herpetologica, 22: 106–112.

Metter, D. E. 1964. A morphological and ecological comparison of two populations of the tailed frog, *Ascaphus truei* Stejneger. Copeia, 1964: 181–195.

Noble, G. K. 1927. The value of life-history data in the study of the evolution of the Amphibia. Ann. N. Y. Acad. Sci., 30:31–128.

Noble, G. K., and P. G. Putnam. 1931. Observations on the life-history of *Ascaphus truei* Stejneger. Copeia, 1931:97–101.

Department of Zoology, Mississippi State University, State College, Mississippi, 39762.