

1974

Specializations of the feeding response of the bullfrog, *Rana catesbeiana*, for the capture of prey submerged in water.

Frederick Cardini
University of Massachusetts Amherst

Follow this and additional works at: <https://scholarworks.umass.edu/theses>

Cardini, Frederick, "Specializations of the feeding response of the bullfrog, *Rana catesbeiana*, for the capture of prey submerged in water." (1974). *Masters Theses 1911 - February 2014*. 1375.
<https://doi.org/10.7275/6870906>

This thesis is brought to you for free and open access by ScholarWorks@UMass Amherst. It has been accepted for inclusion in Masters Theses 1911 - February 2014 by an authorized administrator of ScholarWorks@UMass Amherst. For more information, please contact scholarworks@library.umass.edu.

UMASS/AMHERST



312066013802815

SPECIALIZATIONS OF THE FEEDING RESPONSE OF THE
BULLFROG, RANA CATESBEIANA, FOR THE CAPTURE
OF PREY SUBMERGED IN WATER

A Thesis Presented

By

Frederick Cardini

Submitted to the Graduate School of the
University of Massachusetts in partial
fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August

1974

Psychology

Table of Contents

Approval of committeeii

Acknowledgementsiii

Introduction1

Experiment I4

Experiment II16

Experiment III25

General Discussion39

Bibliography41

Figure Legends45

Appendix I52

Appendix II55

Tables58

Figures88

I acknowledge the service of the members of my thesis committee:

Dr. Bruce R. Levin and Dr. Alastair M. Stuart for their valuable suggestions and criticisms, and Dr. Alan C. Kamil for advice concerning statistics.

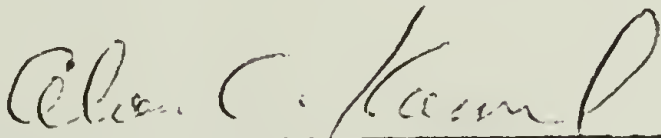
SPECIALIZATIONS OF THE FEEDING RESPONSE OF THE
BULLFROG, RANA CATESBEIANA, FOR THE CAPTURE
OF PREY SUBMERGED IN WATER

A Thesis Presented

by

Frederick Cardini

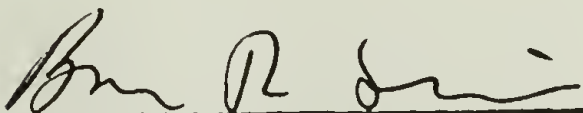
Approved as to style and content by:



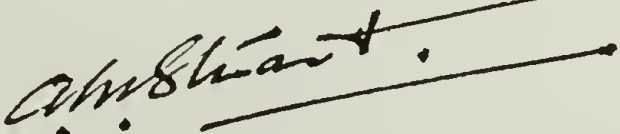
Alan C. Kamil (Chairman of Committee)



John W. Donahoe (Acting Head of Department)



Bruce R. Levin (Committee Member)



Alastair M. Stuart (Committee Member)

July, 1974

Introduction

The bullfrog, Rana catesbeiana Shaw, apparently takes more aquatic prey animals than the green frog, R. clamitans Latreille, the leopard frog, R. pipiens Schreber, and the wood frog, R. sylvatica Le Conte. Table 1 summarizes the results of stomach content analyses performed on these species of frog by various authors. Sample size in many of these studies numbered in the hundreds, and several studies involved the collection of frogs over many months. It is evident that the proportion of animals most likely submerged in water at the time of capture (e. g., fishes, tadpoles, Planorbid snails, Dytiscid beetles) is greater in the bullfrog's food intake than in that of the other frogs. Stomach content analyses involving small samples, or not readily tabulated, also indicate comparatively many aquatic animals in the diet of the bullfrog (Brakeley, 1885; Needham, 1905; Dyché, 1914; Perez, 1951; Cohen and Howard, 1958). Such findings encourage comparison of the feeding behavior of the bullfrog with that of other Rana species. Aquatic organisms are presumably less adherent than dry ones to the mucous tongue surface of a frog, because the mucus is water-soluble (personal observations). As far as is known, the bullfrog initiates the feeding response following sighting prey with the eyes in the air. Due to light refraction as light passes from water to air, an object submerged in water is not located where it appears to be located. Is the consummatory feeding response of the bullfrog specially adapted for capture of submerged prey animals?

Cardini (1973) found that the bullfrog feeding response involves a

tongue extension and retraction generally similar to that of the green frog and leopard frog. It is conceivable that the pattern of differential predation evident in Table 1 is due not to any uniqueness to the bullfrog's feeding motor pattern of characteristics promoting the capture of animals submerged in water. It is well known that the bullfrog is highly aquatic (Dickerson, 1906; Wright and Wright, 1949; Conant, 1958). The bullfrog may take relatively many aquatic prey simply because it relatively frequently encounters these. Nevertheless, the frequent encountering of potential prey submerged in water can selectively favor feeding response characteristics facilitating their capture.

The primary goal of Experiment I was the description and comparison of the motor patterns of the consummatory feeding response of the bullfrog, green frog, leopard frog, and wood frog. Specifically, the topographical comparisons sought response characteristics unique to the feeding strike of the bullfrog that seemed to be adaptations for the capture of prey animals submerged in water. Experiment II tested the capacity of the four frogs to capture prey animals submerged in water. Experiment III examined the response of the four frogs to prey that are, in effect, nonadherent.

General Procedures

Certain conditions were common to the treatment of all experimental frogs. All frogs were housed in standard tropical fish aquaria, with hardware cloth tops, and containing shallow water. Typically, three to six frogs shared a ten gallon tank. Ambient temperature ranged between 68 and 84 degrees, F., but was usually about 75 degrees during daytime working hours. During all experimental testing sessions, ambient temperatures were controlled between 73 and 77 degrees, F., with a thermostatically controlled, fan-forced electric room heater or a thermostatically controlled air-conditioner mounted in the window of the room. A wet bulb thermometer ranged between 60 and 68 degrees, F., during experimental sessions. The room was continuously humidified with a room humidifier. Room illumination was scheduled with electrical time switches; the light-dark cycle was 16 hours light, 8 dark.

Selection of animals for each experiment began with collection or purchase of two to five times the number required. After arrival in the laboratory, the frogs were housed for one to two weeks without being fed. Then each frog was placed alone once a day in a dry aquarium and offered live mealworms (Tenebrio molitor larvae). Only those frogs that on the second or third of these preliminary tests began feeding and ceased giving escape responses to the experimenter's movements were used in the experiment. Occasionally, a frog started in an experiment but had to be removed because it ceased feeding and began showing escape behavior during experimental sessions. Schneider (1954) reported the same phenomenon in European Rana.

Experiment I

Animals

Twelve bullfrogs, green frogs, leopard frogs, and wood frogs, making a total of 48 frogs, served. These were of various body lengths (Table 2). All bullfrogs and wood frogs were collected about Amherst, Massachusetts. Three green frogs and six leopard frogs were purchased (Lake Champlain Frogs Farms, Alburg, Vermont). The remaining green frogs and leopard frogs were collected about Amherst.

Apparatus

The feeding responses of frogs were filmed with a sixteen mm, movie camera (Beaulieu, Model R16). The frogs fed inside a standard tropical fish tank with outside dimensions 77.5 x 32.5 x 31.0 high. The camera, focused at four ft., was mounted on a tripod such that the plane of the film was four ft. from and parallel to a straight white line etched into the slate floor of the tank. The height of the axis of the camera lens was 10 to 15 cm. above the plane of the tank floor.

The large glass wall of the tank nearest the camera was removed to permit unobstructed filming. The other large glass wall was replaced with a sheet of plywood painted flat black, a back-drop for filming. The tank floor was covered, except in the region where the prey was positioned, with gray fiberglass window screen, for traction. Thus, a frog had screen beneath its feet at the start of its feeding leap, and bare, flat slate under it at the consummation of the response. The white line marking the plane of focus was crossed with white hatch marks at intervals of 1.0 cm. in this region of bare slate, to

provide a rule for later distance measurements from film projections.

During filming two sources of illumination were used in addition to the four forty w. fluorescent lamps mounted on the ceiling of the room. One fifteen w. fluorescent lamp mounted in a standard desk reflector was located 31 cm. above the tank floor. One 150 w. incandescent lamp mounted in 27 cm. diameter aluminum photographic reflector was directed towards the region of the tank where the prey were positioned. This bulb was located approximately 31 cm. above the tank floor and 20 cm. in a horizontal direction from the plane of focus to the camera.

Films were viewed and analyzed with a sixteen mm. movie film editor (Craig Projecto-Editor, The Kalart Co., Plainville, Connecticut). The editor projection screen was modified (enlarged and moved farther from the film) to produce a larger image for more precise analysis.

Procedure

After the preliminary feeding tests, frogs were fed live mealworms or beetles (T. molitor) once daily in the apparatus until they began taking these prey within ten seconds following presentation. Then the frogs' feeding responses were filmed. Body weights were not recorded for all frogs in this experiment, but only individuals that visually appeared of the correct body bulk for their species were used in this experiment.

The filming procedure was as follows. A prey animal (mealworm or beetle) was placed on the white line on the tank floor. Then a frog was placed in the tank, on the white line, facing the prey, and at

such a distance from the prey that an approach response was necessary prior to the feeding strike. Therefore, the frog made its feeding strike from a distance from the prey that was the result of its own (approach) behavior. The camera was started as soon as the approach response occurred. Frogs were filmed at 64 frames per second. Two successful strikes per individual frog were filmed. Occasionally a frog struck and missed the prey and then struck again. No such responses were counted. Only initial successful strikes counted in the experiment. Some bullfrogs and leopard frogs consistently missed on the first strike; these animals were removed from the experiment, and none of their data are presented.

Half of the animals of each species of frog were presented live mealworms (2.0 to 2.5 cm. in body length) as prey, and the other half were presented live beetles. Individual frogs received the same prey type during the habituation and filming sessions. Table 2 shows that within prey types various frog body sizes were represented. The mealworms were crushed with forceps about midway along the body prior to positioning in the apparatus. This caused them to writhe vigorously but to remain generally where placed. Beetles had all the legs removed with the similar result of producing a prey stimulus that moved but did not go far. Thus, prey stimuli could be fairly precisely positioned before the camera, ensuring that the feeding behavior occurred on the plane of focus (white line).

The analysis of the films began with the noting of the fundamental similarities between the feeding strikes of the bullfrog, green frog, leopard frog, and wood frog. The feeding response of a frog consists

essentially of three discrete behaviors. The body advances toward the prey and then retreats. The mouth opens and closes. The tongue is extended from the mouth and retracted back into it. How all this is integrated can be seen in Figures 1 and 2. These figures were made from single frame projections of a movie film of a feeding leopard frog or bullfrog. The traced sequences begin at the point in the strike at which the frog has leaped forward and the frog's tongue has been fully extended onto the prey. The sequences end at mouth closure. The time course of this behavior varied from $5/64$ sec. to $27/64$ sec., but most time courses fell between $6/64$ sec. and $13/64$ sec.

Preliminary viewing of a number of such filmed behavioral sequences suggested that the bullfrog feeding response differs from that of the other frogs in three interesting ways: (1) in the later parts of the strike the bullfrog's jaws appear to pass nearer the prey's original location; (2) in the later parts of the strike the bullfrog's head is more bowed; (3) early in the strike the bullfrog's lower jaw apex usually rests on the ground so that almost the entire dorsal aspect of the tongue may come into play as a prey catching surface, whereas in the other frogs only a posterior portion of the dorsal aspect of the tongue is laid down. Comparisons of Figures 1 and 2 will illustrate these differences.

It thus appeared that the bullfrog has a comparatively well developed biting action of the jaws that occurs toward the end of the tongue retraction and is oriented toward the prey's original location. This behavior of the jaws may have the effect of capturing prey animals that do not travel obligingly into the mouth on the tongue when retracted,

namely, aquatic prey. Consistent with this notion is the presence of grasping type teeth on the upper jaw of frogs of the genus Rana. The apparent laying down of the anterior dorsal aspect of the tongue by the bullfrog may be an adaptation to light refraction at the water-air interface. Because of light refraction, a submerged object viewed obliquely, as a frog will view it, appears nearer the viewer than would be the case if the object were not submerged. Given the bullfrog's comparatively aquatic as well as terrestrial diet, the spatial relationship between the visual image and the true location of the bullfrog's prey will presumably vary more than for the other frogs. Adaptation to refraction in the bullfrog may amount simply to laying down of more tongue surface, covering more ground than other frogs. It should be noted, however, that it appears that more tongue surface is laid down by the bullfrog specifically in the region where laying down more tongue surface may be selectively favored by the frog's striking at submerged prey animals, that is, in the region nearer the frog from the prey.

The foregoing considerations and observations guided the selection of motor pattern parameters for comparison. Statistical tests of whether bullfrog jaws close nearer the prey's original location involved as the basic data measurements of the distance from the prey or its original location to the apexes of the jaws. These measurements were made at three points in the strike. These were: tongue extension, defined as that point at which the tongue has been fully extended onto the prey (Figures 1a and 2a); tongue retraction, defined as occurring the instant the tongue is pulled back flush against the buccal floor

(Figures 1e and 2f); mouth closure, defined as the point at which the edges of the jaws meet (Figures 1h and 2h). All distances were measured between the midpoint on a straight line connecting the apexes of the two jaws (a point marking the joined jaw apexes for the measurements at jaw closure) and the intersection of two perpendicular lines, one indicating the ground beneath the prey or its original location, the other passing through the midpoint of the prey or its original location. Distances were measured to the prey's original position, meaning the position of the prey at strike initiation, at tongue retraction and mouth closure, when the prey was no longer at its original location. These distances were measured on single frame projections; white hatch marks (see Apparatus) at 1.0 cm. intervals provided a rule for calculating the true distances. All true distances were divided by the body length of the frog involved. This was done in an attempt to remove the effect of body size on the distance measurements, since larger frogs tended to produce longer prey to jaws distances. Another potential measure of biting, and one uncomplicated by corrections for body size, was the angle made relative to the horizontal by the line between the closed jaws at jaw closure. This angle was measured with a protractor on single frame projections.

Two measurements of tongue application were made, both at tongue extension. One was of the horizontal distance between the midpoint of the prey and the point of the frog's tongue farthest from the frog and making contact with either the prey or the ground. The second measurement was of the horizontal distance between the prey midpoint

and the point on the frog's tongue nearest the frog and making contact with either prey or ground. Both distances were divided by the body length of the frog involved, since frogs of greater body length possess longer tongues.

One set of measurements were made for the purpose of making Figures 3, 5, and 6. At tongue extension, retraction, and at mouth closure the vertical distance from the ground to the apex of each jaw and the horizontal distance from the prey midpoint or the midpoint of its original location to each jaw apex were measured on single frame projections. The true distances were divided by body lengths, as above. Then the means of these quotients were calculated for each species, and these means (coordinates) were used in the plotting of the locations of the jaw apexes in Figures 3, 5, and 6.

Results

Figure 3 shows the locations of the jaw apexes of the bullfrog, green frog, leopard frog, and wood frog, relative to the location of the prey, at tongue extension. Figure 4 shows the mean distances between the prey and jaw apexes of these frogs at tongue extension. No species differences in prey to jaws distance were significant at this point in the strike ($F < 1.00$, $df = 3/40$)(Table 3). The difference in the prey to jaws distance between frogs feeding on beetles and frogs feeding on beetle larvae was not significant ($F = 1.19$, $df = 1/40$). Differences between species of frog did not vary significantly as a function of prey type ($F = 1.06$, $df = 3/40$).

The locations of the frogs' jaws at tongue retraction are shown in Figure 5. The jaw apexes are located relative to the prey's

original location, meaning where the prey was at strike initiation. The mean distances from the prey's original location to the jaw apices of the four frogs at tongue retraction are shown in Figure 4. The bullfrog's jaws were significantly closer to the prey's original location than the jaws of the wood frog ($\underline{F} = 17.38$, $df = 1/40$, $p < 0.001$)(Table 4). The jaws of the leopard frog were also significantly closer to the prey's original location than the wood frog's jaws ($\underline{F} = 7.75$, $df = 1/40$, $p < 0.01$). It should be noted that because all the pairwise comparisons were tested (see Table 4) and because this procedure inflates the type I error rate, all comparisons were tested at the 0.025 level. The difference in the prey to jaws distance between frogs feeding on beetles and those feeding on larvae was not significant ($\underline{F} = 1.25$, $df = 3/40$). Species differences in prey to jaws distance did not vary with prey type ($\underline{F} < 1.00$, $df = 3/40$).

At mouth closure (Figures 4 and 6) the bullfrog's jaws were significantly nearer the prey's original location than were the jaws of the green frog ($\underline{F} = 7.03$, $df = 1/40$, $p < 0.025$)(Table 5), and the wood frog ($\underline{F} = 13.03$, $df = 1/40$, $p < 0.001$). The difference between the prey to jaws distance of frogs feeding beetles and frogs feeding on larvae was not significant ($\underline{F} < 1.00$, $df = 1/40$). Species differences did not vary significantly with prey type ($\underline{F} < 1.00$, $df = 3/40$).

Figures 6 and 7 show the mean jaw-line angles of the four frogs at mouth closure. The jaws of the bullfrog sloped downward significantly more than the jaws of the wood frog ($\underline{F} = 26.21$, $df = 1/40$, $p < 0.001$) (Table 6) and the green frog ($\underline{F} = 22.21$, $df = 1/40$, $p < 0.001$). The

jaws of the leopard frog also sloped downward more than those of the green frog ($\underline{F} = 9.71$, $df = 1/40$, $p < 0.005$) and the wood frog ($\underline{F} = 12.41$, $df = 1/40$, $p < 0.005$).

The location relative to the prey of the region of tongue contact with prey or ground of each of the four frogs is shown in Figure 8. The vertical axis represents the midpoint of the prey. There were no significant differences among the locations of the anterior limits of the tongue contact regions (limits to the left in Figure 8) ($\underline{F} < 1.00$, $df = 3/40$) (Table 7). Locations of the anterior limits did not vary as a function of prey type ($\underline{F} = 3.91$, $df = 1/40$). Species differences did not vary with prey type ($\underline{F} < 1.00$, $df = 3/40$).

The bullfrog's posterior tongue contact limit was significantly farther back from the prey than that of the green frog ($\underline{F} = 8.61$, $df = 1/40$, $p < 0.01$) (Table 8), the leopard frog ($\underline{F} = 7.56$, $df = 1/40$, $p < 0.01$), and the wood frog ($\underline{F} = 9.50$, $df = 1/40$, $p < 0.005$). Locations of the posterior contact limits did not vary with prey type ($\underline{F} = 2.67$, $df = 1/40$). Species differences in locations of the posterior contact limits did not vary with prey type ($\underline{F} = 1.11$, $df = 3/40$). It follows from the findings on the locations of the anterior and posterior limits of the tongue contact regions of the four frogs that the bullfrog applies a significantly greater length of tongue surface in the feeding strike than the other frogs, which do not differ among themselves in this respect.

Because the anatomical connection of the tongue on a frog's lower jaw is at the anterior extent of the jaw (see Figures 1 and 2), it is clear that the unique application of the tongue surface by bullfrogs is

effected by the positioning of the lower jaw apex at tongue extension comparatively near the ground and far back from the prey (cf. Figures 3 and 7).

Discussion

At tongue extension, the jaws of the bullfrog, green frog, leopard frog, and wood frog were essentially equidistant from the prey. Species differences in the distance from the jaws to the prey's original location appeared at tongue retraction; the jaws of the bullfrog and leopard frog were significantly nearer the prey's original location than the wood frog's jaws. At mouth closure the bullfrog's jaws were significantly nearer the prey's original location than were the wood frog's jaws and also the green frog's jaws. At mouth closure the jaws of the bullfrog and leopard frog sloped downward more than the jaws of the wood frog and green frog. The bullfrog's posterior tongue contact limit was found to be located farther back from the prey than that of the other frogs.

Two markedly distinct prey stimuli were used in the present experiment in an attempt thoroughly to characterize differences among the feeding strikes of the four frogs. Species differences between the strikes of frogs feeding on beetles were the same as species differences between the strikes of frogs feeding on the beetle larvae. Differences between the strikes of frogs feeding on beetles and those feeding on larvae were not significant. It seems reasonable to conclude that the differences found between the feeding strikes of the four frogs reflect not elicited effects specific to the particular prey stimuli employed, but rather effects of internal factors controlling the motor

patterns. In other words, we are concluding that had almost any prey stimuli been used, results similar to those gotten here would have been obtained. The present results, therefore, raise the question of why the frog species differ in the internal organizations of their feeding strikes.

The bullfrog is not so exceptional in the behavior of its jaws during the feeding strike as it appears to be in its food intake. By the present analysis, it does not differ significantly from the leopard frog, which seems to take few aquatic prey. This implies that the closeness of the bullfrog's jaws to the prey's original location at late points in the strike and the downward angulation of the jaws at mouth closure are characteristics not selectively favored by striking at aquatic prey animals. Still the jaws of only the bullfrog are closer to the original location of the prey than are the jaws of the wood frog and green frog at late points in the strike. And the bullfrog's jaws are angled downwards more at jaw closure than the jaws of the wood frog and green frog. Are these differences related to the bullfrog's unique diet? The data of Experiment I do not provide an answer to this question. It will be raised again in Experiments II and III.

The differences between the locations of the posterior tongue contact limits of the bullfrog, green frog, leopard frog, and wood frog are the sole behavioral differences discovered here that distinguish the bullfrog as do the species differences in food intake described above. Both bodies of data set the bullfrog apart, and the parallel is consistent with the location of the posterior tongue contact limit in the bullfrog having something to do with its diet aquatic animals.

Further, what we know happens to light as it traverses the water-air boundary suggests that a frog taking significant numbers of both terrestrial and aquatic prey will show exactly the peculiarity of tongue surface application shown by the bullfrog. A greater extent of tongue surface comes into play by the laying down of more of the anterior region of the tongue. It is possible that the comparatively posterior location of the posterior tongue contact limit of the bullfrog is selectively favored by this species' habit of striking at prey submerged in water.

If the effect of the bullfrog's unique tongue application is the capture of prey submerged in water, then it should be possible to demonstrate the bullfrog's superior capacity to capture submerged animals in the laboratory. Experiment II tested the capacity of the bullfrog, green frog, leopard frog, and wood frog to capture animals submerged in shallow water. The bullfrog's tongue placement does not suggest any lesser capacity for capture of ground prey accompanies the hypothesized greater capacity for capture of aquatic prey, since the bullfrog's tongue contact region covers all the ground about the prey covered by the tongue contact regions of the green frog, leopard frog, and wood frog (Figure 8). Experiment II compared also the capacities of the four frogs to capture terrestrial prey.

Experiment II

Animals

Six bullfrogs, green frogs, leopard frogs, and wood frogs, making a total of 24 frogs, served. These were all of approximately the same body length (Table 9). All of the bullfrogs and wood frogs were collected in the area about Amherst, Massachusetts. All but one of the green frogs and three of the leopard frogs were collected about Amherst. The remaining frogs were purchased (Lake Champlain Frog Farms, Alburg, Vermont).

Apparatus

Frogs were tested in a tropical fish tank, with outside dimensions 51.5 x 17.0 x 21.0 cm. high. The floor of the tank was modified as follows. A sheet of plexiglass 48.5 x 7.5 x 1.0 cm. thick was placed on the tank floor flush with a long side of the tank. Thus, a half of the tank floor became 1.0 cm. higher than the other. The entire floor of the tank was then covered with gray fiberglass window screen, for traction. Water was poured into the tank until a depth of 1.0 cm. was achieved in the lower half, the other half remaining above the water. The choice of a depth of 1.0 cm. of water was based upon observations of the depth of water frogs of the above body lengths were observed to rest in, in the habitat, and upon pilot work showing that none of the four frog species could capture prey animals submerged in a depth of water equal to one half of their body length. One small glass wall of the aquarium was removed leaving the tank open at one end.

Procedure

Five to seven days after the preliminary feeding tests, each frog's body weight was measured, and those frogs were used that had a body weight reasonably approximating natural body weight. This judgment was based on a comparison of the frog's body weight with the body weights of newly captured individuals of the same species and of similar body length. The frog was then placed in the apparatus without water and fed to satiety on dead mealworms. The mealworms had just been killed by immersion in hot water. They were dragged before the frog one at a time, impaled on the end of a fine monofilament spin-fishing line (2-pound test). The line was inserted into the mealworm's anus. As soon as the frog took each mealworm, the line was gradually pulled from the frog's mouth.

Six to eight days later the frog was tested. Prior to testing, all frogs' body weights were again measured, and only frogs with approximately natural body weights were used in the testing. Each frog was placed in the apparatus and testing began. The experimenter manually dragged a dead mealworm before the frog on the dry side of the tank floor. The prey was dragged at approximately one cm. per second. If the frog's first strike was successful, the line was gently pulled free from the frog's mouth and a stop watch started. The experimenter scored the response as successful. If the frog failed to capture the mealworm on its first strike, the mealworm was jerked away rapidly and out of the tank, and the watch started. The experimenter scored the response as unsuccessful. After 1.25 min. elapsed, which allowed sufficient time for the freeing of the frog's tongue from the previous

mealworm (if captured), the next mealworm was presented, submerged. The submerged mealworm was dragged as the dry one before the frog, and the experimenter responded to successful and unsuccessful strikes as above. Testing in this manner continued, with prey being presented alternately dry or submerged until either the frog showed a sign of satiety or twenty mealworm presentations were made. The frog was judged sated upon the occurrence of escape responses or the cessation of feeding. If twenty mealworm presentations were made, four additional mealworms were offered the frog, and if it ate all four, the experimenter concluded that satiety did not occur during the testing, and the experiment for that frog was completed. If a frog appeared sated prior to the conclusion of twenty mealworm presentations, or prior to eating the four additional mealworms, its responses to all but the last four mealworms eaten were judged to be uninfluenced by satiety factors. Only responses free of satiety effects were scored in the experiment. Frogs that became sated were tested again six to eight days later. This procedure continued until there were recorded for each frog the results of ten strikes at mealworms dragged on the dry side of the tank floor, and ten strikes at mealworms dragged in 1.0 cm. of water.

Throughout testing the line was drawn, in dragging the mealworms, through the end of the tank from which the glass wall had been removed. This was to keep the line as near the floor of the tank as possible, in an attempt to minimize the raising of the submerged mealworms off the bottom. All mealworms used in testing were between 1.5 and 2.0 cm. in body length.

Results

Table 10 shows the results of dividing the number of successful strikes at submerged mealworms by the number of successful strikes at dry mealworms for individual frogs. The absence of quotients greater than or equal to one means that all frogs failed to capture submerged mealworms as frequently as dry mealworms. Failures to capture dry mealworms were occasional in all four frog species (Table 11). Because of these findings it was assumed that some factors contributing to failures operate independently of whether or not the prey is submerged in water. These factors presumably underly the failures to capture dry mealworms as well as some of the failures to capture submerged mealworms. The effect of these factors is a general strike failure rate. Since there were more successful strikes at dry mealworms, it was assumed that some factors contributing to failures operate only when the prey is submerged and that these factors simply add their effect, a strike failure rate, to the general failure rate. Following this model, the failure rate associated specifically with prey submersion for each frog may be isolated as follows. The number of dry mealworms not captured is subtracted from the number of submerged mealworms not captured. This operation theoretically removes from the total number of submerged mealworms not captured those not captured due to factors generally contributing to failures. The remaining number of submerged mealworms not captured were not captured because they were submerged. This number is then divided by ten minus the number of dry mealworms not captured to give the strike failure rate due to factors associated specifically with prey submersion. The results

are presented as strike success rates, the complements of the failure rates.

The mean strike success rate with submerged mealworms for the bullfrog was significantly greater than that of the green frog ($\underline{F} = 30.50$, $df = 1/20$, $p < 0.001$)(Table 12; Figure 9), and of the leopard frog ($\underline{F} = 69.88$, $df = 1/20$, $p < 0.001$), and of the wood frog ($\underline{F} = 88.88$, $df = 1/20$, $p < 0.001$). The green frog's strike success rate with submerged mealworms was significantly greater than the leopard frog's ($\underline{F} = 8.13$, $df = 1/20$, $p < 0.01$) and the wood frog's ($\underline{F} = 15.25$, $df = 1/20$, $p < 0.001$).

The bullfrog's and green frog's superior capacities with submerged mealworms do not seem to carry with them lesser capacities for the capture of dry mealworms, or terrestrial prey. The species differences in capacity to capture dry mealworms (Table 11) were not significant ($\underline{F} = 1.83$, $df = 3/20$)(Table 13).

Discussion

The bullfrog appears to possess a feeding strike comparatively effective for the capture of prey animals below the surface of water. The results of the direct tests of the present experiment and of the stomach content analyses indicate this conclusion. The peculiar tongue placement by bullfrogs further supports this conclusion in indicating the mechanism mediating the capture of animals submerged in water. Though attempts to film frogs feeding on submerged mealworms were unsuccessful, it is unlikely that these were caught on the adherent surface of the tongue as were the dry mealworms. All four frog species used in the present experiment were incapable of capturing

a wet mealworm lying on the dry side of the tank floor, even when allowed to strike repeatedly. Mealworms submerged in water were probably captured by being caught in a region of negative pressure beneath the tongue as it was retracted into the frog's mouth. This suggests that the bullfrog's superior capacity to capture submerged prey animals may be due to the locations of its jaws at late points in the strike as well as its unique tongue placement. Submerged prey can be pulled along by the tongue retraction only so long as there is water between tongue and prey. The comparative proximity of the bullfrog's jaws to the prey's original location at late points in the strike may frequently result in the jaws closing while they are below the water surface. This in turn would result in a biting or grasping capture of a prey that could not have been captured with the tongue alone. It should be noted that during testing in Experiment II it was observed that both the jaws of bullfrogs frequently entered the water during feeding strikes.

The green frog was more successful in capturing submerged mealworms than was expected on the basis of its tongue placement, for in this it did not differ from the leopard frog or the wood frog. Observations made during testing suggested a resolution to the disparity with the tongue placement findings. Leopard frogs and wood frogs appeared to strike only the water surface with the tongue when striking at submerged mealworms. Rarely did these species create a disturbance in the water sufficient to move the mealworm. Green frogs, like bullfrogs, usually caused the submerged mealworm to shift about with their strikes (when they failed to capture the mealworm),

indicating a deeper strike with the tongue. Green frogs may have captured more submerged mealworms than leopard frogs or wood frogs because green frogs actually struck at the mealworms whereas the strikes of leopard frogs and wood frogs appeared to abort at the water surface.

The case of the wood frog is further remarkable because not only did no wood frog, including three pilot animals, ever capture a mealworm submerged in water, but the striking of the water with the tongue appeared aversive to this species. Only rarely did a wood frog, in pilot work, follow up a failure to capture a submerged mealworm with a second strike, and this response is characteristic of the other three frogs. Further, some wood frogs ceased after three to six strikes at submerged mealworms altogether to strike at these, though continuing to eat dry mealworms. (When this occurred during experimental testing, which it did in three frogs, the failures to respond were scored as unsuccessful strikes as long as the frog continued to eat dry mealworms.)

The differences between the bullfrog's capacity for capture of submerged mealworms and that of the leopard frog and the wood frog cannot be attributed to the peculiarity of the bullfrog's tongue application or jaw closure during the feeding strike. That the leopard frog's and wood frog's tongues apparently failed usually to extend to the submerged mealworms may also have resulted in these differences. Nevertheless, the difference between the submerged mealworm capture rates of the green frog and bullfrog may have resulted from the differences between the tongue application and jaw

behavior during the feeding strike of these species, since green frogs and bullfrogs did not appear to differ in the extent to which their tongues went into the water. Thus, the results of the present experiment do single out the peculiarities of the bullfrog's tongue application and jaw movements during the feeding strike as the possible mechanisms mediating its comparatively effective capture of submerged prey animals.

Disparities between submerged mealworm capture rates and stomach content analyses remain to be explained. Green frogs captured more submerged mealworms than did leopard frogs or wood frogs, but stomach content analyses do not indicate differences between these species in proportion of aquatic prey. The complete inability of wood frogs to capture submerged mealworms is inconsistent with the number of aquatic prey found in wood frog stomachs by Munz (1920). Variance between laboratory and field findings may involve a host of factors. Capacities detected by laboratory tests simply may not be put to use in the field in the way we apprehend them. Subadult green frogs appear to be less aquatic than adults; subadults are found in the vicinity of permanent water, but are less frequently than adults found actually sitting in the water (Jenssen and Klimstra, 1966; personal observations). Collection of relatively many young green frogs for stomach content analyses may generate a picture of predation on mainly terrestrial organisms (Jenssen and Klimstra, 1966), though the species may be quite capable of taking aquatic prey. The capacity for capture of submerged prey animals found in the present experiment may contribute to fitness mainly in adult green frogs.

Conversely, capacities operant in the field may go undetected in the laboratory. Munz (1920) examined stomach contents of only recently metamorphosed frogs. Possibly at this stage of development the wood frog possesses a significant capacity for capture of submerged prey, especially since the transforming frogs pass some time about the shoreline. It is also possible that wood frogs and leopard frogs, regardless of stage of development, are capable of capturing submerged prey, though only at lesser depths of water than represented in the present experiment.

Finally, an important factor behind the laboratory-field paradoxes may be geographic variation. Green frogs of the Amherst area may take aquatic prey, as the present experiment indicates they possess the capacity, but green frogs of other regions as Kentucky (Bush, 1959) or New York State (Hamilton, 1948; Whitaker, 1961) may take no aquatic prey. Or wood frogs of the region of Ithaca, New York may prey upon submerged organisms (Munz, 1920) but those of Amherst may not.

Experiment III

The results of Experiments I and II indicated the bullfrog's feeding strike is adapted for capture of aquatic prey animals. Tongue placement appears adapted to light refraction. The behavior of the jaws appears adapted to the incapacity of the tongue to convey (submerged) prey far from their original location. Further evidence consistent with this second hypothesis was obtained in the present experiment.

Occasionally during the making of film records for Experiment I a frog was filmed as it struck and failed to capture the prey, then struck again. It seemed upon casual inspection of the films that when a green frog, leopard frog, or wood frog struck at a prey after having struck and failed to capture the same prey, its strike was topographically modified. The topographic modification of the strike appeared to consist of closing of the jaws nearer the prey's original location and increased downward angulation of the jaws late in the strike. It was reasoned that feeding strike modification following an unsuccessful strike may be advantageous only if prey infrequently captured by a frog's normal strike are frequently captured by the modified strike. It followed that the adaptation of the frog feeding strike to nonadherent prey may be the development of a biting action of the jaws. It should be noted that this also follows from a consideration of the mechanics of the situation; the toothed jaws are probably a more effective tool for picking up nonadherent objects than

the mucous tongue. Because the modified strikes of these frogs appeared similar to the normal strike of the bullfrog, it was thought that the selective advantage of the bullfrog's strike is the same as that of these modified strikes, the capture of relatively nonadherent prey animals.

Experiment III examined the effect of failure to capture a prey that is nonadherent upon the topography of the feeding strike of the green, frog, leopard frog, wood frog, and the bullfrog.

Animals

Six bullfrogs, green frogs, leopard frogs, and wood frogs, making a total of 24 frogs, served. These were of various body lengths (Table 14). All bullfrogs and wood frogs were collected about Amherst, Massachusetts. Three leopard frogs and two green frogs were purchased (Lake Champlain Frog Farms, Alburg, Vermont). The remaining green frogs and leopard frogs were collected about Amherst.

Apparatus

The apparatus used in Experiment I was used in Experiment III.

Procedure

The procedure was identical to that of Experiment I, with the following exceptions. The prey were mealworms in the habituation and experimental sessions for all frogs. During experimental sessions the mealworms were fastened to the tank floor so that the frogs were unable to capture them. Thin (2-pound test) monofilament spin-fishing line was tied snugly around the mealworm at two points, near its head and near its posterior, respectively. The free ends of the ties were then taped to the tank floor. The distance between the

mealworm and the tapes was approximately 2.5 cm., so that the mealworm appeared much as it did in Experiment I, lying on the slate tank floor. Mealworms writhed in place after being tied down. Each frog was filmed as it made its very first three successive strikes at the tied down mealworm. Prior to their ever responding to a tied down mealworm, all frogs were filmed once feeding on a mealworm that was not tied down. A strike at a normal mealworm, meaning one that was not tied down, was included in the comparison as the baseline.

Results

Because the aim of the present experiment was to examine the effect of failure to capture a nonadherent prey during a feeding strike upon the topography of subsequent feeding strikes of each of the four frog species, the data from each species were analyzed separately. Comparisons were made between the strike at the normal mealworm and the strikes at the tied down mealworm.

Figures 10, 11, and 12 show the locations of the jaw apexes of the green frog at tongue extension, tongue retraction, and mouth closure during the four strikes. Figure 13 shows the distances of the jaws from the mealworm at the three points in the strike during each of the strikes. During feeding strikes at the tied down mealworm the jaws of the green frog passed significantly closer to the mealworm than during strikes at the normal mealworm ($F = 3.78$, $df = 3/15$, $p < 0.05$)(Table 15). The interaction of strike by point in the strike was not significant ($F = 1.68$, $df = 6/30$), indicating that the primary effect of the tied down mealworm was that the jaw movement as a whole was carried out nearer the prey. Application of the Newman-

Keuls procedure to these data revealed that during the second and third strikes at the tied down mealworm the green frog's jaws passed significantly closer to the mealworm than during the strike at the normal mealworm ($p < 0.05$), and that during the third strike at the tied down mealworm the jaws came closer to the mealworm than during the first strike at this prey ($p < 0.05$).

The increased downward angulation of the green frog's jaws at mouth closure (Figures 12 and 14) during strikes at the tied down mealworm was significant ($F = 6.80$, $df = 3/15$, $p < 0.005$)(Table 16). A Newman-Keuls test of these data showed that the angulation of the jaws during the second and third failing strikes differed significantly from the angulation of the jaws during the strike at the normal mealworm ($p < 0.05$).

The locations of the leopard frog's jaw apexes at the three points in the strike during each of the strikes are shown in Figures 15, 16, and 17. Figure 18 shows for the leopard frog the distances of the jaws from the mealworm. The leopard frog's jaws, as the green frog's, passed nearer the tied down mealworm than the normal mealworm ($F = 9.41$, $df = 3/15$, $p < 0.001$)(Table 17). The strike by point in the strike interaction was not significant ($F = 2.29$, $df = 6/30$); the primary effect of the tied down mealworm again appeared to be that the usual jaw movement occurred closer to the prey. Testing of these data by the method of Newman-Keuls indicated that on the three strikes at the tied down mealworm the jaws of the leopard frog came closer to the prey than during the strike at the normal mealworm ($p < 0.05$), and that the jaws came closer to the prey on the third strike at the

tied down mealworm than during the first strike at this prey ($p < 0.05$). The significant difference between the strike at the normal mealworm and the first strike at the tied down mealworm indicates modification of the first strike at the tied down mealworm. Such modification may be a result of a difference in the visual appearance of the tied down mealworm from that of the normal mealworm. In other words, the carrying out of the feeding strike jaw movement nearer the prey may be caused by factors other than failure to capture the prey. But the interpretation that failure to capture prey resulted in the leopard frog's jaws passing nearer the prey on a subsequent feeding strike is allowed, though not necessitated, by the significant difference between the prey to jaws distance of the first and third strikes at the tied down mealworm.

The increase in the downward angulation of the leopard frog's jaws at jaw closure (Figures 17 and 19) was significant ($F = 11.32$, $df = 3/15$, $p < 0.001$)(Table 18). A Newman-Keuls test of these data showed that the downward angulation on all three strikes at the tied down mealworm was significantly greater than on the strike at the normal mealworm ($p < 0.05$) and that the angulation of the third strike at the tied down mealworm was significantly greater than that on the first strike at this prey ($p < 0.05$).

The wood frog's jaw apex locations are shown in Figures 20, 21, and 22. Distances from prey to jaws are shown in Figure 23. The wood frog's jaws passed significantly nearer the tied down mealworm than the normal mealworm ($F = 6.98$, $df = 3/15$, $p < 0.005$)(Table 19). The strike by point in the strike interaction was not significant ($F =$

1.63, $df = 6/30$). The Newman-Keuls test showed that the three strikes at the tied down mealworm differed significantly in prey to jaws distance from the strike at the normal mealworm ($p < 0.05$), and that there were no significant differences among these three strikes. There is no evidence here for any effect of failure to capture prey on the wood frog's feeding strike. A significant decrease in the prey to jaws distance appeared on the first strike at the tied down mealworm, and no further change in this parameter was evident on subsequent strikes.

Figures 22 and 24 show the angulation of the wood frog's jaws at mouth closure. Striking at the tied down mealworm resulted in significantly increased downward angulation of the jaws ($F = 9.50$, $df = 3/15$, $p < 0.001$)(Table 20). But again the first strike at a tied down mealworm appeared modified to the same extent as subsequent strikes; a Newman-Keuls test of the data showed that the downward angulation of the jaws on the three strikes at the tied down mealworm was significantly greater than that on the strike at the normal mealworm ($p < 0.05$) and that the angulation on the three failing strikes did not vary significantly.

The locations of the jaw apexes of the bullfrog during the four strikes are shown in Figures 25, 26, and 27. Prey to jaws distances are shown in Figure 28. The bullfrog's jaws passed significantly nearer the tied down than the normal mealworm ($F = 6.15$, $df = 3/15$, $p < 0.01$)(Table 21). The Newman-Keuls test showed that all three strikes at the tied down mealworm differed significantly in prey to jaws distance from the strike at the normal mealworm ($p < 0.05$) and that the

first and third strikes at the tied down mealworm also differed significantly ($p < 0.05$). Strike modification was apparent during the first strike at the tied down mealworm, but further modification occurred, possibly as a result of failure, on subsequent strikes. Since the strike by point in the strike interaction was not significant in the bullfrog ($F = 1.31$, $df = 6/30$), the primary effect of the tied down mealworm appeared to be, as in the green frog and leopard frog, the carrying out of the usual feeding jaw movement nearer the prey.

Figures 27 and 29 show the increase in the downward angulation of the bullfrog's jaws at mouth closure. The effect was significant ($F = 9.86$, $df = 3/15$, $p < 0.001$)(Table 22). But there was no statistically significant effect of failure. The Newman-Keuls test revealed that the differences between the three strikes at the tied down mealworm were not significant, but all three differed significantly from the strike at the normal mealworm ($p < 0.05$).

Figures 30, 31, 32, and 33 show the locations of the frogs' tongue contact regions relative to the mealworm on each of the four strikes. The distance from the mealworm midpoint to the anterior tongue contact limit did not vary significantly between strikes in the green frog ($F < 1.00$, $df = 3/15$)(Table 23), the wood frog ($F = 1.28$, $df = 3/15$)(Table 24), and the bullfrog ($F = 2.58$, $df = 3/15$)(Table 25). In the leopard frog the distance from prey midpoint to anterior tongue contact limit varied significantly ($F = 4.94$, $df = 3/15$, $p < 0.025$)(Table 26). The distance between the mealworm midpoint and the posterior contact limit did not vary significantly between strikes in the

leopard frog ($\underline{F} < 1.00$, $df = 3/15$)(Table 27), the wood frog ($\underline{F} < 1.00$, $df = 3/15$)(Table 28), and the bullfrog ($\underline{F} = 1.17$, $df = 3/15$)(Table 29). In the green frog the location of the posterior tongue contact limit varied significantly between strikes ($\underline{F} = 3.58$, $df = 3/15$, $p < 0.05$)(Table 30).

Discussion

During their strikes at the tied down mealworm, the jaws of the green frog, leopard frog, wood frog, and bullfrog passed nearer the mealworm than during their strike at the normal mealworm, respectively. In the leopard frog, wood frog, and bullfrog, the jaws passed significantly nearer the tied down mealworm during the first strike at this than during the strike at the normal mealworm, respectively. The jaws of the green frog, leopard frog, and bullfrog passed nearer the tied down mealworm during the third strike at this than during the first, respectively.

There was increased downward angulation of the jaws at mouth closure during strikes at the tied down mealworm in all four species of frog. The downward angulation during the first strike at the tied down mealworm was greater than that during the strike at the normal mealworm in the leopard frog, wood frog, and bullfrog. The downward angulation during the third strike at the tied down mealworm was greater than that during the first strike at this in the leopard frog.

The location of the anterior tongue contact limit varied significantly between strikes in the leopard frog. In the green frog the location of the posterior tongue contact limit varied between strikes.

The topographic modification of frogs' first strikes at the tied

down mealworm suggests, as mentioned earlier, that factors other than failure to capture prey on a previous strike can influence the form of frogs' strikes. The modifications of jaw movement appearing during the first strikes were of the same nature as those appearing during subsequent strikes. Therefore, in cases where a significant difference appeared between the strike at the normal mealworm and the first strike at the tied down mealworm, there had to be also a significant modification of the third strike at the tied down mealworm compared to the first, for an interpretation of an effect of failure on strike topography to be possible. A difference between the first and third strikes at the tied down mealworm does not necessarily mean the difference was caused by the failure to capture the prey during the first and second strikes, however. Possibly the mealworm's behavior changed upon being struck by the frog. This does not, however, seem likely. Examination of film records revealed no systematic changes (to the human eye) in the writhing of the tied down mealworms following being struck by frogs. Further, the strikes observed in the film records of Experiment I, following failing strikes, appeared modified yet the prey in such cases was sometimes untouched during the first strike by the attacking frog. It does not appear likely that modification of the behavior of tied down mealworms was a cause of the modification of strikes.

The general finding of the present experiment is that the feeding strikes of the green frog, leopard frog, bullfrog, and possibly the wood frog, following strikes failing to capture nonadherent prey differ topographically from their normal strikes, respectively, in the

same manner in which the normal strike of the bullfrog differs from the normal strike of the other frogs. On strikes following strikes failing to capture a nonadherent prey animal, the jaws of the green frog, leopard frog, and bullfrog passed and therefore closed nearer the prey. The results of Experiment I showed that the bullfrog's normal strike is characterized by comparative closeness of the jaws to the prey's original location at late points in the strike, particularly jaw closure. Failing to capture nonadherent prey resulted, in the green frog and leopard frog, in increased downward angulation of the jaws at mouth closure. In the bullfrog and wood frog, the increases in downward angulation of the jaws following failing strikes were not statistically significant. But because all four Rana species invariably showed increased downward jaw angulation on each subsequent strike at the tied down mealworm (see Figures 14, 19, 24, and 29), the increased angulation in the bullfrog and wood frog was probably not random error variance but an organized response elicited by failure to capture the nonadherent mealworm. The results of Experiment I showed the downward angulation at mouth closure of the bullfrog's jaws to be significantly greater than that of the jaws of the green frog and wood frog. These parallels between the peculiarities of the normal feeding strike of the bullfrog and the peculiarities of frog feeding strikes elicited by failure to capture nonadherent prey are consistent with the hypothesis that the bullfrog's normal strike is adapted for capture of relatively nonadherent prey.

The mechanical advantage of the bullfrog strike and the modified

strikes is quite evident. The closing of the jaws, the upper one bearing grasping teeth, nearer the prey's original location should increase the probability of a (biting) capture of the prey in the event the prey fails to travel into the mouth on the tongue. The downward angulation of the jaws brings them nearer and orients them towards the prey's original location (cf. Figures 1, 2, 6, 12, 17, 22, and 27) further facilitating capture. It should be noted that during the development of a method of fastening a mealworm to the tank floor, frogs, particularly bullfrogs and leopard frogs, frequently succeeded in biting off a section of a mealworm fastened to the tank floor. (The method was perfected prior to the making of any films and no frogs succeeded in biting off a section of the mealworm, nor in capturing the whole mealworm, during Experiment III.)

That the feeding strike of the bullfrog was also modified following failures to capture prey is not inconsistent with the foregoing hypothesis. There is no reason to think the bullfrog's normal feeding strike the ultimate adaptation of the Rana feeding strike for the capture of nonadherent prey animals. The bullfrog's strike is probably specialized for capture of prey on the average less adherent than the prey of other frogs. Topographic modification following failure to capture nonadherent prey in the bullfrog probably has essentially the same effect as this does in other frogs, the capture of prey exceptionally nonadherent compared to the frog's usual prey.

Because Experiment III tested the frogs' response to nonadherent prey, and because a priori no modification in tongue placement was envisioned that could facilitate capture of nonadherent prey, no

effects of failure to capture nonadherent prey were expected. It appears that failure to capture nonadherent prey had no effect on tongue placement. In the leopard frog the significant variance of the location of the anterior tongue contact limit was due, at least in part, to the difference between the locations of the anterior contact limits of the first strike at the tied down mealworm and the strike at the normal mealworm (see Figure 31). A significant difference between the strike at the normal mealworm and the first strike at the tied down mealworm suggests two possible explanations: (1) the tied down mealworm behaved differently from the normal mealworm, and so elicited a different strike; (2) the first strike at the tied down mealworm was modified by sensory feedback received by the frog during the response. This second hypothesis can be rejected as an explanation for the location of the anterior contact limit of the leopard frog's first strike at the tied down mealworm because tongue placement was measured at tongue extension, that point in the strike at which the tongue has just been laid down upon the prey and before any retraction of the tongue can be seen. It seems unlikely that the tied down mealworm's nonadherence could be detected at this early point in the strike. Instead, the leopard frog's altered tongue placement on this strike was probably elicited by the tied down mealworm's behavioral peculiarities (see below). And because no further increases in the distance from the mealworm midpoint to the leopard frog's anterior tongue contact limit occurred on the subsequent strikes at this prey, no effect of failure on the leopard frog's tongue placement can be inferred. It is not possible to interpret as an

effect of failure the shifting back of the leopard frog's anterior tongue contact limit on the second and third strikes at the tied down mealworm, because this may instead reflect a resumption of normal tongue placement.

Similarly, in the green frog the shifting back of the posterior tongue contact limit occurred maximally on the first strike at the tied down mealworm. Again no effect of failure on tongue placement is evident.

The jaws of the bullfrog, leopard frog, and wood frog passed significantly nearer the tied down mealworm during the first strike at this than during the strike at the normal mealworm. It is not as easy to explain these results as to explain tongue placement modification. For jaw movements were measured at late as well as early points in the strike, allowing the possibility of strike modification by sensory feedback received during the strike as well as by sensory information received before the strike began. That is, possibly the nonadherence of the tied down mealworm was detected early in the strike, for example as the tongue retraction began, and this resulted in modification of later parts of the strike such that the jaws closed nearer the prey. Of course, the strike by point in the strike interaction was not significant in any frog species, implying that alteration of this nature did not occur. In all four frogs, however, strikes at tied down mealworms differed from normal strikes in that the decrease in the prey to jaws distance at mouth closure was greater than the decrease at tongue extension (see Figures 13, 18, 23, and 28). The occurrence of this same pattern in the data of all four

frog species seems an improbable result if due to chance. Therefore, there seems to be significant evidence consistent with the hypothesis of feeding strike alteration by sensory feedback received during the strike. And because the variance between the prey to jaws distance of the first strike at the tied down mealworm and the strike at the normal mealworm was contributed to by the variance between these strikes at mouth closure, the significant difference between these strikes may reflect the effect of sensory feedback received during the strikes. Alternatively, it is possible that all differences between these strikes of the bullfrog, leopard frog, and wood frog were due to differences between the behaviors of the eliciting stimuli, the normal and tied down mealworms.

What were the differences in behavior between normal and tied down mealworms? It might be noted that the well-documented reliance of frogs upon the movement of their prey for elicitation of feeding behavior was the initial basis for suspecting a behavioral difference was the critical one between normal and tied down mealworms. Tied down mealworms writhed less vigorously than did normal mealworms, and tied down mealworms did not travel at all. Normal mealworms, though injured so as to hinder locomotion, did usually travel to some extent due to their writhing. Assuming that the behavior of tied down mealworms did elicit feeding strike modifications, that these were of the same character as the modifications elicited by failure to capture nonadherent prey animals suggests that the prey of frogs that move the least or least rapidly are the most difficult to pick up with the tongue.

General Discussion

The bullfrog apparently takes more aquatic prey than the green frog, the leopard frog, and the wood frog. This is probably not solely a function of the bullfrog's remaining nearer permanent water than other frogs, for it apparently possesses a greater capacity for capture of submerged prey animals. How bullfrogs manage to capture comparatively many aquatic prey animals is indicated insofar as the feeding strike of the bullfrog differs topographically from the strike of the other frogs in two particulars which on other grounds appear to be adaptations for the capture of prey animals submerged in water. Because of light refraction at the water-air interface, a prey animal submerged in water appears to be situated beyond its actual location, when viewed obliquely. The bullfrog's tongue placement is such that the posterior contact limit is farther back from a terrestrial prey than is that of the other frogs. When directed at prey submerged in water, such a tongue placement presumably will more frequently result in the tongue laying upon the prey than will the tongue placement of the other frogs. Prey animals submerged in water do not adhere to the mucous surface of frogs' tongues. Prey submerged in water are probably pulled towards the bullfrog's mouth when caught in a region of negative pressure below the retracting tongue. Prey so caught cannot be significantly lifted above the water surface, and the bullfrog's jaws closing comparatively near the prey's original location may have the effect of capturing the prey by closing on it below the water surface. That the bullfrog's jaws closing comparatively near the prey's

original location is an adaptation to prey that are not effectively captured on the tongue is further supported by the finding that the response to nonadherent prey in Rana appears to be a closing of the jaws nearer the prey's original location.

The measurements made in Experiment I of tongue placement and jaw apex locations at tongue placement showed the bullfrog to protrude the tongue from the mouth to essentially the same extent as the green frog, leopard frog, and wood frog (cf. Figures 3, 4, and 8). Yet the greatest development of a biting action in the bullfrog amounts to the least dependence in this species upon the tongue for prey capture. It is interesting to note a general correlation in the Anura between anatomical reduction of the tongue with aquatic habitat, the completely aquatic Pipidae entirely lacking the structure (Noble, 1931), and in the Caudata between the degree of development of the tongue with terrestrial habitat (Regal, 1966). The amphibian tongue as a prey capture apparatus appears selectively favored in terrestrial habitats, where prey with a dry, adherent surface predominate.

References

- Brakeley, J. H. Notes on carp and frog-culture. Bull. U. S. Fish Com. 5: 209- 213, 1885.
- Brooks, G. R. An analysis of the food habits of the bullfrog, Rana catesbeiana, by body size, sex, month, and habitat. Va. J. Sci. 15: 173- 186, 1964.
- Bush, F. M. Foods of some Kentucky herptiles. Herpetologica. 15: 73- 77, 1959.
- Cardini, F. Characteristics and adaptedness of feeding behaviors of North American anurans. Paper presented at meeting of the Animal Behavior Society, Amherst, Mass., 1973.
- Cohen, N. W. and W. E. Howard. Bullfrog food and growth at the San Joaquin experimental range, California. Copeia. 1958: 223- 225.
- Conant, R. A Field Guide to Reptiles and Amphibians of the United States and Canada East of the 100th Meridian. Boston: Houghton Mifflin, 1958.
- Dickerson, M. C. The Frog Book. New York: Doubleday, Page and Co., 1906.
- Drake, C. J. The food of Rana pipiens Schreber. The Ohio Naturalist. 14: 257- 269, 1914.
- Dyche, L. L. Ponds, pond fish, and pond fish culture. Bull. No. 1 Kan. Dept. Fish and Game. 1914.
- Hamilton, W. J. The food and feeding behavior of the green frog, Rana clamitans Latreille, in New York State. Copeia. 1948: 203- 207.

- Hedeen, S. E. Food and feeding behavior of the mink frog, Rana septentrionalis Baird, in Minnesota. Amer. Midl. Nat. 88: 291-300, 1972.
- Jenssen, T. A. and W. D. Klimstra. Food habits of the green frog, Rana clamitans, in southern Illinois. Amer. Midl. Nat. 76: 169-182, 1966.
- Knowlton, G. F. Some insect food of Rana pipiens. Copeia. 1944: 119.
- Korschgen, L. J. and T. S. Baskett. Foods of impoundment- and stream-dwelling bullfrogs in Missouri. Herpetologica. 19: 89- 99, 1963.
- Korschgen, L. J. and D. L. Moyle. Food habits of the bullfrog in central Missouri farm ponds. Amer. Midl. Nat. 54: 332- 341, 1955.
- Linzey, D. W. Food of the leopard frog, Rana p. pipiens, in central New York. Herpetologica. 23: 11- 17, 1967.
- Munz, P. A. A study of the food habits of the Ithacan species of anura during transformation. Pomona College J. Ent. and Zool. 12: 33-56, 1920.
- Needham, J. G. The summer food of the bullfrog (Rana catesbeiana Shaw) at Saranac Inn. Bull. No. 86, New York State Museum. 1905.
- Noble, G. K. The Biology of the Amphibia. New York: McGraw-Hill, 1931.
- Perez, M. E. The food of Rana catesbeiana Shaw in Puerto Rico. Herpetologica. 7: 102- 104, 1951.
- Regal, P. J. Feeding specializations and the classification of terrestrial salamanders. Evol. 20: 392- 407, 1966.
- Schneider, D. Beitrag zu einer Analyse des Beute- und Fluchtverhaltens einheimischer Anuren. Biol. Zbl. 73: 225- 282, 1954.

Surface, H. A. First report on the economic features of the amphibians and reptiles of Pennsylvania. Zool. Bull. Pa. Dept. Agric.

3: 67- 152, 1913.

Whitaker, J. O. Habitat and food of mousetrapped young Rana pipiens and Rana clamitans. Herpetologica. 17: 173- 179, 1961.

Wright, A. H. and A. A. Wright. Handbook of Frogs and Toads of the United States and Canada. Ithaca: Comstock Publishing Co., 1949.

Figure Legends

Figure 1. The feeding response of a leopard frog, R. pipiens. The response was filmed at 64 frames per sec. The individual frames were projected and the images of the frog and prey were traced. The tracings begin at the point in the response at which the tongue has just been fully extended onto the prey, and end at the point at which the edges of the jaws meet.

Figure 2. The feeding response of a bullfrog, R. catesbeiana. Conventions as in Figure 1.

Figure 3. The locations of the upper jaw apex and lower jaw apex of the bullfrog, green frog, leopard frog, and wood frog relative to the prey at the point in the strike at which the tongue has just been fully extended onto the prey. The vertical axis indicates the midpoint of the prey. The horizontal axis indicates the ground level. The strike is viewed from the side. The coordinates of the locations of the jaw apexes were found as follows. The true vertical distances between the ground and each jaw apex of an individual frog were measured on single frame projections. The means of both these quantities were each divided by the body length of the individual frog in question. The resulting pair of quotients for each individual frog were separately summed within species and the sums divided by twelve to give the mean height on body length for each species' upper and lower jaw apex. The horizontal coordinates were found analogously, with distances being measured from the prey midpoint instead of the ground.

The points showing the locations of the jaw apexes of each species were connected with a straight line to give an indication of the angulation of the jaws with the horizontal.

Figure 4. The distances of the jaws of the bullfrog, green frog, leopard frog, and wood frog from the prey at tongue extension (E), tongue retraction (R), and mouth closure (C). True distances were measured on single frame projections as the distance from the intersection of two perpendicular lines, one indicating the ground beneath the prey and the other indicating the midpoint of the prey, to the midpoint of a straight line connecting the jaw apexes or to a point marking the joined jaw apexes at mouth closure. Average true distance at each point in the strike for each individual frog was divided by the frog's body length. The resulting quotients were summed within points in the strike and within species, and these sums were each divided by twelve to give the species means shown.

Figure 5. Locations of the upper jaw apex and lower jaw apex of the bullfrog, green frog, leopard frog, and wood frog relative to the prey's original location at the point in the strike at which the tongue is retracted. Conventions as in Figure 3.

Figure 6. The locations of the joined jaw apexes of the bullfrog, green frog, leopard frog, and wood frog relative to the prey's original location at the point in the strike at which the mouth has

just closed. The oblique lines connected to the points indicate the line between the closed jaws, that is, the angulation of the jaws at mouth closure. Conventions as in Figure 3.

Figure 7. Angle with the horizontal made by the line between the closed jaws of the bullfrog, green frog, leopard frog, and wood frog at mouth closure. The angle between the horizontal and the line between the jaws was measured on single frame projections.. The mean angles for individual frogs were averaged within species to give the species means shown.

Figure 8. Location of the region of contact made by the tongue of the bullfrog, green frog, leopard frog, and wood frog with the prey or ground relative to the location of the prey, at tongue extension. The vertical axis indicates the midpoint of the prey. The positive region on the horizontal axis is the region beyond the prey midpoint from the frog. The negative region on the horizontal axis is the region nearer the frog from the prey midpoint. Locations of the anterior and posterior limits of the tongue contact regions were found as follows. True distances between the prey midpoint and the two limits of the contact region were measured on single frame projections. The mean distances to both for each individual frog were divided by the frog's body length. Both quotients were summed within species and the two sums for each species were divided by twelve to give the species means shown.

Figure 9. Success rates of the bullfrog, green frog, leopard frog, and wood frog when striking at mealworms submerged in shallow water. The ratios of the number of submerged mealworms captured on the number of dry mealworms captured by individual frogs were averaged within species to give the species mean ratios shown.

Figure 10. Locations relative to the prey of the upper jaw apex and lower apex of the green frog at tongue extension during a strike at a normal mealworm (N), and during the first (1), second (2), and third (3) successive strikes at a tied down mealworm. The vertical axis indicates the midpoint of the mealworm. The horizontal axis indicates the ground level. The strikes are viewed from the side. The coordinates of the locations of the jaw apexes were found as follows. The true vertical distances between the ground and each jaw apex at tongue extension of each individual green frog during each of the strikes were measured on single frame projections. Each distance measurement was divided by the body length of the frog involved. The resulting quotients involving the upper and lower jaw apexes were summed separately within strikes, and the sums divided by six to give the mean height on body length of each jaw apex at tongue extension during each of the strikes. The horizontal coordinates were found analogously, with distances being measured from the prey midpoint instead of the ground. The points showing the locations of the jaw apexes were connected with a straight line to give an indication of the angulation of the jaws with the horizontal.

Figure 11. Locations relative to the prey of the upper jaw apex and lower jaw apex of the green frog at tongue retraction during a strike at a normal mealworm (N), and during the first (1), second (2), and third (3) successive strikes at tied down mealworm. Conventions as in Figure 10.

Figure 12. Locations relative to the prey of the joined jaw apexes of the green frog at mouth closure during a strike at a normal mealworm (N), and during the first (1), second (2), and third (3) strikes at a tied down mealworm. The oblique lines connected to the points indicate the line between the closed jaws, that is, the angulation of the jaws at mouth closure. Conventions as in Figure 10.

Figure 13. The distances of the jaws of the green frog from the prey at tongue extension (E), tongue retraction (R), and mouth closure (C) during a strike at a tied down mealworm (N), and during the first (1), second (2), and third (3) strikes at a tied down mealworm. True distances were measured on single frame projections as the distance from the intersection of two perpendicular lines, one indicating the ground beneath the prey and the other indicating the midpoint of the prey, to the midpoint of a straight line connecting the jaw apexes or to a point marking the joined jaw apexes at mouth closure. True distance at each point in the strike for each individual frog was divided by the frog's body length. The resulting quotients were summed within points in the strike and within strikes, and these sums were each divided by six to give the means at each point in each of the strikes.

Figure 14. Angle with the horizontal made by the line between the closed jaws of the green frog at mouth closure during a strike at a normal mealworm (N), and during the first (1), second (2), and third (3) successive strikes at a tied down mealworm. The angle between the horizontal and the line between the closed jaws was measured on single frame projections. The angles of individual frogs were averaged within strikes to give the means of each strike.

Figure 15. Locations relative to the prey of the upper jaw apex and lower jaw apex of the leopard frog, at tongue extension. Conventions as in Figure 10.

Figure 16. Locations relative to the prey of the upper jaw apex and lower jaw apex of the leopard frog at tongue retraction. Conventions as in Figure 10.

Figure 17. Locations relative to the prey of the joined jaw apexes of the leopard frog at mouth closure. Conventions as in Figure 12.

Figure 18. The distances of the jaws of the leopard frog from the prey. Conventions as in Figure 13.

Figure 19. Angle with the horizontal made by the line between the closed jaws of the leopard frog at mouth closure. Conventions as in Figure 14.

Figure 20. Locations relative to the prey of the upper jaw apex and lower jaw apex of the wood frog at tongue extension. Conventions

as in Figure 10.

Figure 21. Locations relative to the prey of the upper jaw apex and lower jaw apex of the wood frog at tongue retraction. Conventions as in Figure 10.

Figure 22. Locations relative to the prey of the joined jaw apices of the wood frog at mouth closure. Conventions as in Figure 10.

Figure 23. The distances of the jaws of the wood frog from the prey. Conventions as in Figure 13.

Figure 24. Angle with the horizontal made by the line between the closed jaws of the wood frog at mouth closure. Conventions as in Figure 14.

Figure 25. Locations relative to the prey of the upper jaw apex and lower jaw apex of the bullfrog at tongue extension. Conventions as in Figure 10.

Figure 26. Locations relative to the prey of the upper jaw apex and lower jaw apex of the bullfrog at tongue retraction. Conventions as in Figure 10.

Figure 27. Locations relative to the prey of the joined jaw apices of the bullfrog at mouth closure. Conventions as in Figure 10.

Figure 29. Angle with the horizontal made by the line between the closed jaws of the bullfrog at mouth closure. Conventions as in Figure 14.

Figure 30. Locations of the region of contact made by the tongue of the green frog with the prey or ground relative to the location of the prey at tongue extension during a strike at a normal mealworm (N), and during the first (1), second (2), and third (3) strikes at a tied down mealworm. The vertical axis indicates the midpoint of the prey. The positive region of the horizontal axis is the region beyond the prey midpoint from the frog. The negative region on the horizontal axis is the region nearer the frog from the prey midpoint. Locations of the anterior and posterior limits of the tongue contact regions were found as follows. True distances between the prey midpoint and the two limits of the contact regions were measured on single frame projections. The distances to both contact limits were divided by the body length of the frog involved. Both quotients were summed within strikes and the sums divided by six to give the means shown.

Figure 31. Locations of the region of contact made by the tongue of the leopard frog. Conventions as in Figure 30.

Figure 32. Locations of the region of contact made by the tongue of the wood frog. Conventions as in Figure 30.

Figure 33. Locations of the region of contact made by the tongue of the bullfrog. Conventions as in Figure 30.

Appendix I

Experiment I showed the bullfrog applies tongue surface comparatively far back from the prey. Experiment II showed the bullfrog to be especially effective in capturing mealworms submerged in water. If this capacity of the bullfrog is due to the peculiarity of its tongue surface application, then the displacement of the visual image of the submerged mealworms in Experiment II must have been sufficient to cause green frogs to apply the tongue surface forward of the prey more frequently than bullfrogs. That this may have been the case can be demonstrated as follows. First, it should be noted that because mealworms were almost always dragged before frogs in a path perpendicular to the frogs' body axis, and because the mealworms were about 0.2 cm. thick, image displacements of as little as 0.2 cm. could cause a frog to miss, to fail to capture a submerged mealworm. We have from Experiment I the finding that the posterior tongue contact limit of green frogs, on the average, lies 0.123 cm. times the body length of the frog back from the prey midpoint. In the bullfrog the analogous figure is 0.237 cm. times the frog's body length. If we multiply the body lengths of green frogs in Experiment II (Table 9) by 0.123, we obtain the following estimates of the distance between the prey midpoint and the posterior tongue contact limit for the strike of each frog (in cm.): 0.6; 0.7; 0.7; 0.7; 0.7; 0.8. Multiplying the body lengths of the bullfrogs in Experiment II by 0.237 gives (in cm.): 1.2; 1.2; 1.2; 1.4; 1.5; 1.5. If the more posterior locations of the bullfrogs' posterior contact

limits were involved in the bullfrogs' more effective capture of submerged mealworms, then the effect of light refraction must have been such that images of submerged mealworms appeared beyond the actual locations of the mealworms by a distance at least 0.1 cm. (half the thickness of a mealworm) greater than that between the prey midpoint and posterior tongue contact limit of green frogs, but not greater than the distance between the prey midpoint and posterior tongue contact limit of bullfrogs. In other words, refraction had to cause mealworms to lie in the region covered by bullfrogs' tongues but not covered by green frogs' tongues.

The displacement of the visual images of submerged mealworms, due to light refraction, was calculated in light of the facts that during Experiment II frogs just prior to striking held their eyes two to three cm. above the water surface and three to eight cm. from the prey in a horizontal direction. Employing 0.8 cm. as the depth of the mealworms, application of trigonometry and Snell's law showed that when a frog's eyes were located three cm. above the water surface and three in a horizontal direction from the mealworm, the mealworm was 0.2 cm. nearer the frog than it presumably appeared to be to the frog. When the frog's eyes were located two cm. above the water surface, and eight cm. from the mealworm horizontally, the mealworm was actually 1.5 cm. nearer the frog than it presumably appeared to be. Thus, light refraction caused image displacements 0.1 cm. greater than the distance from the prey midpoint to the posterior tongue contact limit of green frogs, but not greater than this distance of bullfrogs. It is possible, therefore, that bullfrogs in Experiment

It captured more submerged mealworms because the comparatively posterior location of their posterior tongue contact limit resulted in comparatively frequent proximity of tongue surface and mealworm. Further, because maximum image displacement (1.5 cm.) was greater than the distance from prey midpoint to posterior tongue contact limit (plus 0.1 cm.) of some bullfrogs, there is evidence here consistent with the fact that bullfrogs failed to capture submerged mealworms. In other words, possibly bullfrogs, like green frogs, sometimes struck forward of the mealworm and therefore failed to capture.

In conclusion, it should be stressed that although the magnitude of image displacement due to light refraction is consistent with the hypothesis that comparatively posterior location of the bullfrog's posterior tongue contact limit had the effect of facilitating the capture of mealworms submerged in shallow water, such consistency should not be construed as proof of this hypothesis. The calculations made concerning the effect of light refraction constitute a test of the foregoing hypothesis. Because the results of the calculations are logically consistent with the hypothesis, and because the hypothesis is otherwise reasonable, it may be regarded, at best, as the best estimate of the truth. In short, it is not necessarily true.

Appendix II

The foregoing research might be followed up with at least two further experiments regarding how the bullfrog feeding strike is specifically adapted for the capture of prey animals submerged in water. These are described here briefly.

1. The most important experiment would be the filming of the strikes of the four frog species as they strike at prey submerged in water, an experiment attempted during the foregoing research. This experiment was unsuccessful for two reasons. First, the intensity of illumination required for adequate illumination of behavior occurring underwater caused most frogs to attempt to escape the apparatus rather than feed. Second, the turbulence set up in the water by the striking frogs caused distortion of the visual image of behavior occurring underwater. The first problem might be solved by the collection of very large numbers of frogs, which might produce sufficient numbers of animals that will feed under high light intensities. The experiment might be limited to very large bullfrogs and green frogs to produce larger images on film which, in turn, might offset the distortion caused by turbulence. Also frogs might be tested at lower body temperatures than was the case in the foregoing experiments; this should slow the feeding strike and so decrease turbulence. This experiment alone can provide direct evidence on what features of the bullfrog strike are responsible for this species' comparative effectiveness in capturing submerged prey.

2. Another (indirect) means of asking what features of the bullfrog feeding strike contribute to the success rate with submerged prey

is to film the strikes of bullfrogs feeding upon terrestrial prey, as mealworms, and then to test the correlations of various topographical features of the strikes of individuals with their success rates at capturing submerged prey. If, for example, bullfrogs with a more posteriorly located posterior tongue contact limit were more successful in capturing submerged prey, this would support the hypothesis that the comparatively posterior location of the posterior tongue contact limit in the bullfrog is an adaptation for the capture of submerged prey. Or, if individual bullfrogs with a tendency to close the jaws nearer the prey succeeded in capturing more submerged prey, the implication would be that the bullfrog's jaw biting action is an adaptation for the capture of submerged prey. Several variants of this design might be conducted. The results of the foregoing experiments lead to the prediction that bullfrogs that close the jaws closer to the prey's original location have a greater capacity for the capture of prey animals in shallow water. Thus, by varying the depth of the water in which prey were submerged, one should be able to generate and eliminate strike success rate differences between bullfrogs differing in the closeness of their jaws to the prey at mouth closure. At some deepest depth, there should be no differences in the frogs' capacity for capture of the submerged prey, since all individuals would be presumably closing the jaws below the water surface. As the water was made shallower, only those bullfrogs still closing the jaws beneath the surface would continue to be relatively effective in capturing the prey. The results of the foregoing research also lead to the prediction that individual bullfrogs that tend to apply tongue surface

more posteriorly would be relatively effective in feeding on prey in deeper water, in which image displacement due to light refraction would be greater. Again by varying the depth, one should be able to generate and eliminate individual differences between the strike success rates of bullfrogs differing in the location relative to the prey of their posterior tongue contact limits.

Since Amherst green frogs also seem to possess a significant capacity for the capture of submerged prey, the above experiments might also be conducted using these. For if a relatively posteriorly located posterior tongue contact limit or a closing of the jaws relatively near the prey's original location facilitates the capture of submerged prey animals, the facilitation should be evident regardless of frog species.

Table 1. Percentage of prey most likely submerged in water at the time of capture, with source of data.

<u>R. catesbeiana</u>	<u>R. clamitans</u>	<u>R. pipiens</u>	<u>R. sylvatica</u>
26.7 (Korschgen and Moyle, 1955)*	5.6 (Jenssen and Klimstra, 1966)*	1.7 (Linzey, 1967)*	0.0 (Surface, 1913)"
14.0 (Korschgen and Baskett, 1963)*	0.0 (Bush, 1959)*	7.0 (Knowlton, 1944)"	13 (Munz, 1920)"
7.5 (Brooks, 1964)'	0.0 (Whitaker, 1961)"	0.0 (Whitaker, 1961)"	
0.0 (Bush, 1959)*	0.3 (Surface, 1913)"	0.6 (Hedeen, 1972)"	
9.8 (Surface, 1913)"	8 (Munz, 1920)"	0.2 (Drake, 1914)"	
25 (Munz, 1920)"	0.8 (Hamilton, 1948)*	1.4 (Surface, 1913)"	
	0.0 (Hamilton, 1948)*	11 (Munz, 1920)"	

*Volume of the submerged prey over that of the total prey times 100.

'Weight of the submerged prey over that of the total prey times 100.

"Number of submerged prey over the total number of prey times 100.

Table 2. Body lengths (snout tip to vent) of frogs that served in Experiment I.

<u>R. catesbeana</u>	<u>R. clamitans</u>	<u>R. pipiens</u>	<u>R. sylvatica</u>
4.6 cm.*	5.4 cm.*	4.7 cm.*	4.5 cm.*
5.8*	5.6*	5.2*	4.7*
6.3*	5.7*	5.4*	4.9*
6.5*	7.8*	5.8*	5.0*
9.7*	8.0*	6.3*	5.4*
10.3*	8.2*	7.3*	5.5*
5.3'	4.7'	5.9'	5.1'
6.2'	5.7'	6.0'	5.3'
6.3'	5.8'	6.0'	5.4'
8.2'	8.0'	6.0'	5.8'
10.9'	8.2'	6.5'	5.9'
11.5'	9.5'	6.8'	6.0'

*Tested with mealworms.

'Tested with beetles.

Table 3. Analysis of variance of prey to jaws distance data at tongue extension in Experiment II.

SV	df	SS	MS	F
species	3	0.014	0.0047	<1.00
prey	1	0.009	0.009	1.19
species x prey	3	0.024	0.0080	1.06
animals/species x prey	40	0.302	0.0076	

Table 4. Analysis of variance of distance from jaws to prey original location at tongue retraction in Experiment I.

SV	df	SS	MS	F
species	3	0.140	0.047	5.88*
prey	1	0.010	0.01	1.25
species x prey	3	0.020	0.007	<1.00
animals/species x prey	40	0.320	0.008	
<u>catesbeiana</u> and <u>sylvatica</u>	1	0.139	0.139	17.38'
<u>catesbeiana</u> and <u>clamitans</u>	1	0.035	0.035	4.38
<u>catesbeiana</u> and <u>pipiens</u>	1	0.016	0.016	2.00
<u>sylvatica</u> and <u>pipiens</u>	1	0.062	0.062	7.75"
<u>sylvatica</u> and <u>clamitans</u>	1	0.034	0.034	4.25
<u>pipiens</u> and <u>clamitans</u>	1	0.004	0.004	<1.00

*p less than 0.005

'p less than 0.001

"p less than 0.01

Table 5. Analysis of variance of distance from jaws to prey original location at mouth closure in Experiment I.

SV	df	SS	MS	F
species	3	0.460	0.153	4.78*
prey	1	0.010	0.010	<1.00
species x prey	3	0.050	0.017	<1.00
animals/species x prey	40	1.270	0.032	
<u>catesbeiana</u> and <u>sylvatica</u>	1	0.417	0.417	13.03'
<u>catesbeiana</u> and <u>clamitans</u>	1	0.225	0.225	7.03"
<u>catesbeiana</u> and <u>pipiens</u>	1	0.083	0.083	2.59
<u>sylvatica</u> and <u>pipiens</u>	1	0.128	0.128	4.00
<u>sylvatica</u> and <u>clamitans</u>	1	0.029	0.029	<1.00
<u>pipiens</u> and <u>clamitans</u>	1	0.035	0.035	1.09

*p less than 0.01

'p less than 0.001

"p less than 0.025

Table 6. Analysis of variance of jaw-line angle at mouth closure in Experiment I.

SV	df	SS	MS	F
species	3	5513.70	1837.90	12.21*
prey	1	0.75	0.75	<1.00
species x prey	3	814.61	271.54	1.80
animals/species x prey	40	6021.69	150.54	
<u>catesbeiana</u> and <u>sylvatica</u>	1	3946.26	3946.26	26.21*
<u>catesbeiana</u> and <u>clamitans</u>	1	3342.94	3342.94	22.21*
<u>catesbeiana</u> and <u>pipiens</u>	1	384.00	384.00	2.55
<u>sylvatica</u> and <u>pipiens</u>	1	1868.26	1868.26	12.41'
<u>sylvatica</u> and <u>calmitans</u>	1	25.01	25.01	<1.00
<u>pipiens</u> and <u>clamitans</u>	1	1460.94	1460.94	9.71'

*p less than 0.001
'p less than 0.005

Table 7. Analysis of variance of distance between prey midpoint and anterior limit of the tongue contact region in Experiment I.

SV	df	SS	MS	F
species	3	0.010	0.003	< 1.00
prey	1	0.027	0.027	3.91
species x prey	3	0.011	0.004	< 1.00
animals/species prey	40	0.275	0.007	

Table 8. Analysis of variance of distance between prey midpoint and the posterior limit of the tongue contact region in Experiment I.

SV	df	SS	MS	F
species	3	0.116	0.039	4.33*
prey	1	0.024	0.024	2.67
species x prey	3	0.030	0.010	1.11
animals/species x prey	40	0.355	0.009	
<u>catesbeiana</u> and <u>sylvatica</u>	1	0.086	0.086	9.50'
<u>catesbeiana</u> and <u>clamitans</u>	1	0.078	0.078	8.61*
<u>catesbeiana</u> and <u>pipiens</u>	1	0.068	0.068	7.56*
<u>sylvatica</u> and <u>pipiens</u>	1	0.001	0.001	<1.00
<u>sylvatica</u> and <u>clamitans</u>	1	0.000	0.000	< 1.00
<u>pipiens</u> and <u>clamitans</u>	1	0.001	0.001	< 1.00

*p less than 0.01
'p less than 0.005

Table 9. Body lengths (snout tip to vent) of frogs that served in Experiment II.

<u>R. catesbeiana</u>	<u>R. clamitans</u>	<u>R. pipiens</u>	<u>R. sylvatica</u>
5.0 cm.	5.1 cm.	5.6 cm.	5.1 cm.
5.2	5.5	5.7	5.2
5.2	5.7	5.7	5.3
5.8	5.8	5.9	5.7
6.1	6.0	6.0	5.8
6.4	6.1	6.6	6.0

Table 10. Number of successful strikes at submerged mealworms divided by the number of successful strikes at dry mealworms; individual data.

<u>R. catesbeiana</u>	<u>R. clamitans</u>	<u>R. pipiens</u>	<u>R. sylvatica</u>
.80	.10	.00	.00
.10	.33	.00	.00
.89	.14	.00	.00
.10	.50	.33	.00
.50	.00	.00	.00
.50	.14	.00	.00

Table 11. Number of successful strikes at dry mealworms divided by the number of dry mealworm presentations (10).

<u>R. catesbeiana</u>	<u>R. clamitans</u>	<u>R. pipiens</u>	<u>R. sylvatica</u>
1.0	1.0	0.8	1.0
1.0	0.9	1.0	1.0
0.9	0.7	1.0	0.9
1.0	0.8	1.0	1.0
0.8	1.0	1.0	1.0
0.8	0.7	0.8	1.0

Table 12. Analysis of variance of data of Table 10.

SV	df	SS	MS	F
species	3	0.855	0.285	35.63*
animals/species	20	0.160	0.008	
<u>catesbeiana</u> and <u>clamitans</u>	1	0.244	0.244	30.50*
<u>catesbeiana</u> and <u>pipiens</u>	1	0.559	0.559	69.88*
<u>catesbeiana</u> and <u>sylvatica</u>	1	0.711	0.711	88.88*
<u>sylvatica</u> and <u>pipiens</u>	1	0.009	0.009	1.13
<u>sylvatica</u> and <u>clamitans</u>	1	0.122	0.122	15.25*
<u>clamitans</u> and <u>pipiens</u>	1	0.065	0.065	8.13'

*p less than 0.001
'p less than 0.01

Table 13. Analysis of variance of data of Table 11.

SV	df	SS	MS	F
species	3	0.0550	0.0183	1.83
animals/species	20	0.200	0.010	

Table 14. Body lengths of frogs that served in Experiment III.

<u>R. catesbeiana</u>	<u>R. clamitans</u>	<u>R. pipiens</u>	<u>R. sylvatica</u>
4.6 cm.	4.4 cm.	4.3 cm.	4.5 cm.
6.2	4.8	6.0	4.6
6.3	5.5	6.3	5.4
8.2	5.7	6.5	5.5
9.9	7.8	7.3	5.9
10.5	8.2	7.9	6.0

Table 15. Analysis of variance of prey to jaws distance data of
R. clamitans in Experiment III.

SV	df	SS	MS	F
strike	3	0.269	0.0897	3.78*
point in the strike	2	0.187	0.0935	
animals	5	0.303		
strike x point	6	0.0770	0.0128	1.68
strike x animals	15	0.356		
point x animals	10	0.128		
strike x point x animals	30	0.228	0.0076	

*p less than 0.05

Table 16. Analysis of variance of jaw-line angle with the horizon at mouth closure of R. clamitans in Experiment III.

SV	df	SS	MS	F
animals	5	3643.37		
strike	3	3152.04	1050.68	6.80*
strike x animals	15	2316.21	154.41	

*p less than 0.005

Table 17. Analysis of variance of prey to jaws distance data of R.
pipiens in Experiment III.

SV	df	SS	MS	F
strike	3	0.285	0.0950	9.41*
point in the strike	2	0.0940	0.0470	
animals	5	0.339		
strike x point	6	0.0450	0.0075	2.29
strike x animals	15	0.152	0.0101	
point x animals	10	0.0430		
strike x point x animals	30	0.0980	0.00327	

*p less than 0.001

Table 18. Analysis of variance of jaw-line angle with the horizontal at mouth closure of R. pipiens in Experiment III.

SV	df	SS	MS	F
animals	5	916.96		
strike	3	2157.00	719.00	11.32*
strike x animals	15	952.37	63.49	

*p less than 0.001

Table 19. Analysis of variance of prey to jaws distance data of R. sylvatica in Experiment III.

SV	df	SS	MS	F
strike	3	0.423	0.141	6.98*
point in the strike	2	0.224	0.112	
animals	5	0.457		
strike x point	6	0.860	0.0143	1.63
strike x animals	15	0.303	0.0202	
point x animals	10	0.159		
strike x point x animals	30	0.264	0.0088	

*p less than 0.005

Table 20. Analysis of variance of jaw-line angle with the horizontal at mouth closure of R. sylvatica in Experiment III.

SV	df	SS	MS	F
animals	5	1723.75		
strike	3	1584.37	528.12	9.50*
strike x animals	15	833.50	55.57	

*p less than 0.001

Table 21. Analysis of variance of prey to jaws distance data of
R. catesbeiana in Experiment III.

SV	df	SS	MS	F
strike	3	0.346	0.115	6.15*
point in the strike	2	0.0140	0.0070	
animals	5	0.310		
strike x point	6	0.0280	0.00467	1.31
strike x animals	15	0.281	0.0187	
point x animals	10	0.054		
strike x point x animals	30	0.107	0.00357	

*p less than 0.01

Table 22. Analysis of variance of jaw-line angle with the horizontal at mouth closure of R. catesbeiana in Experiment III.

SV	df	SS	MS	F
animals	5	1126.85		
strike	3	1478.29	492.76	9.86*
strike x animals	15	750.02	50.00	

*p less than 0.001

Table 23. Analysis of variance of distance from mealworm midpoint to the anterior tongue contact limit in R. clamitans in Experiment III.

SV	df	SS	MS	F
animals	5	0.0600		
strike	3	0.00890	0.00297	<1.00
strike x animals	15	0.0918	0.00612	

Table 24. Analysis of variance of distance from mealworm midpoint to the anterior tongue contact limit in R. sylvatica in Experiment III.

SV	df	SS	MS	F
animals	5	0.125		
strike	3	0.0120	0.00400	1.28
strike x animals	15	0.0470	0.00313	

Table 25. Analysis of variance of distance from mealworm midpoint to the anterior tongue contact limit in R. catesbeiana in Experiment III.

SV	df	SS	MS	F
animals	5	0.0918		
strike	3	0.0537	0.0179	2.58
strike x animals	15	0.105	0.0070	

Table 26. Analysis of variance of distance from mealworm midpoint to the anterior tongue contact limit in R. pipiens in Experiment III.

SV	df	SS	MS	F
animals	5	0.0793		
strike	3	0.0267	0.0089	4.94*
strike x animals	15	0.0270	0.0018	

Table 27. Analysis of variance of distance from mealworm midpoint to the posterior tongue contact limit in R. pipiens in Experiment III.

SV	df	SS	MS	F
animals	5	0.0740		
strike	3	0.00250	0.000833	<1.00
strike x animals	15	0.0815	0.00543	

Table 28. Analysis of variance of distance from mealworm midpoint to the posterior tongue contact limit of R. sylvatica in Experiment III.

SV	df	SS	MS	F
animals	5	0.0590		
strike	3	0.0110	0.00367	< 1.00
strike x animals	15	0.0750	0.00500	

Table 29. Analysis of variance of distance from mealworm midpoint to the posterior tongue contact limit in R. catesbeiana in Experiment III.

SV	df	SS	MS	F
animals	5	0.2321		
strike	3	0.0294	0.00980	1.17
strike x animals	15	0.1256	0.00837	

Table 30. Analysis of variance of distance from mealworm midpoint to the posterior tongue contact limit in R. clamitans in Experiment III.

SV	df	SS	MS	F
animals	5	0.0303		
strike	3	0.0443	0.01480	3.58*
strike x animals	15	0.0624	0.00416	

*p less than 0.05

Figure 1

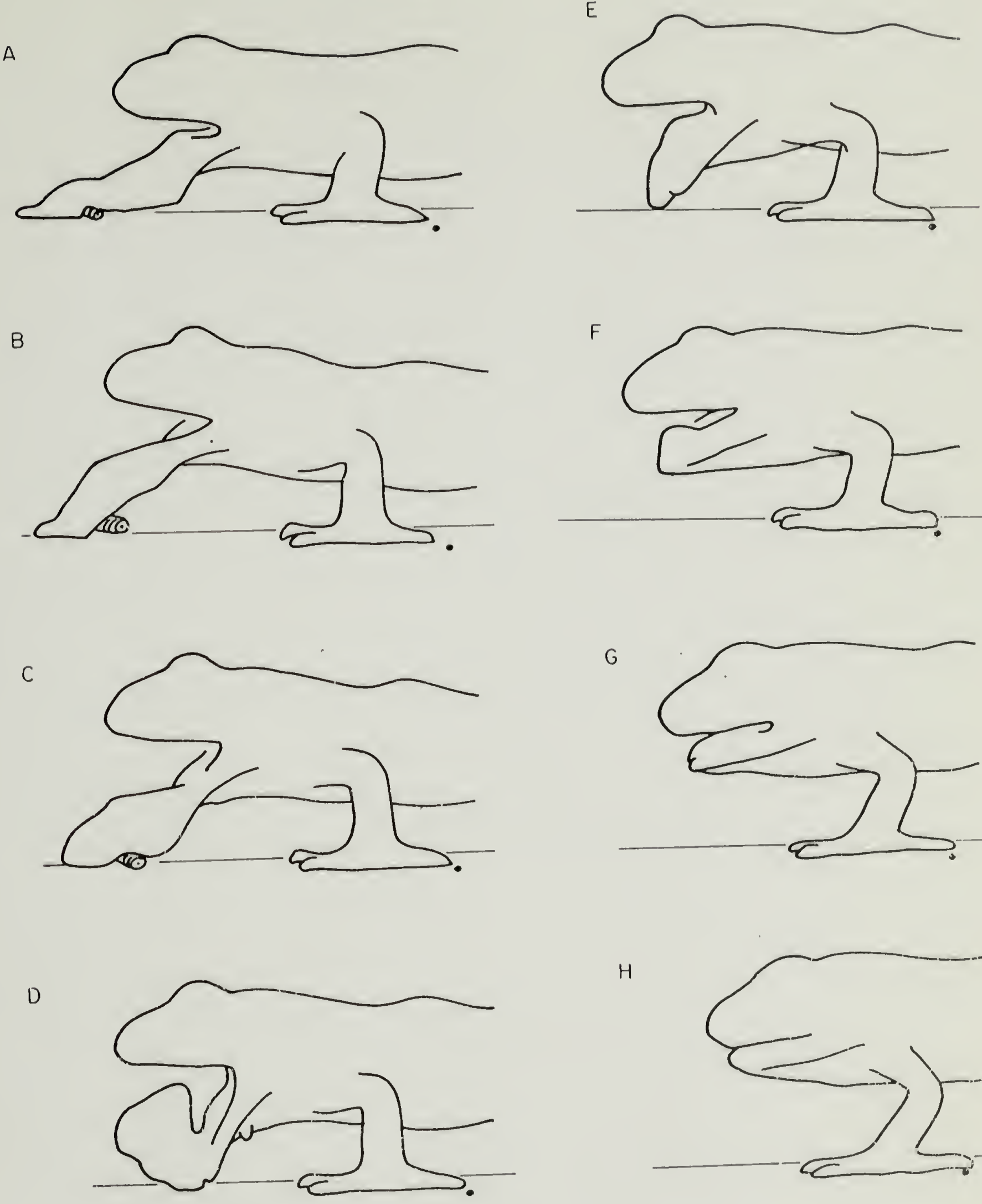


Figure 2

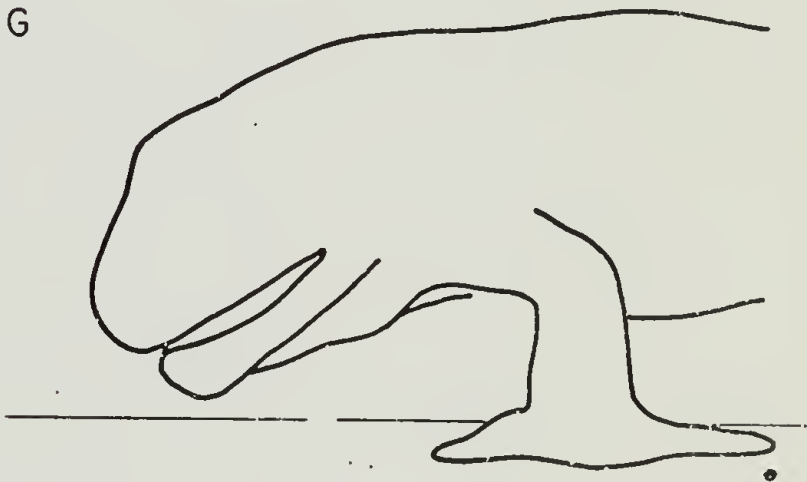
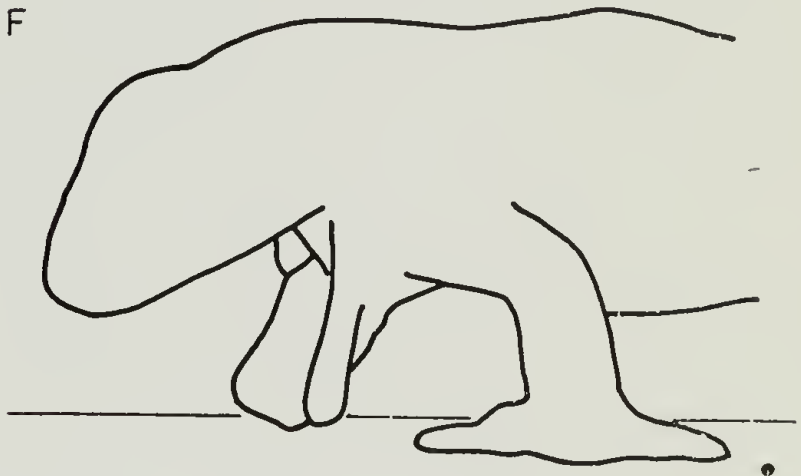
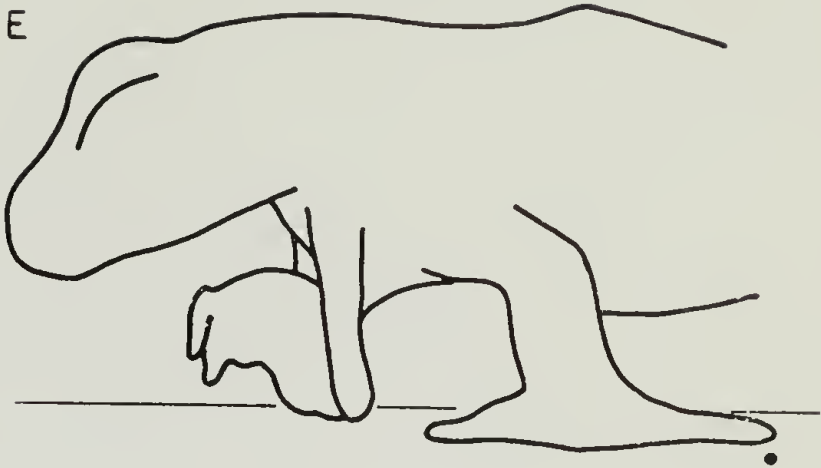
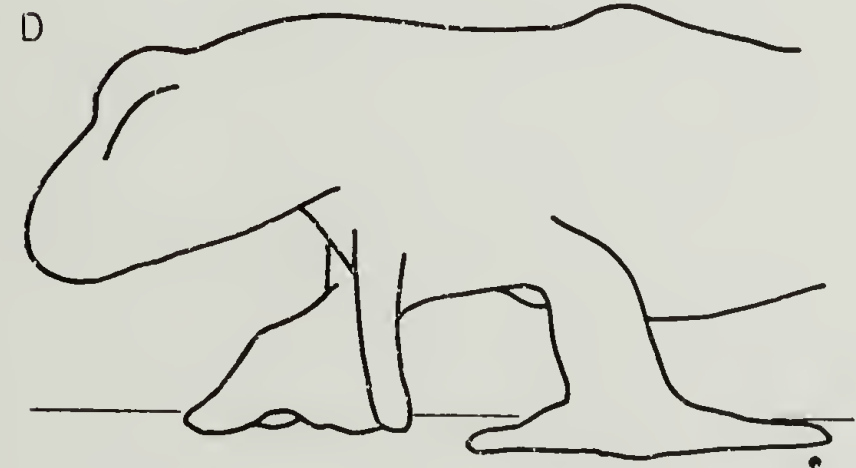
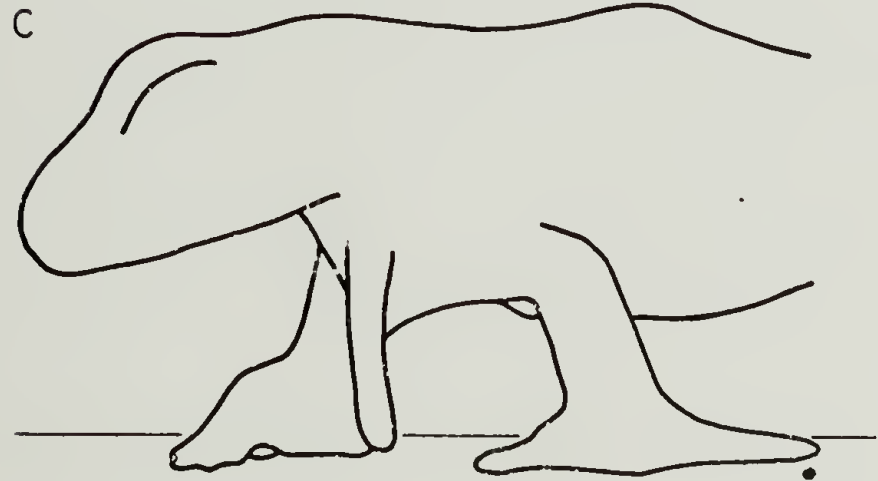
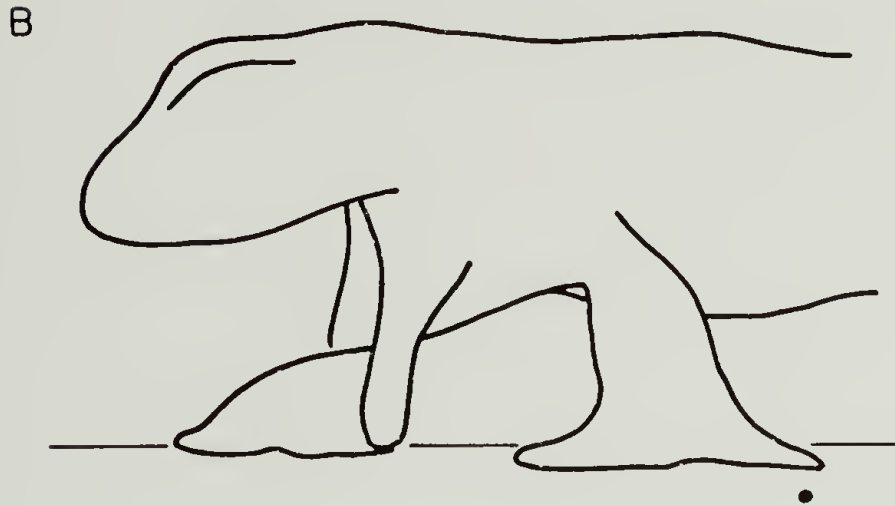


Figure 3

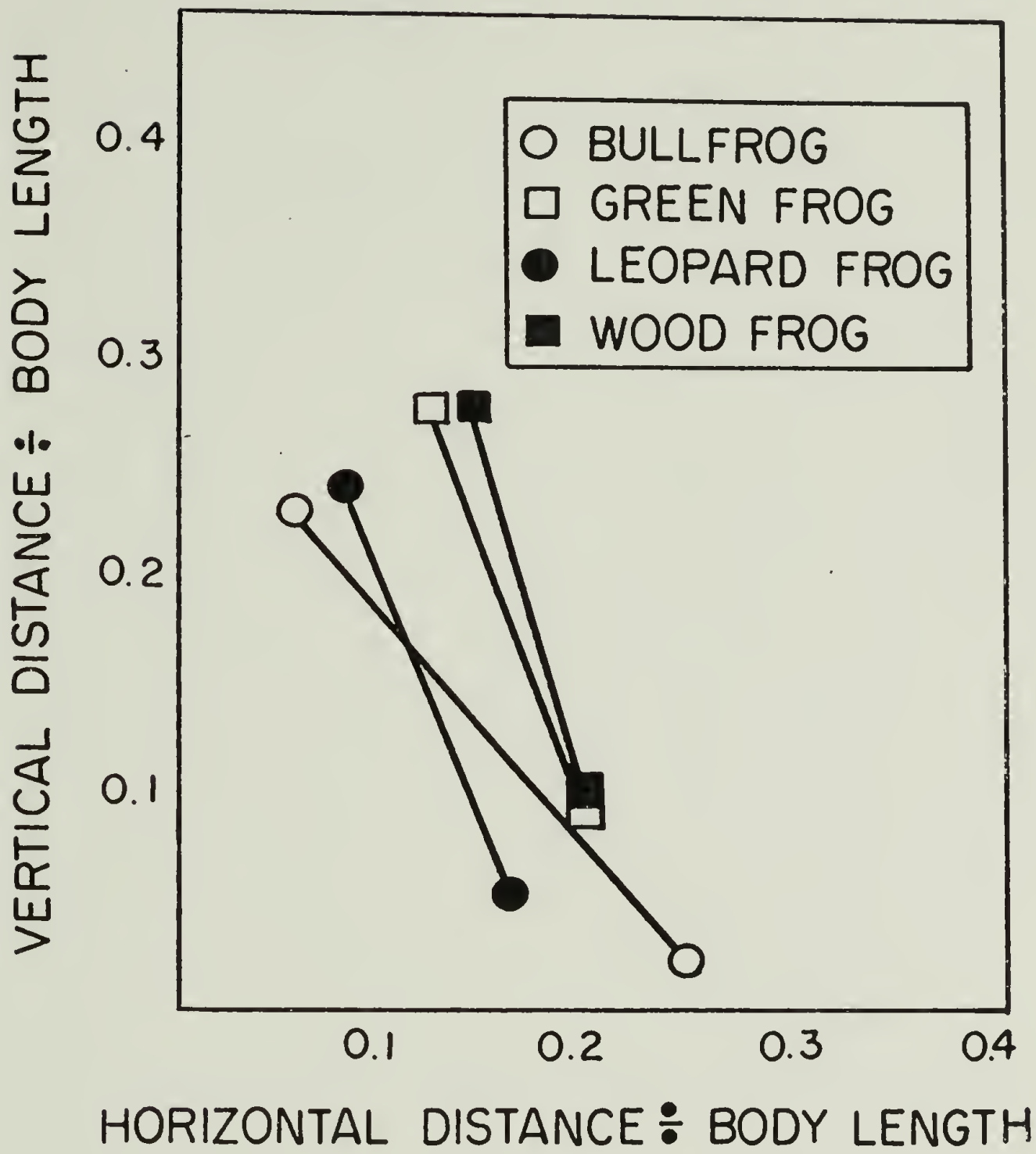


Figure 4

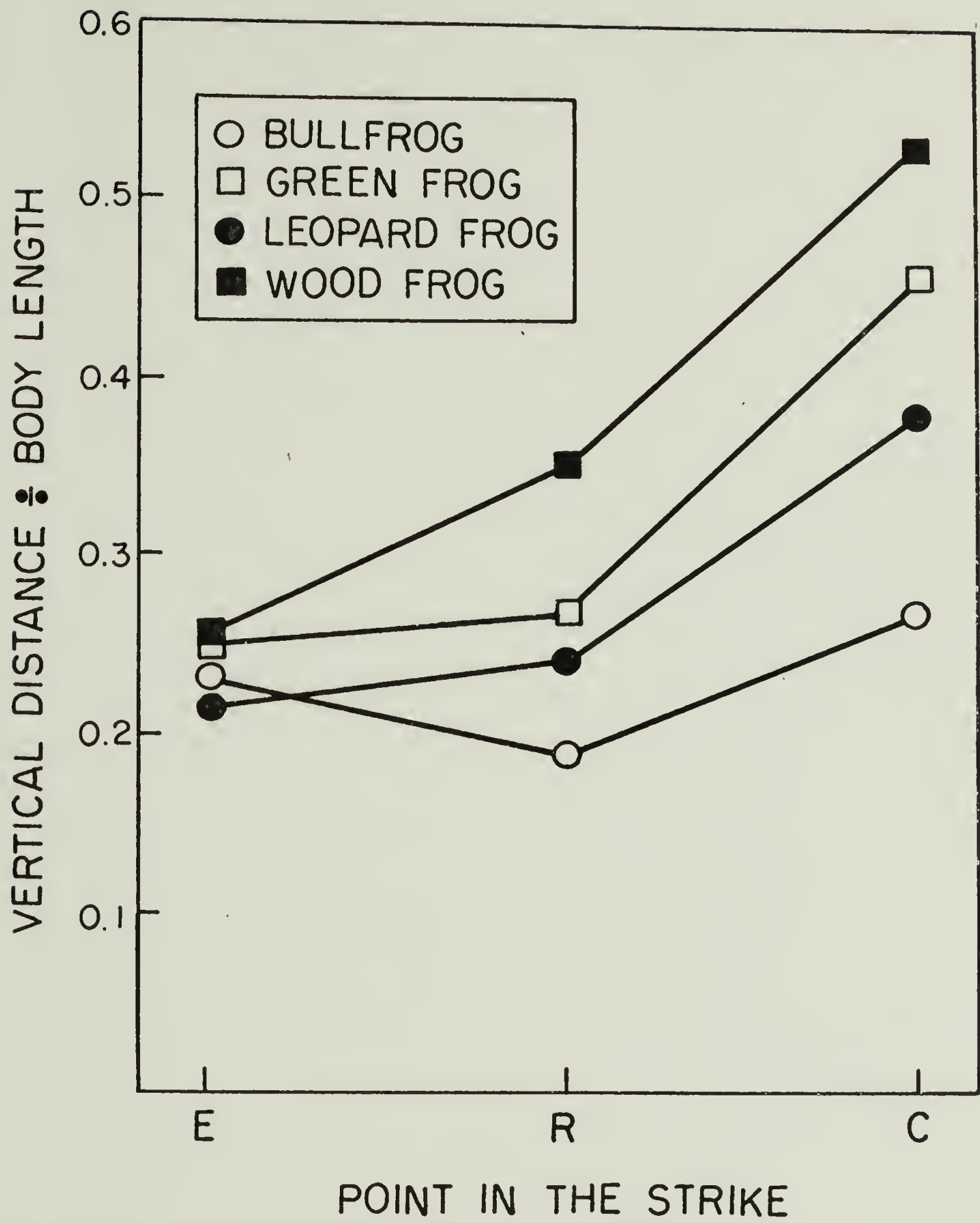


Figure 5

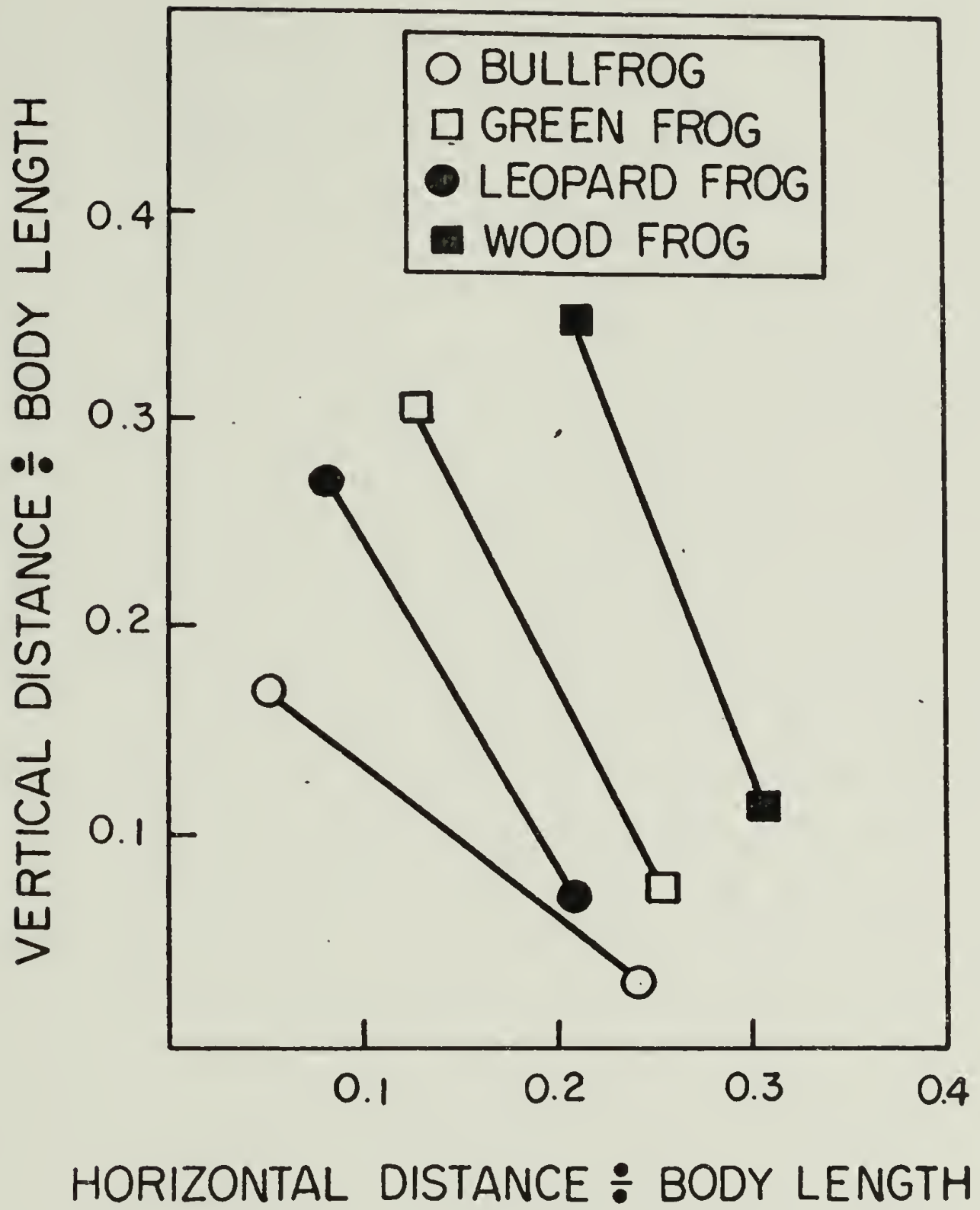


Figure 6

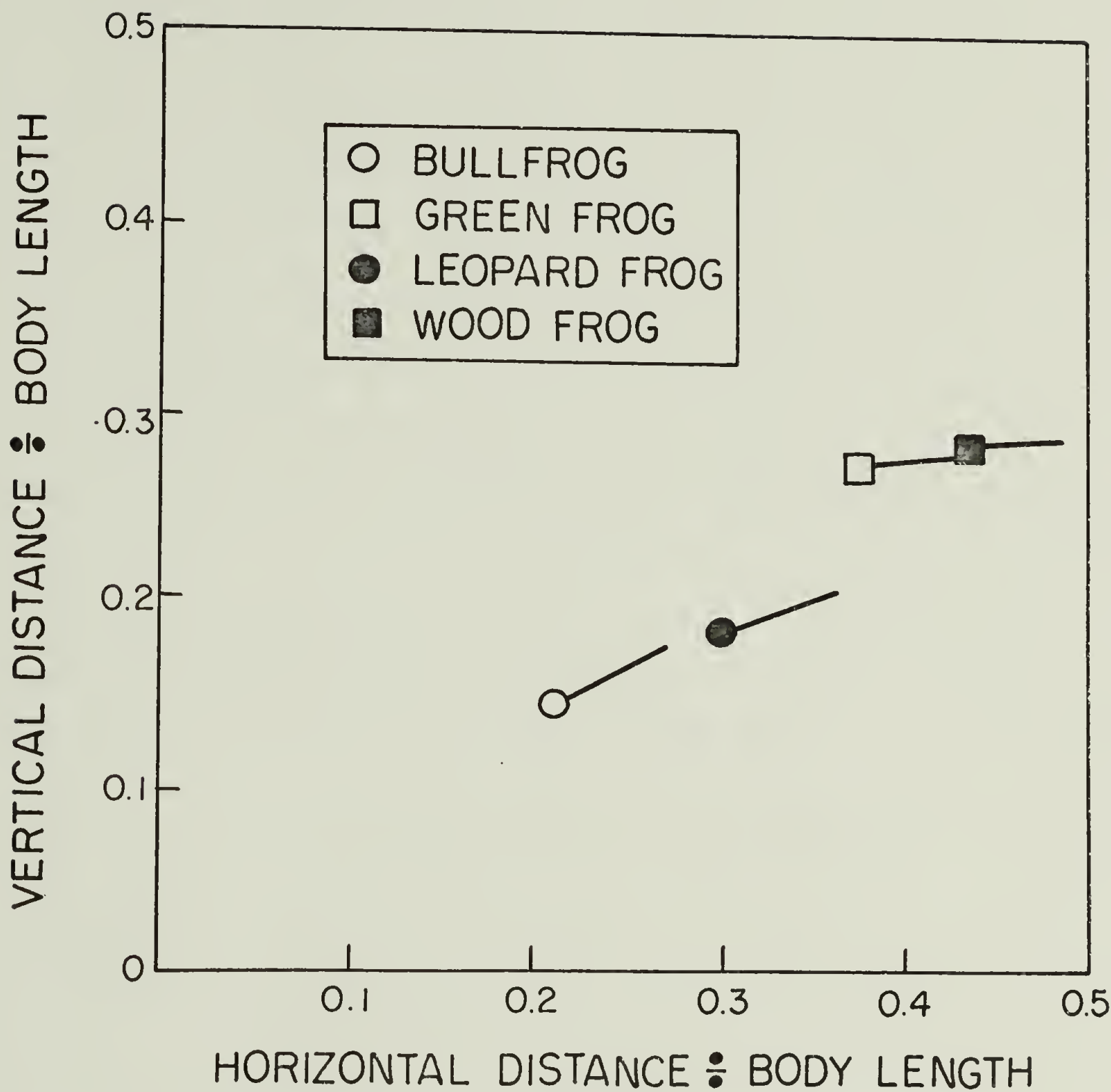


Figure 7

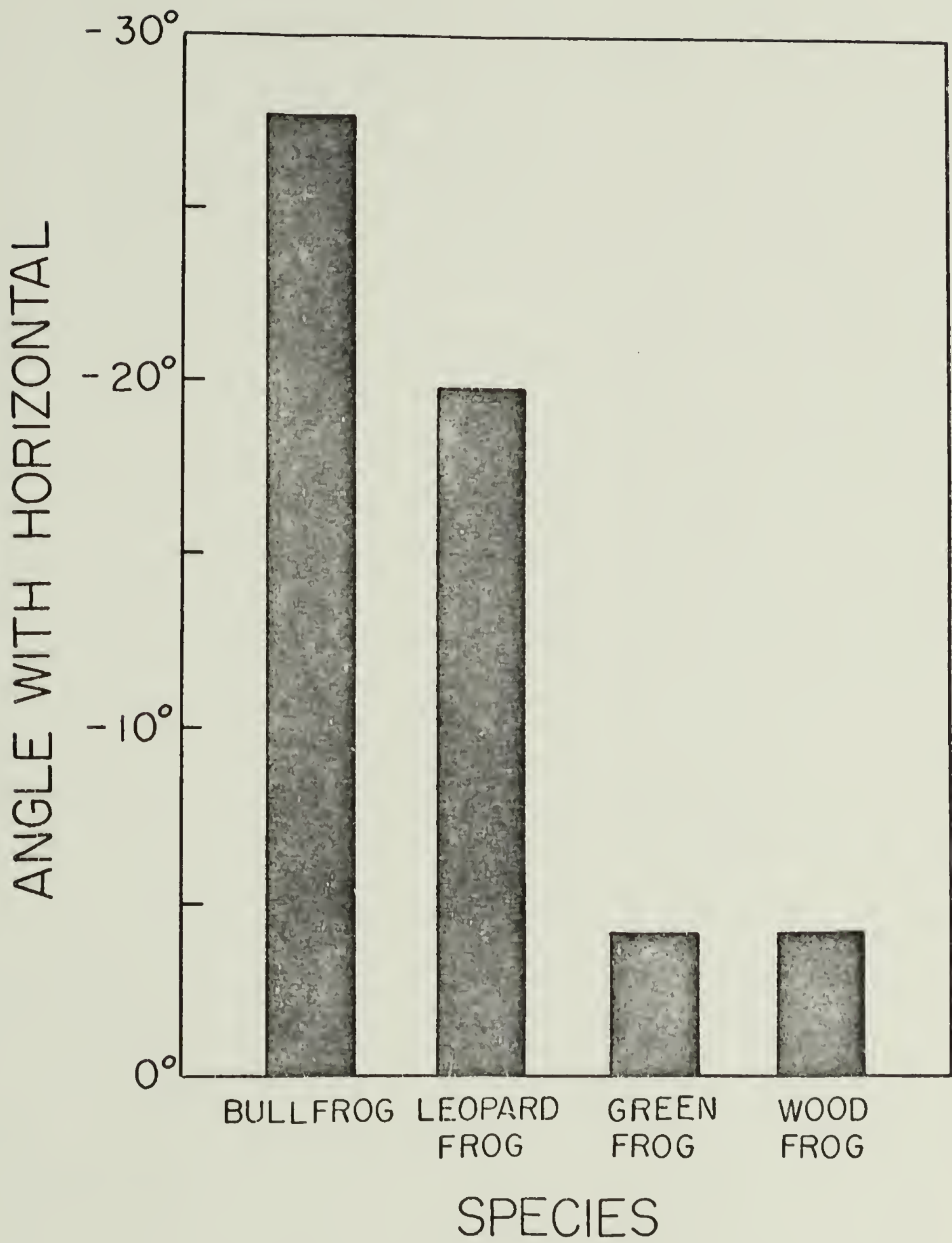


Figure 8

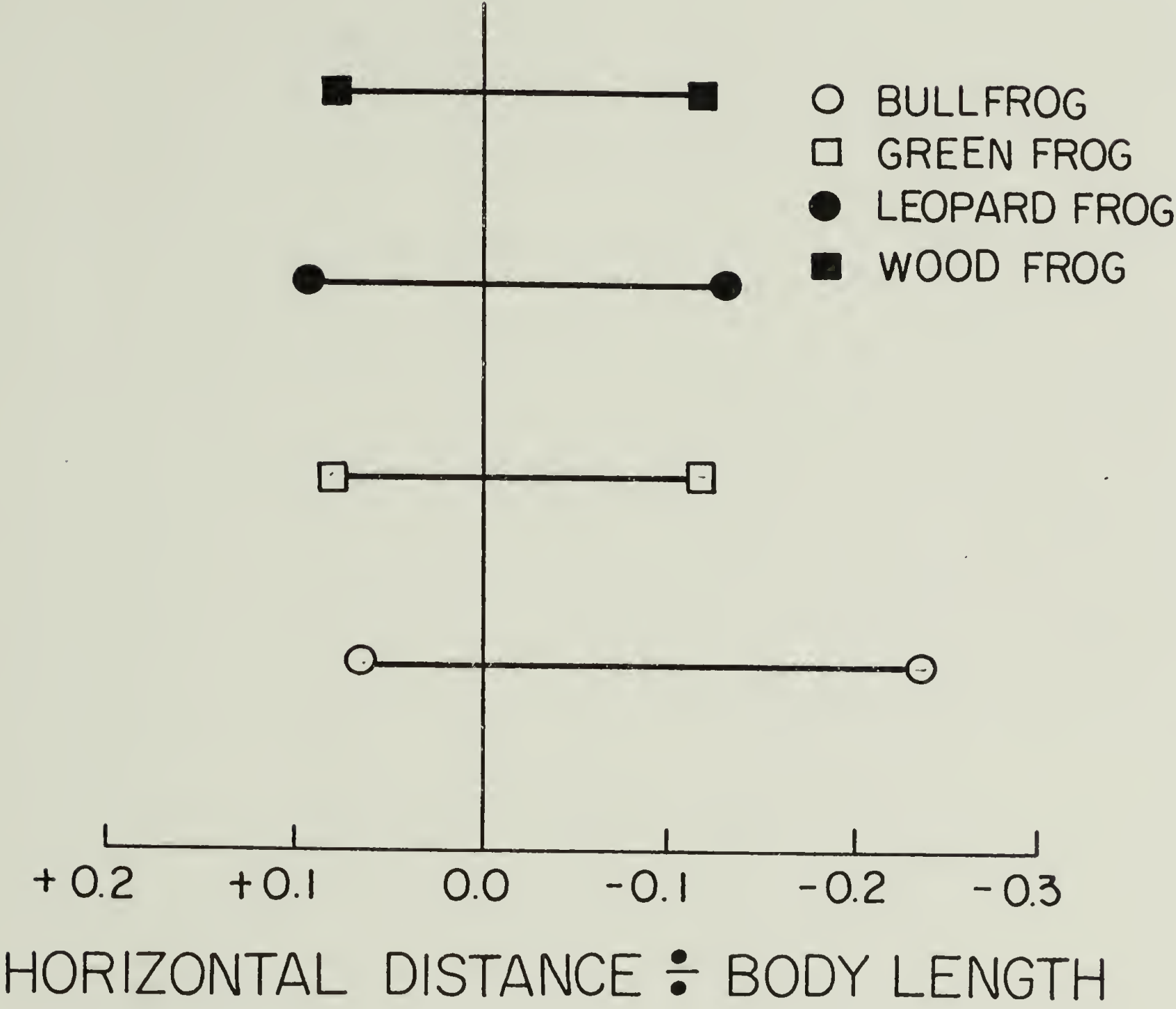


Figure 9

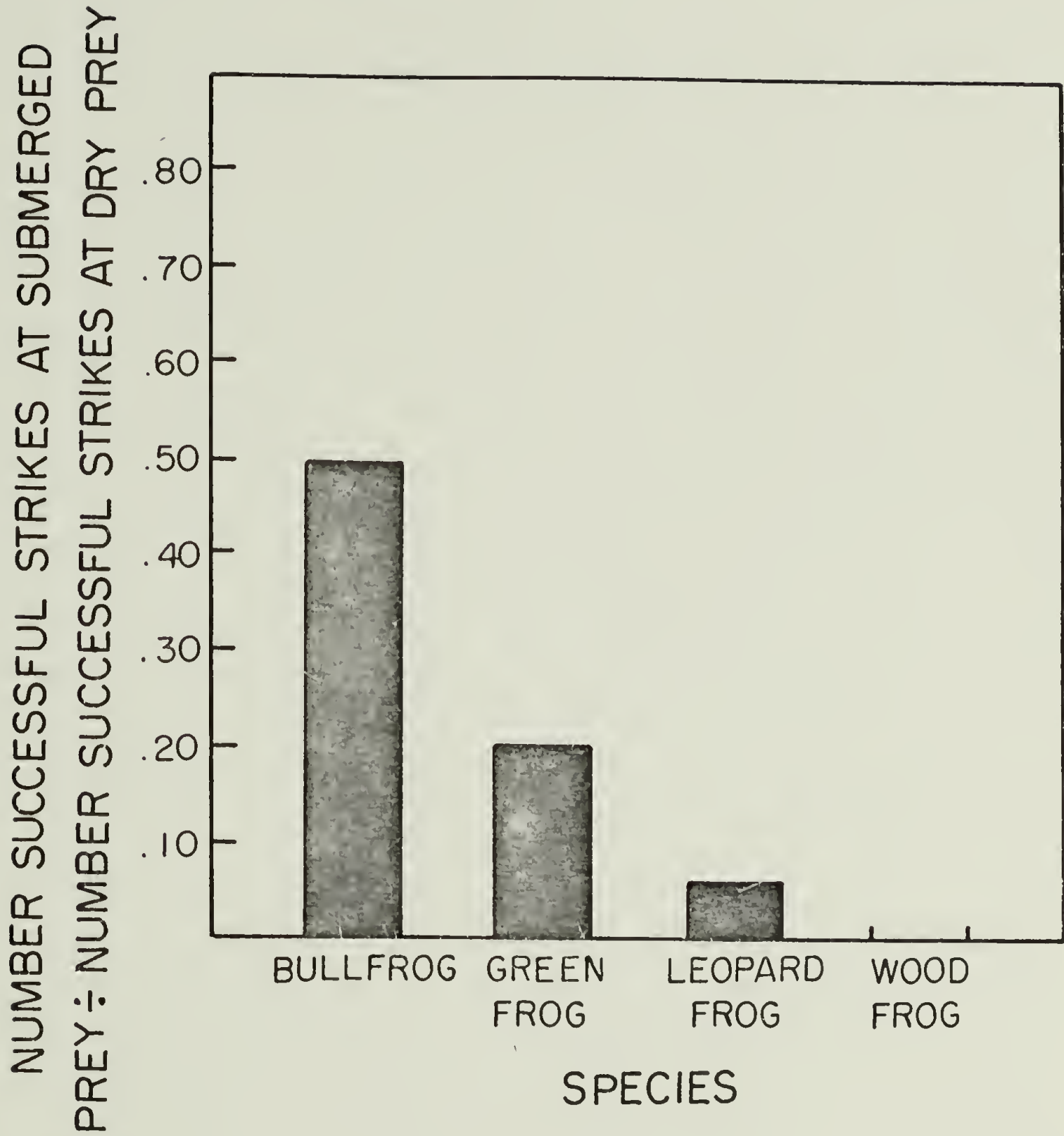


Figure 10

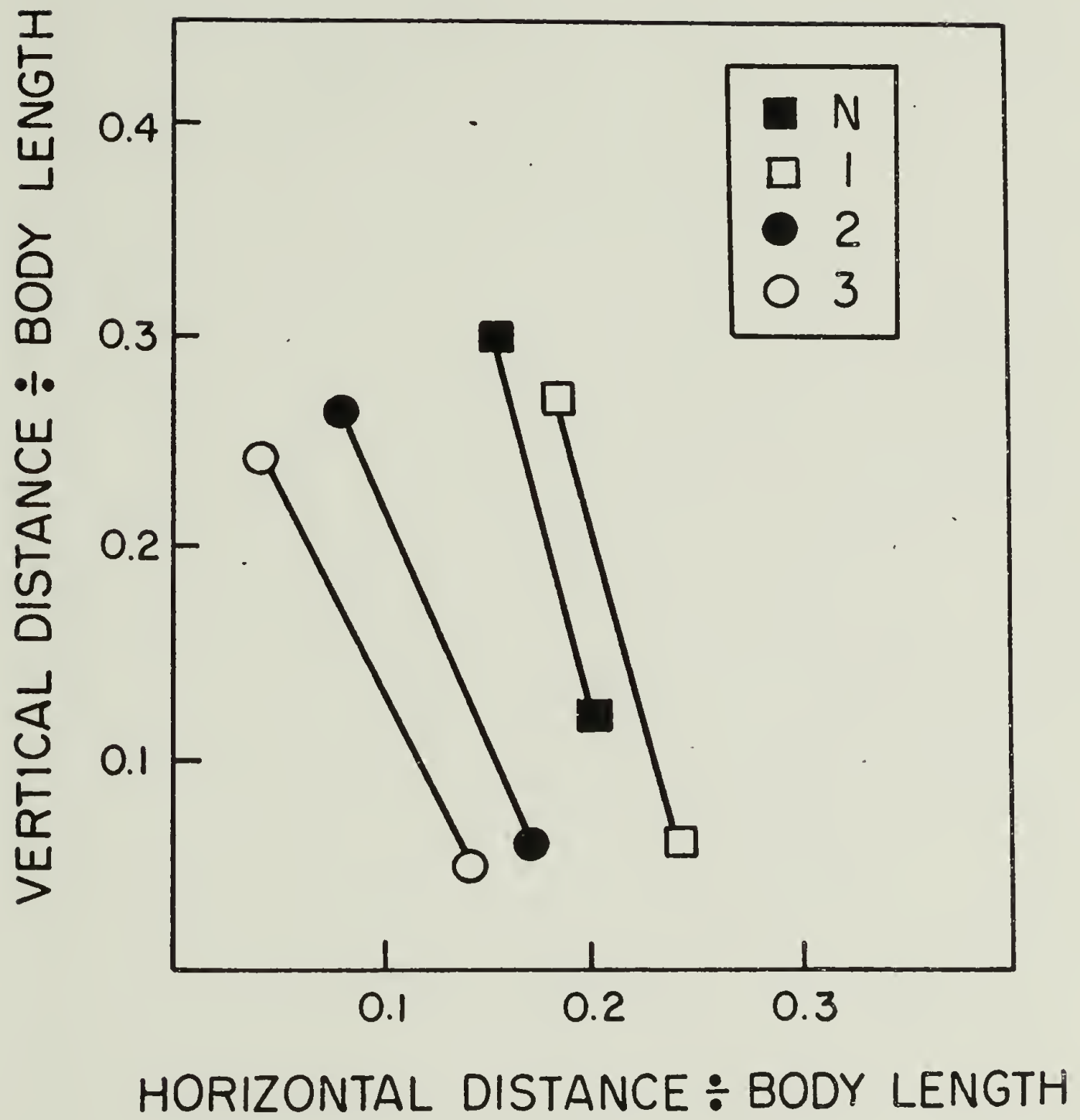


Figure 11

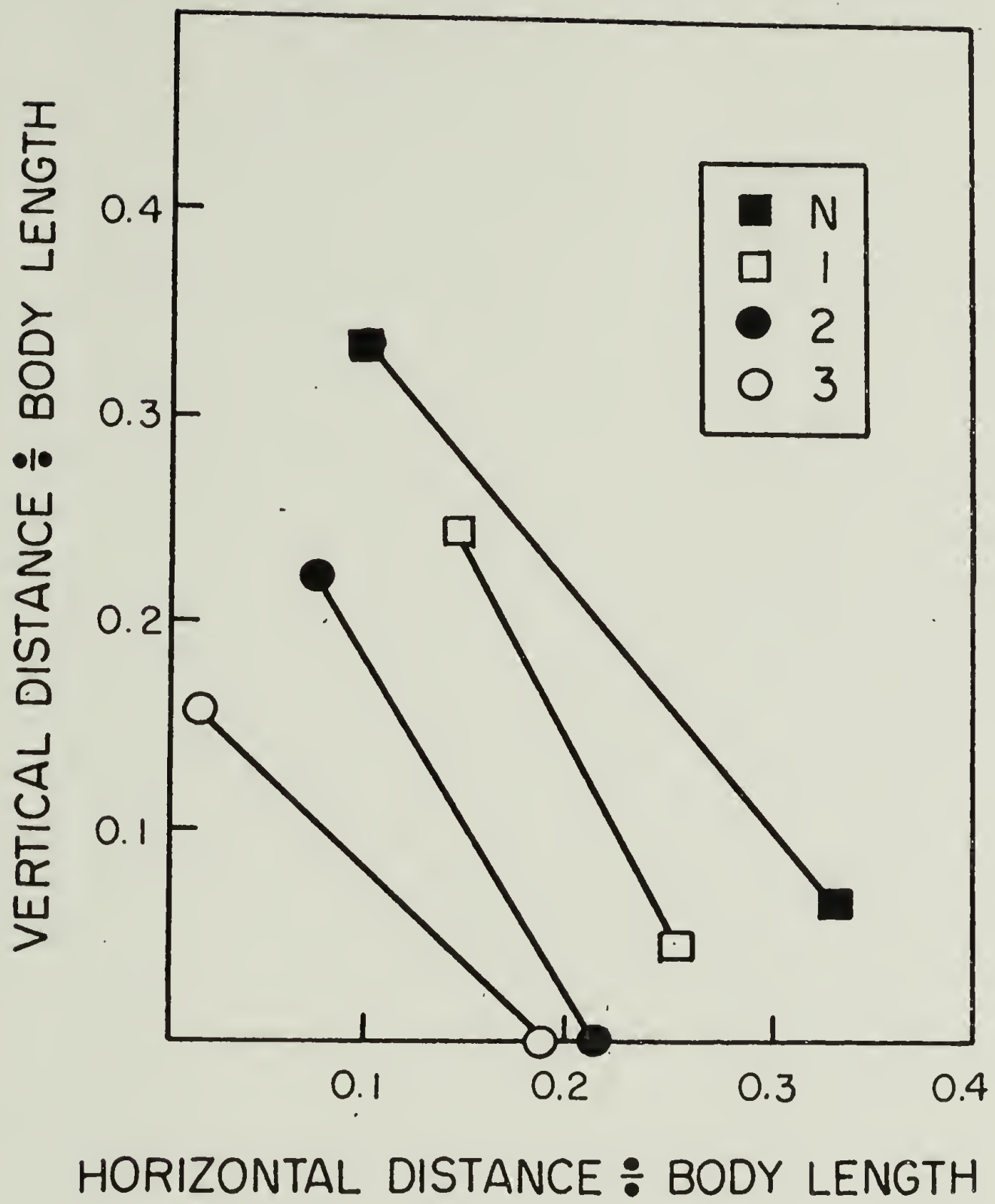


Figure 12

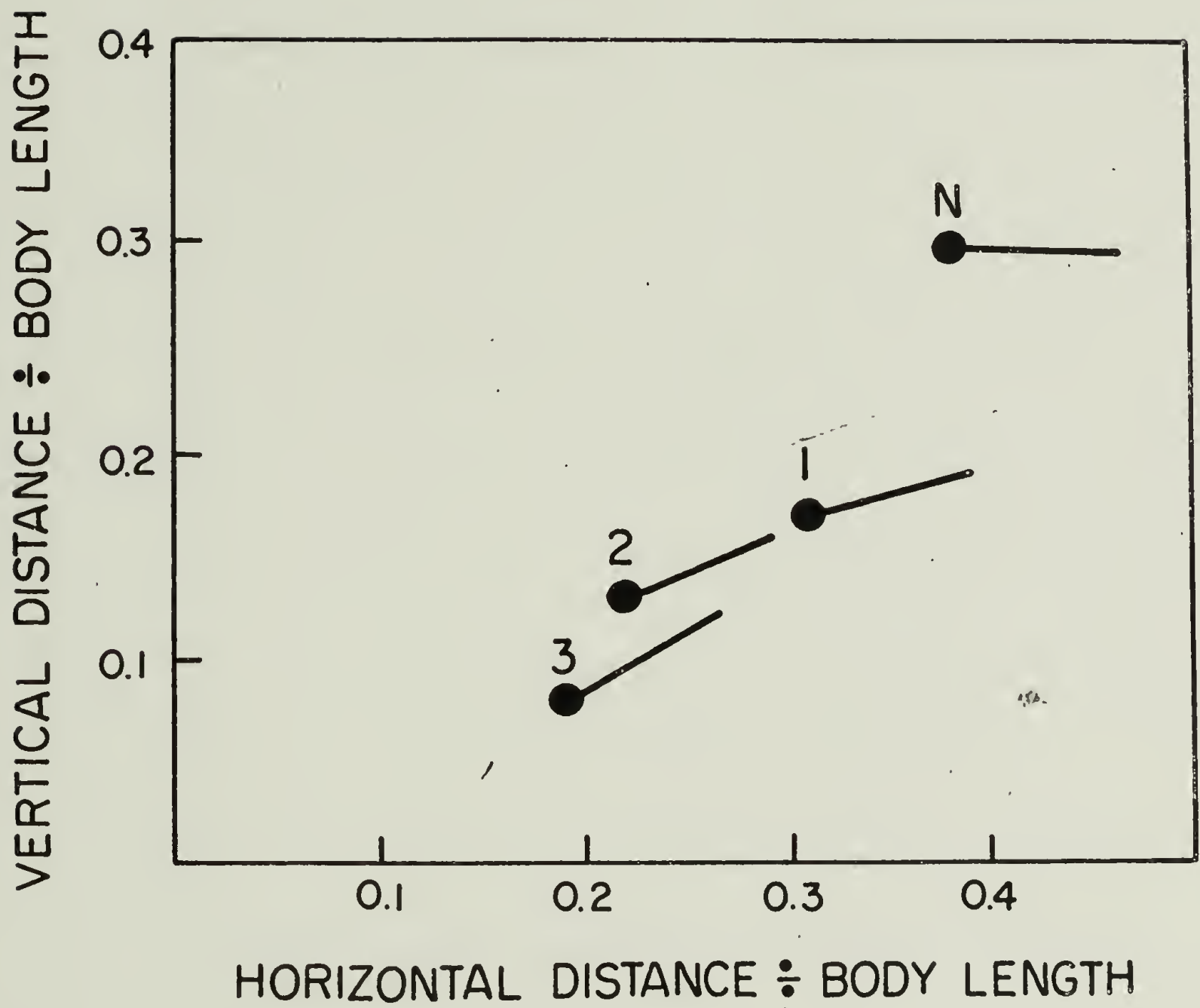


Figure 13

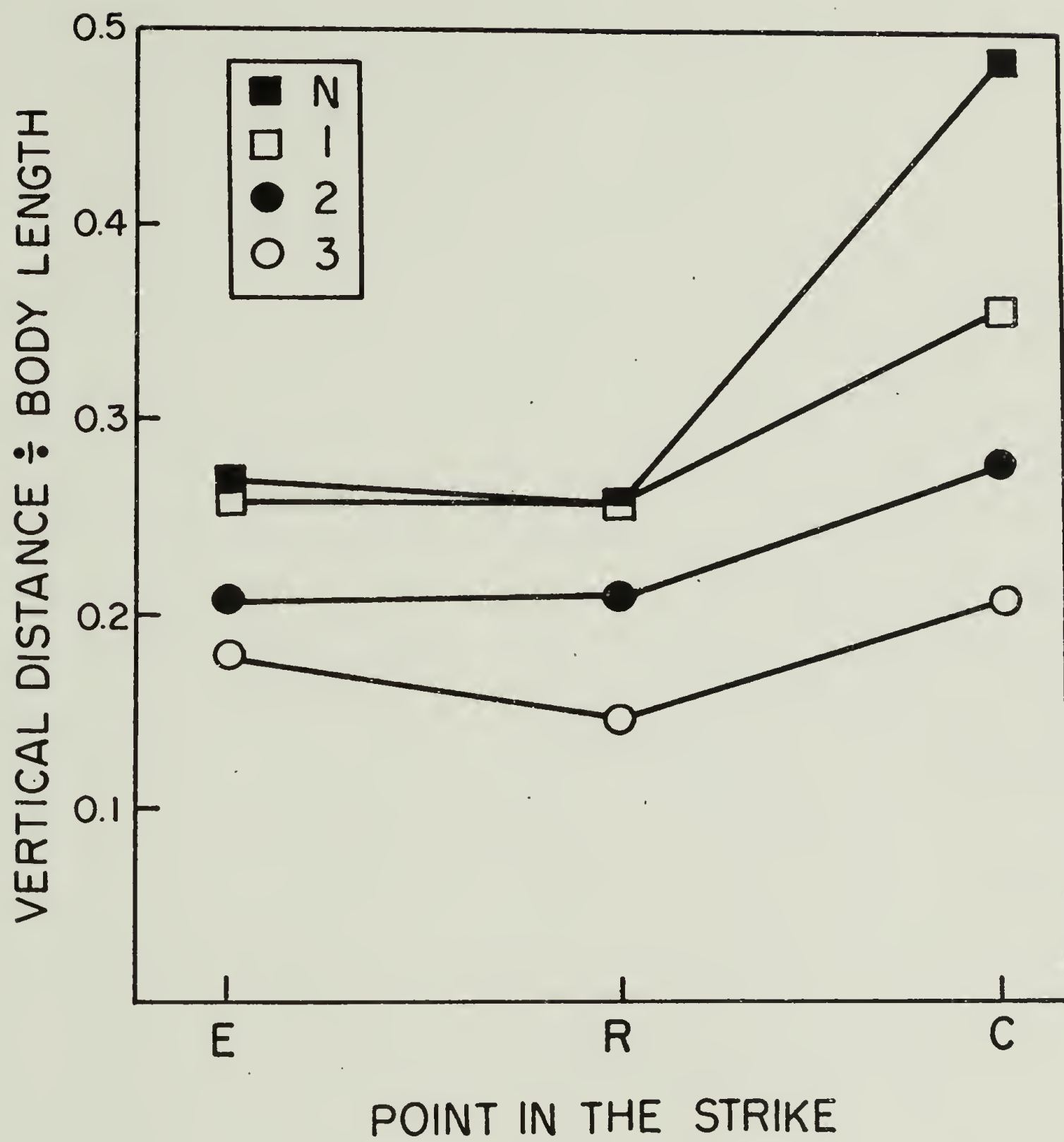


Figure 14

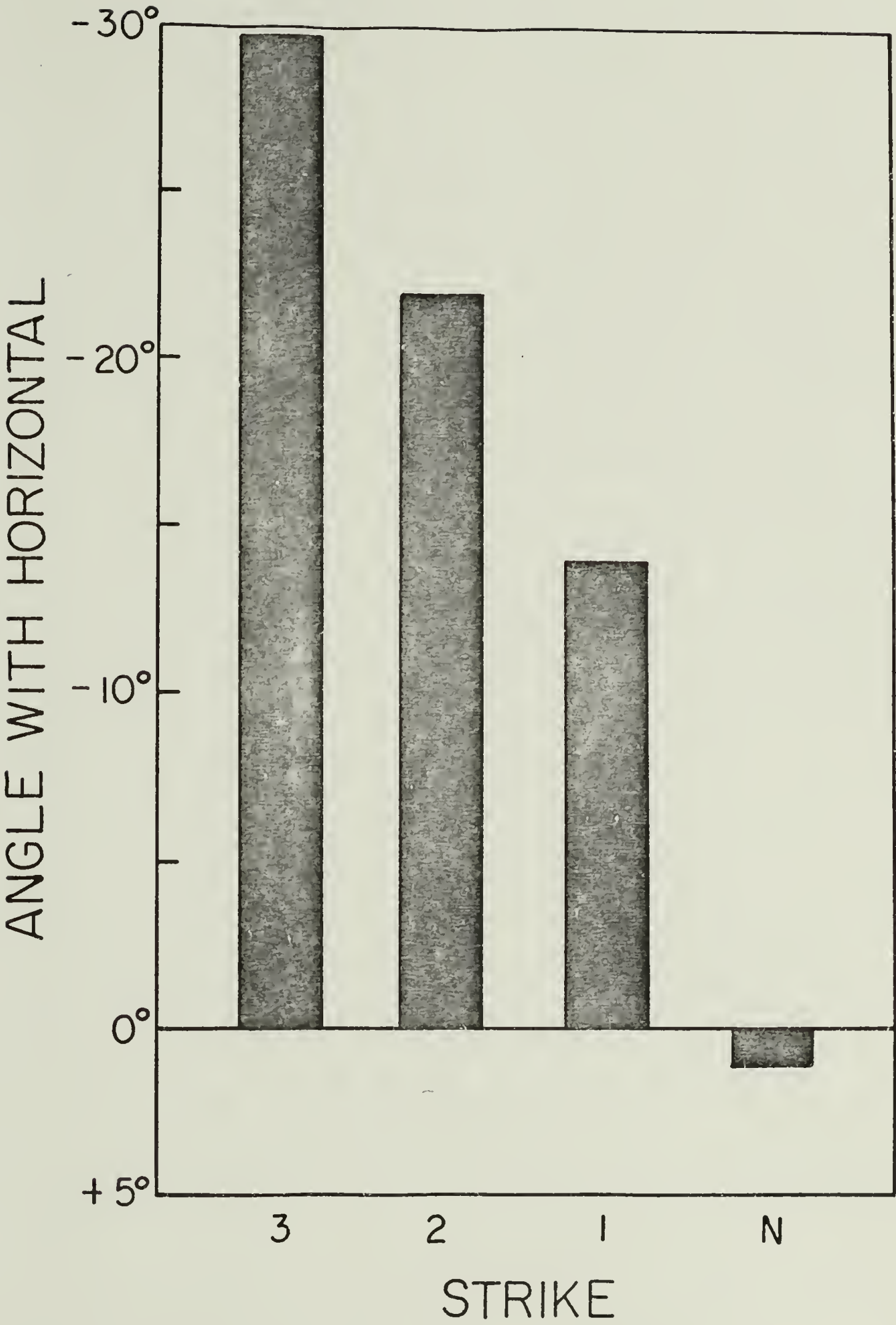


Figure 15

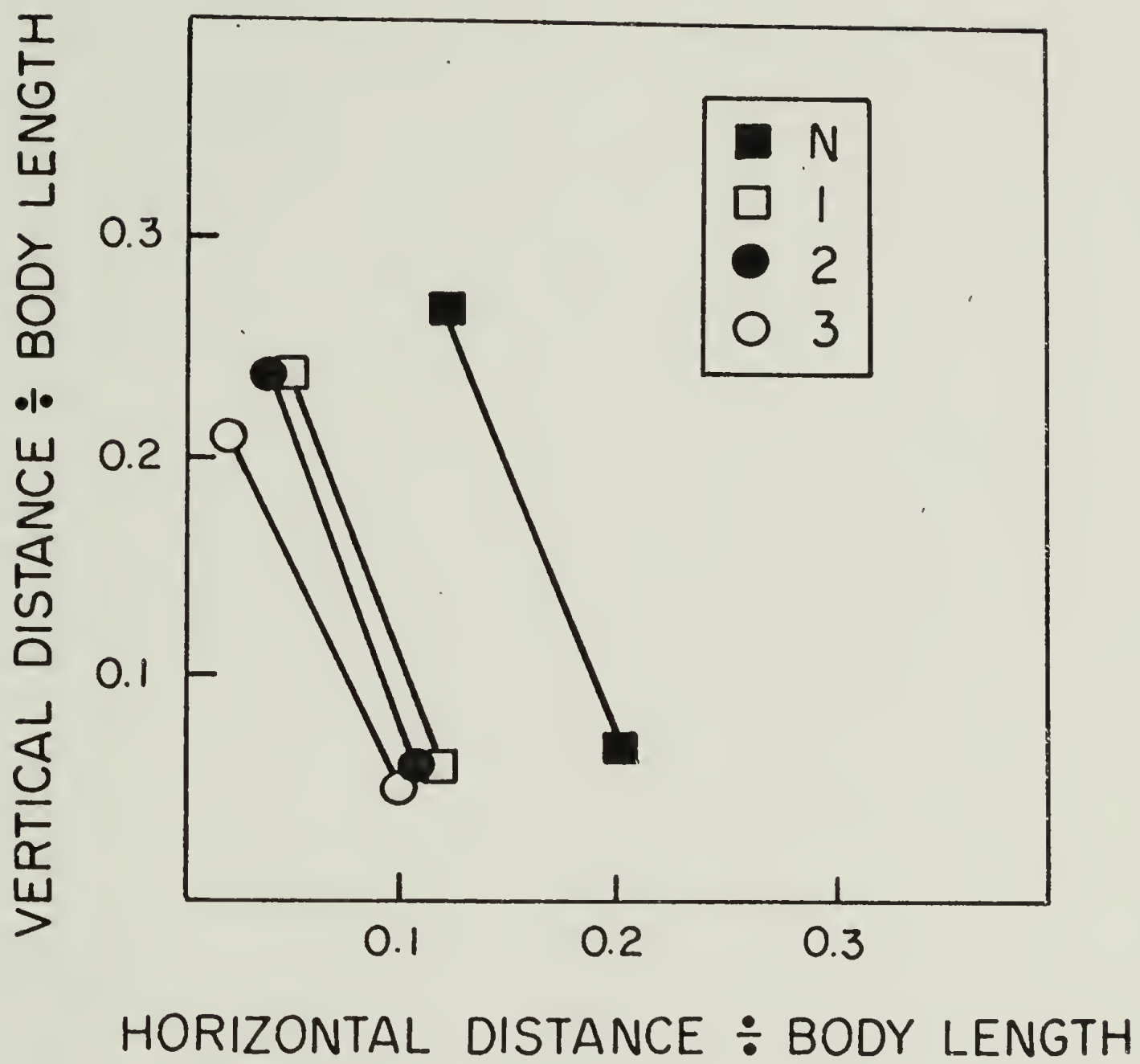


Figure 16

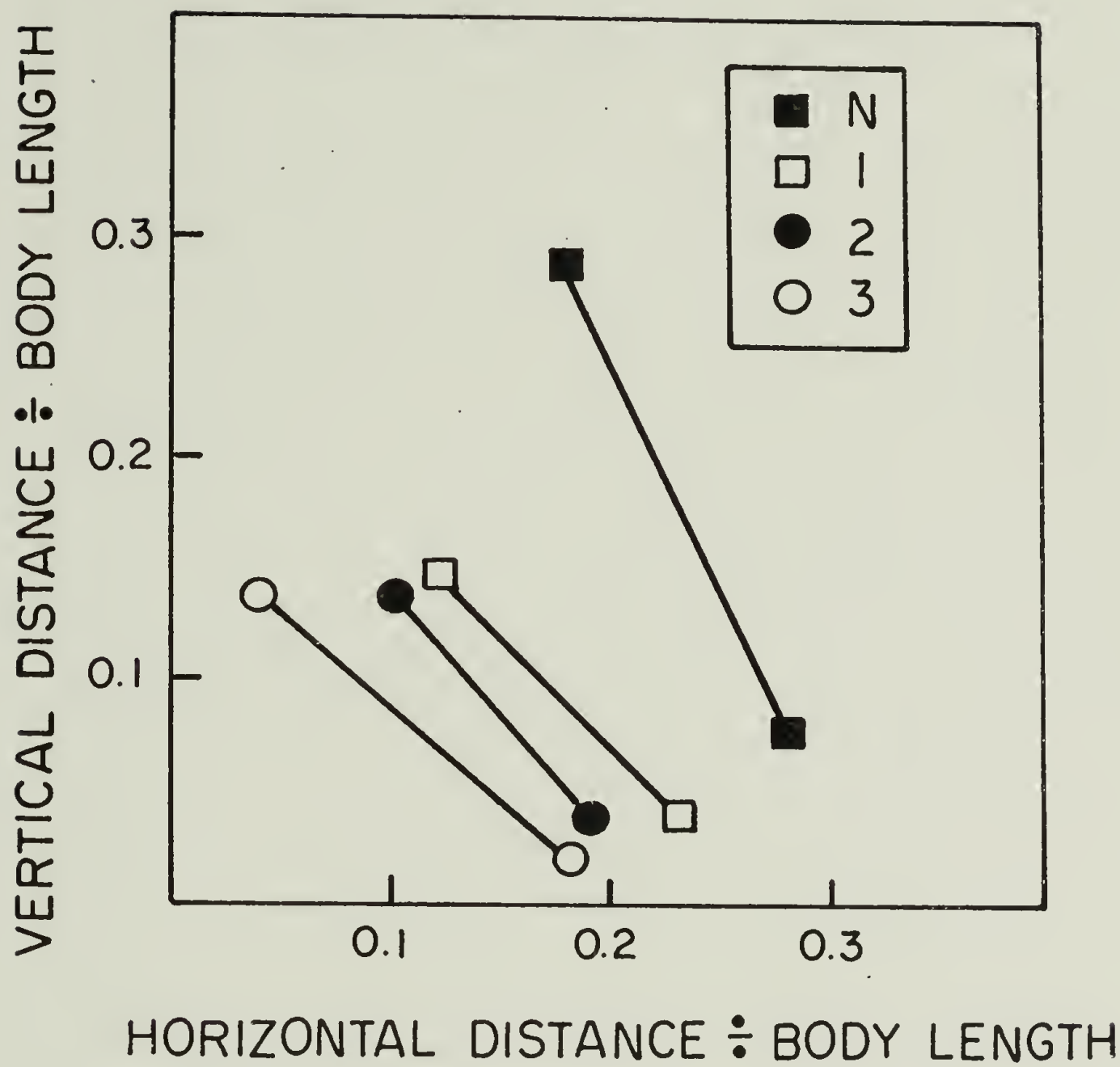


Figure 17

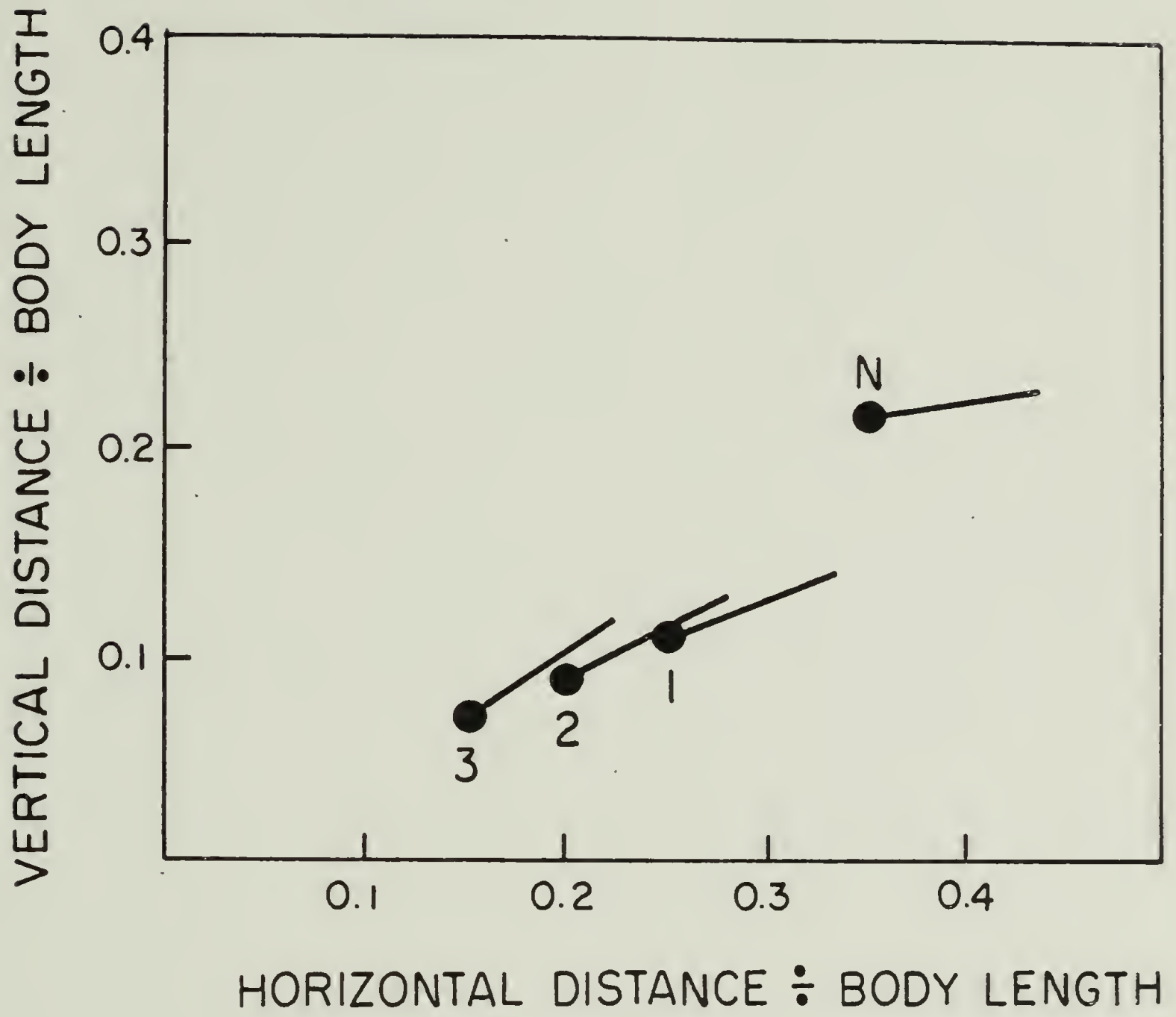


Figure 18

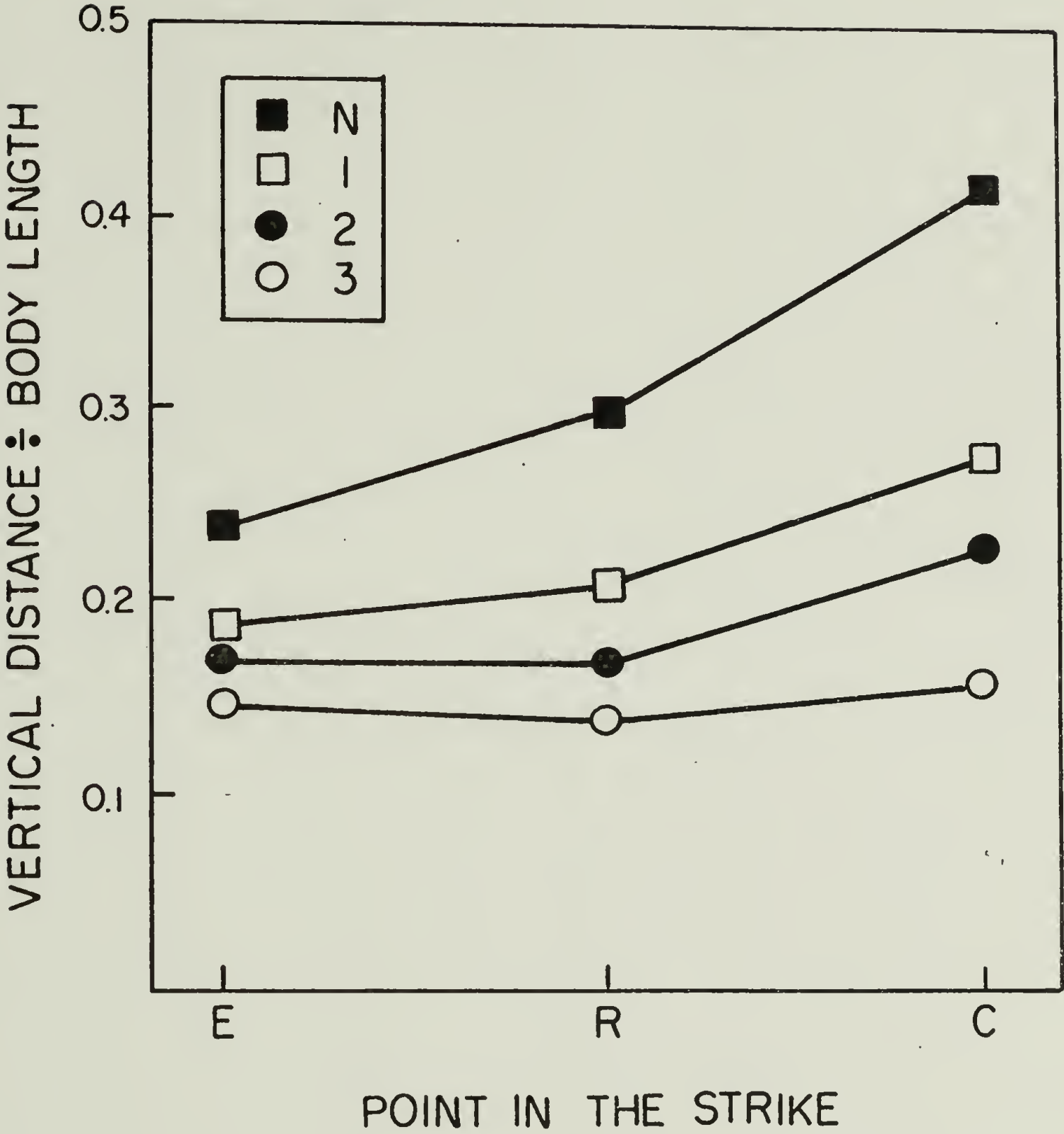


Figure 19

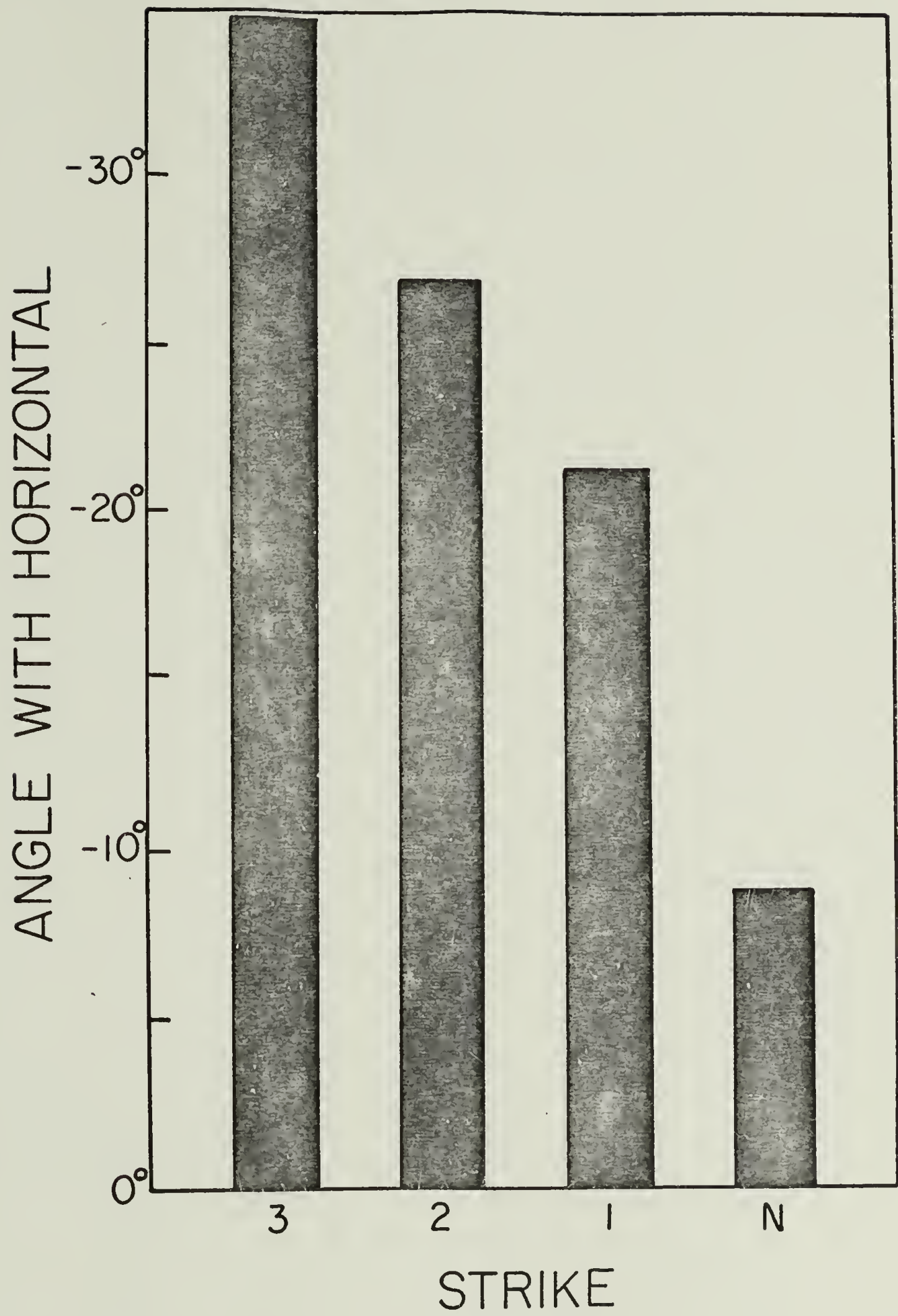


Figure 20

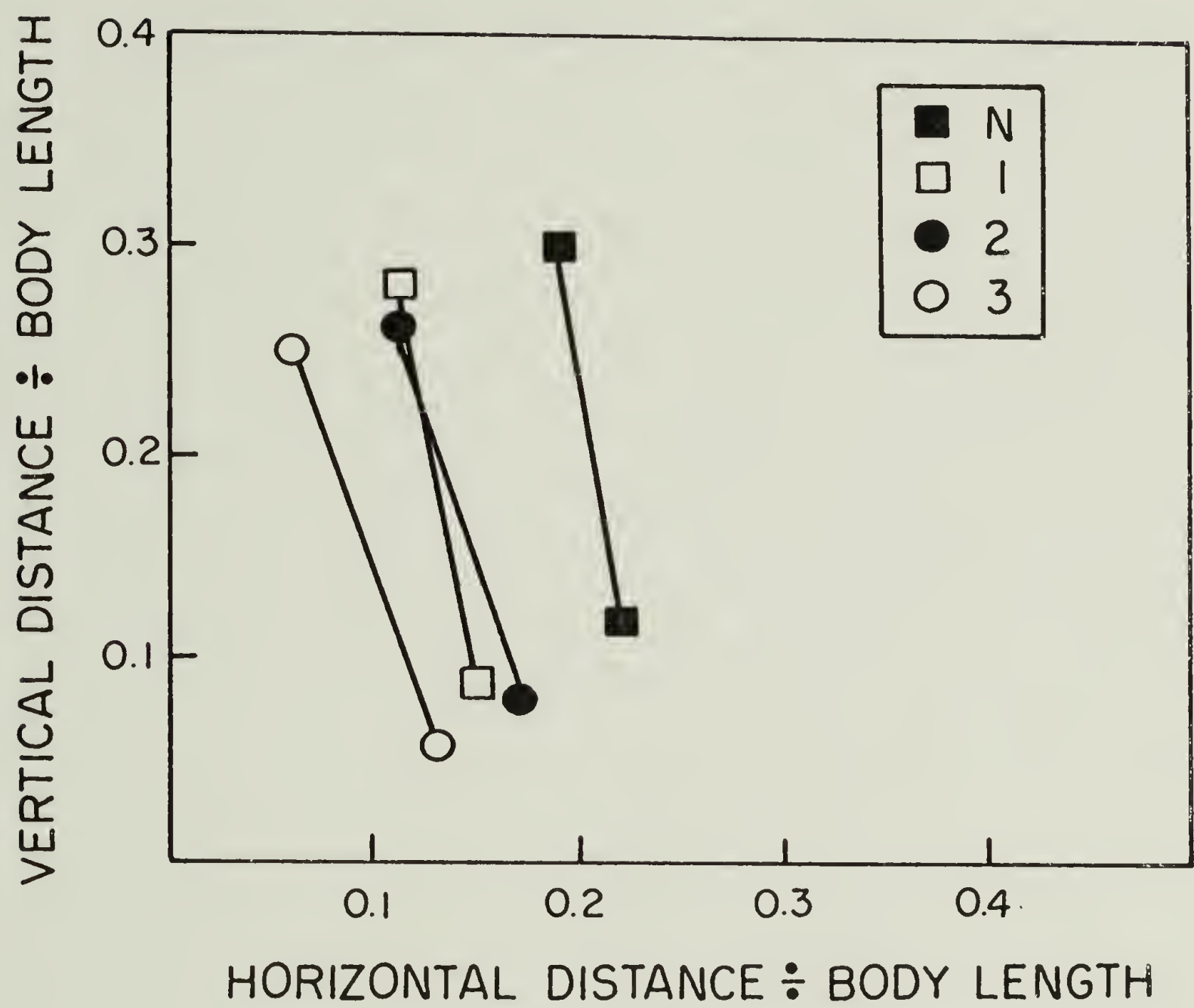


Figure 21

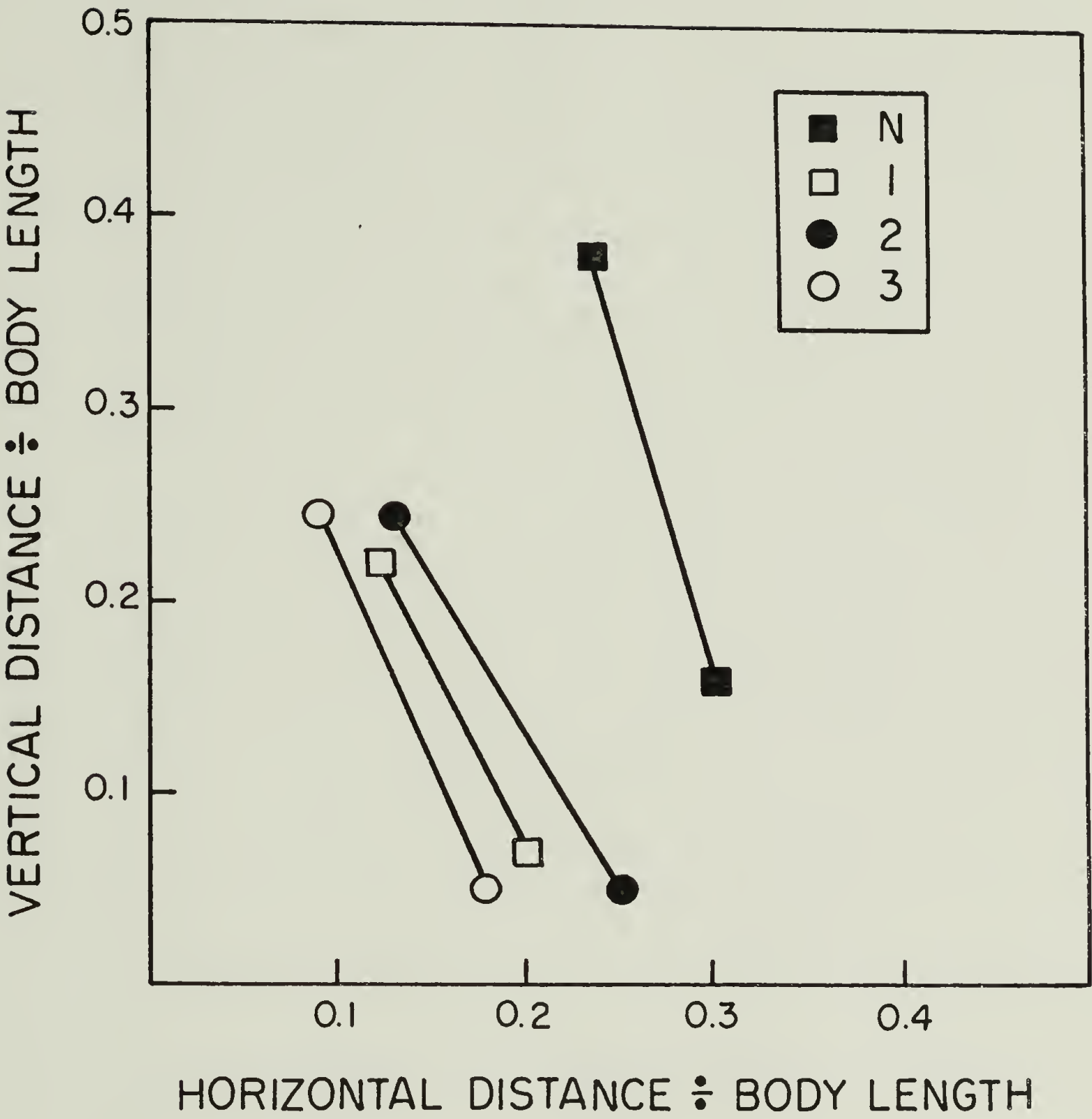


Figure 22

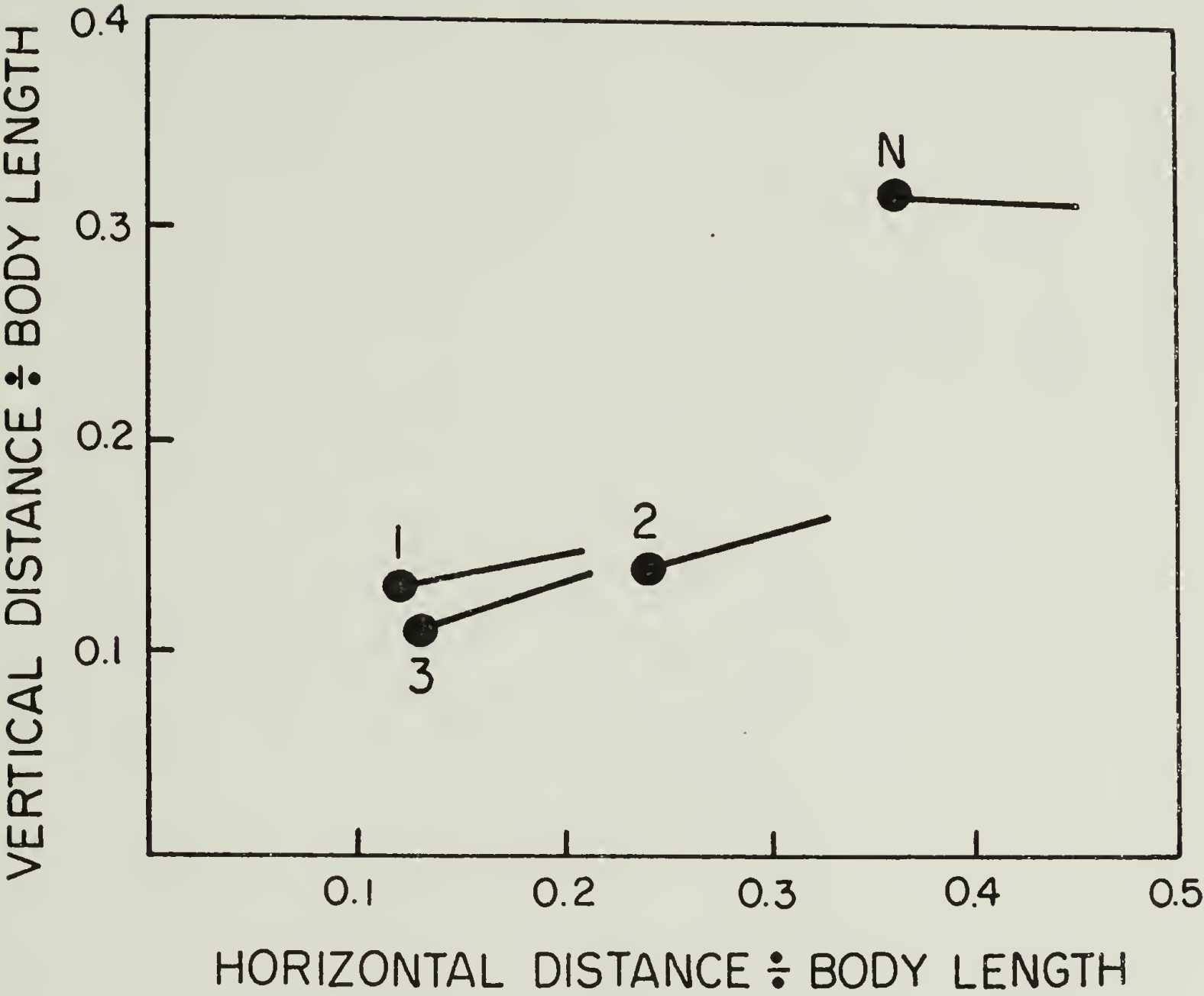


Figure 23

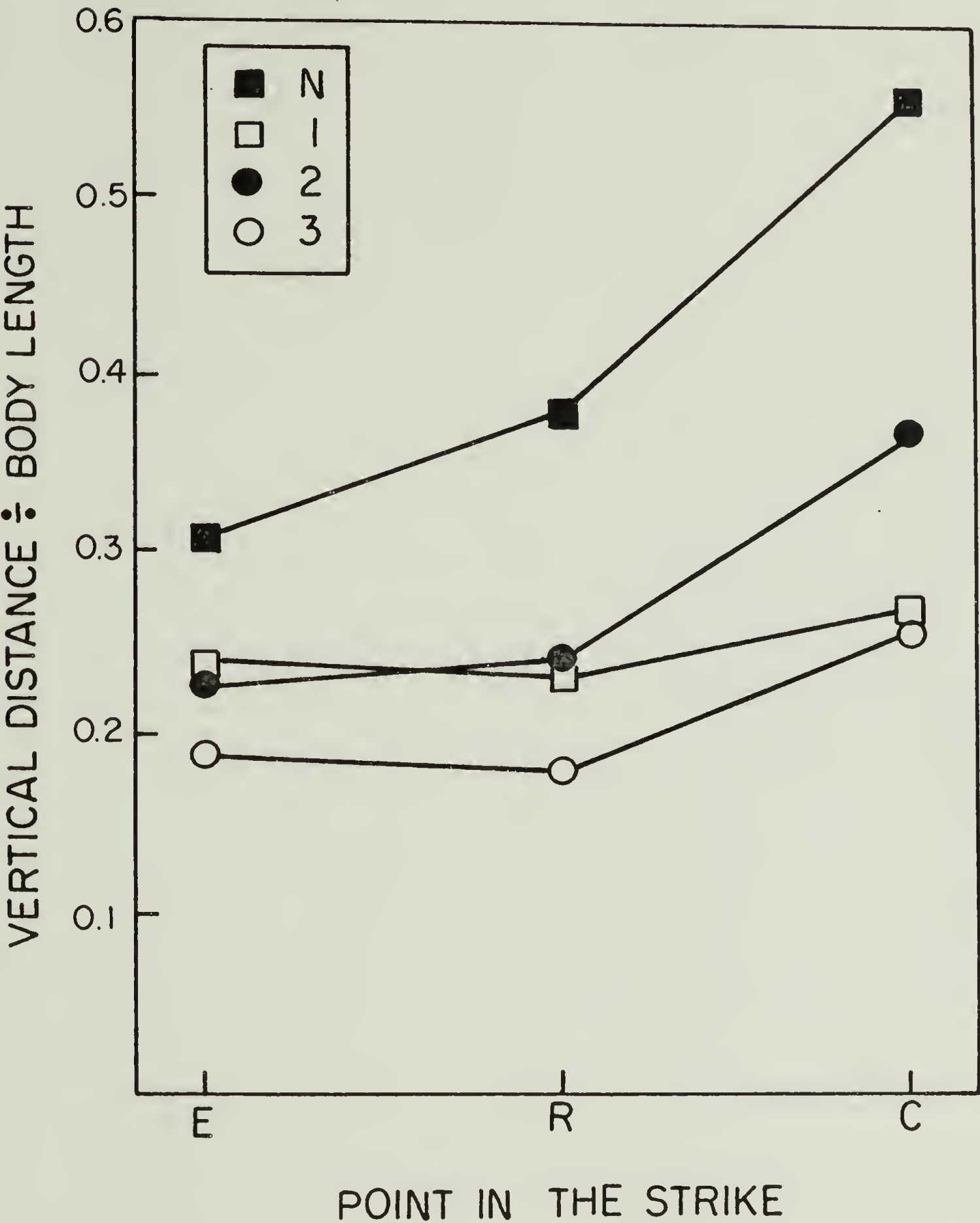


Figure 24

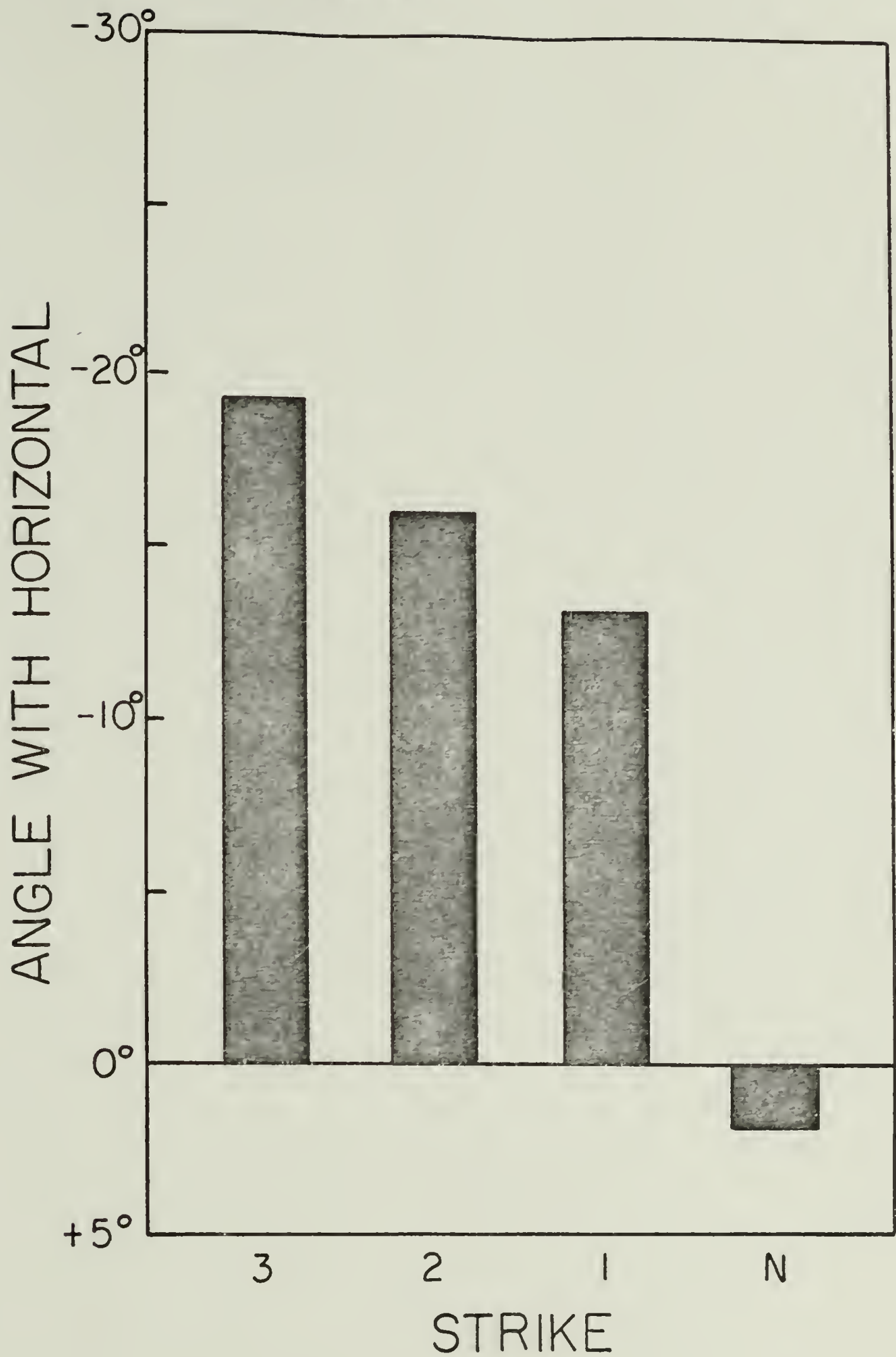


Figure 25

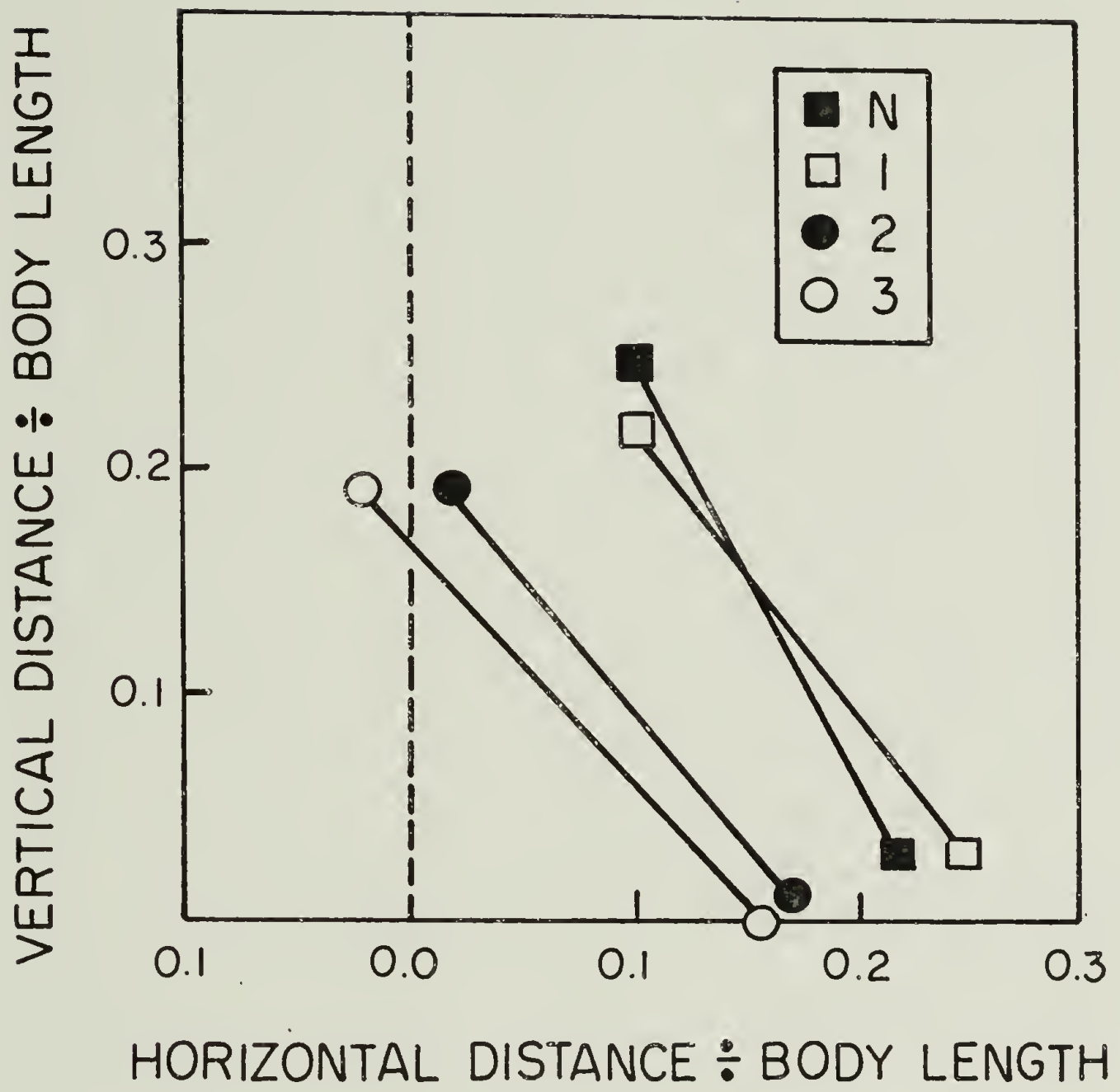


Figure 26

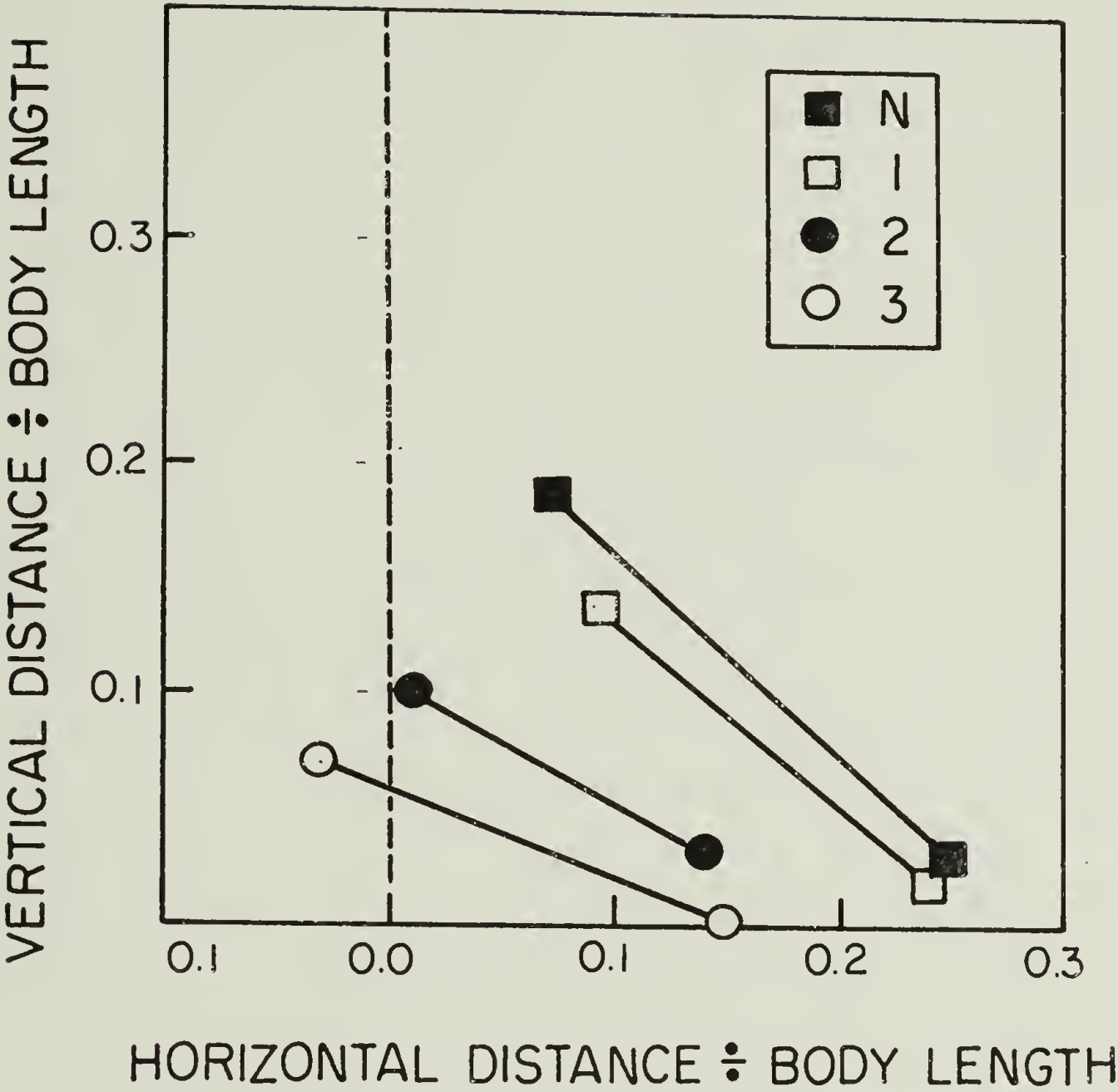


Figure 27

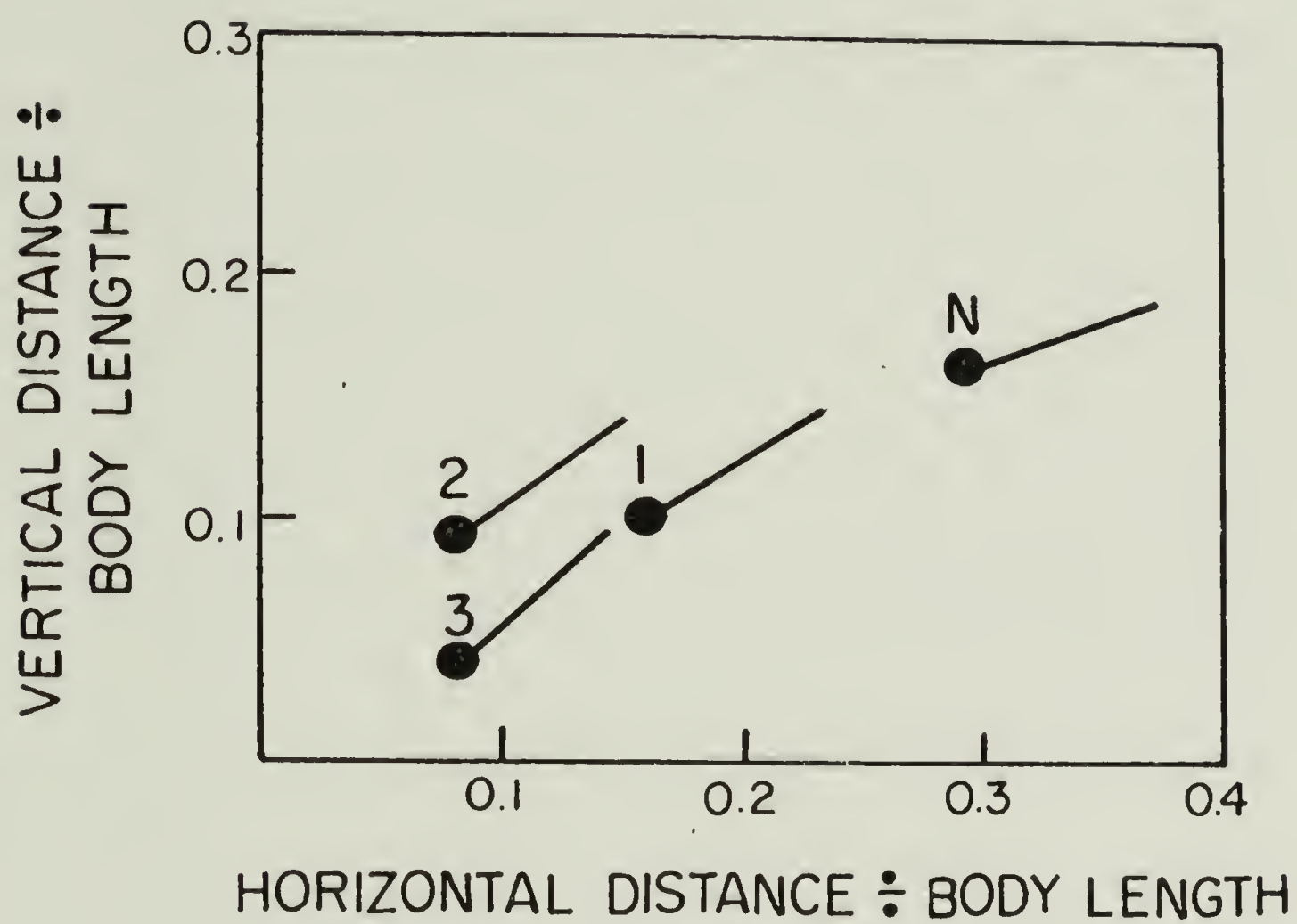
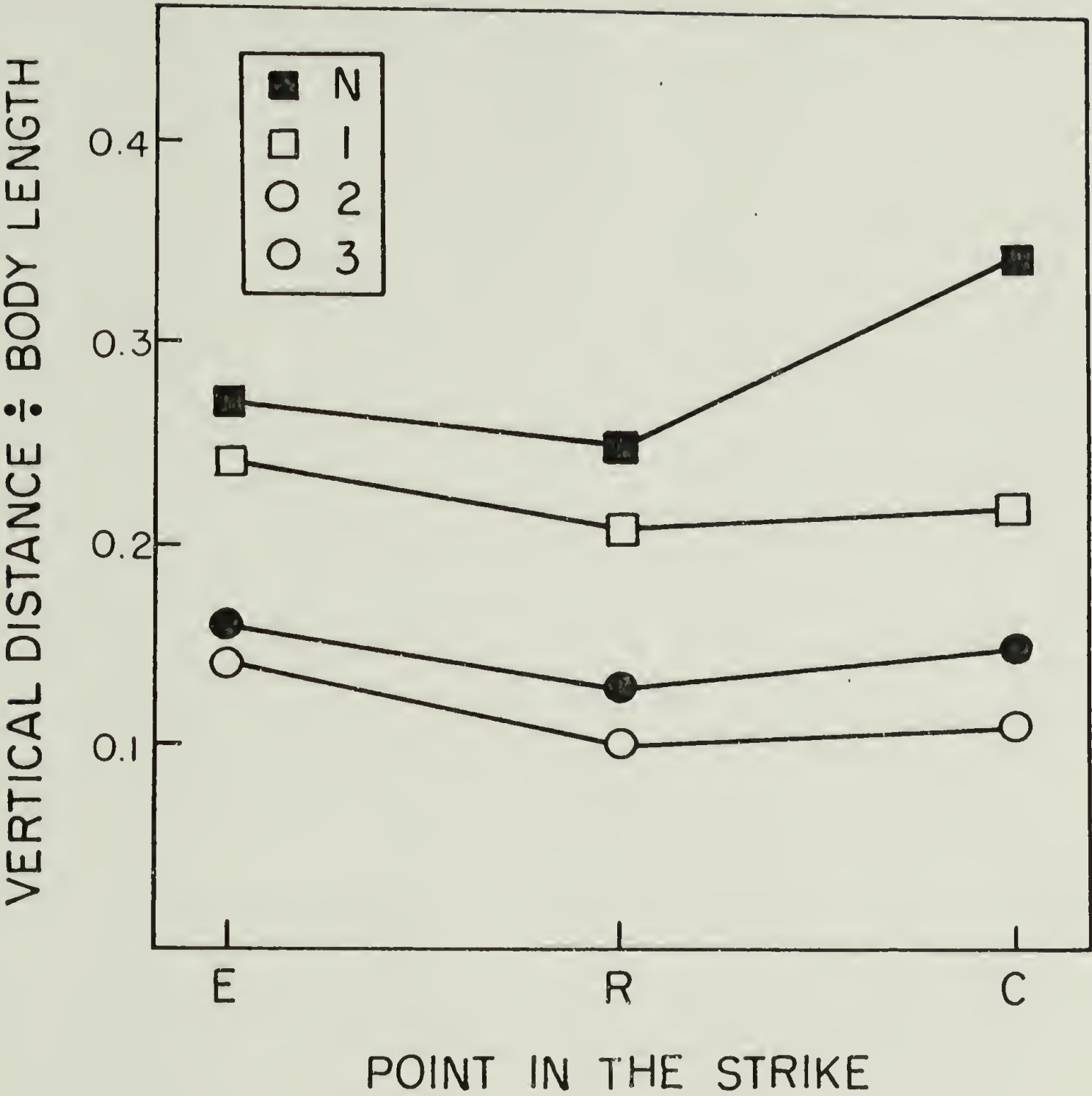


Figure 28



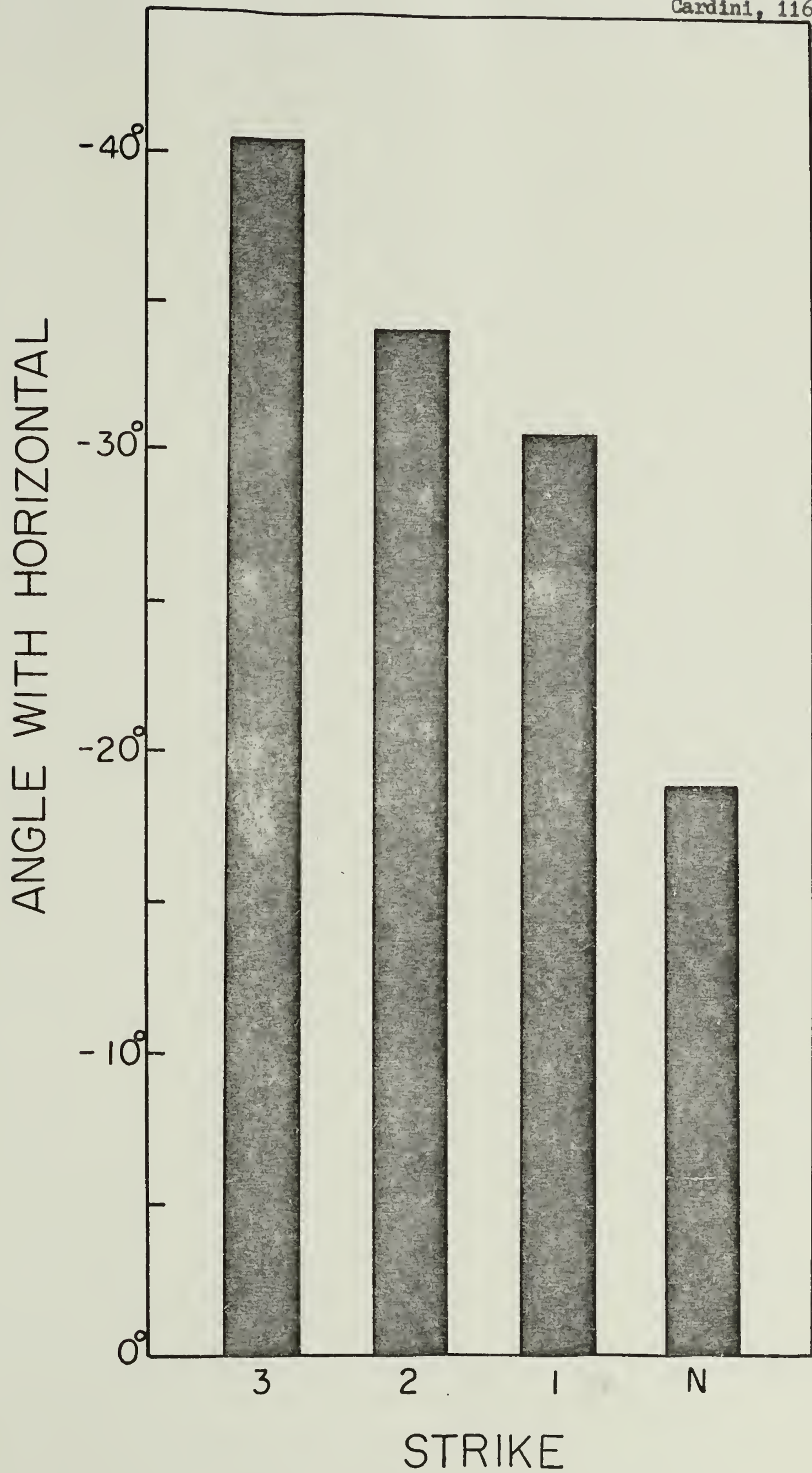


Figure 30

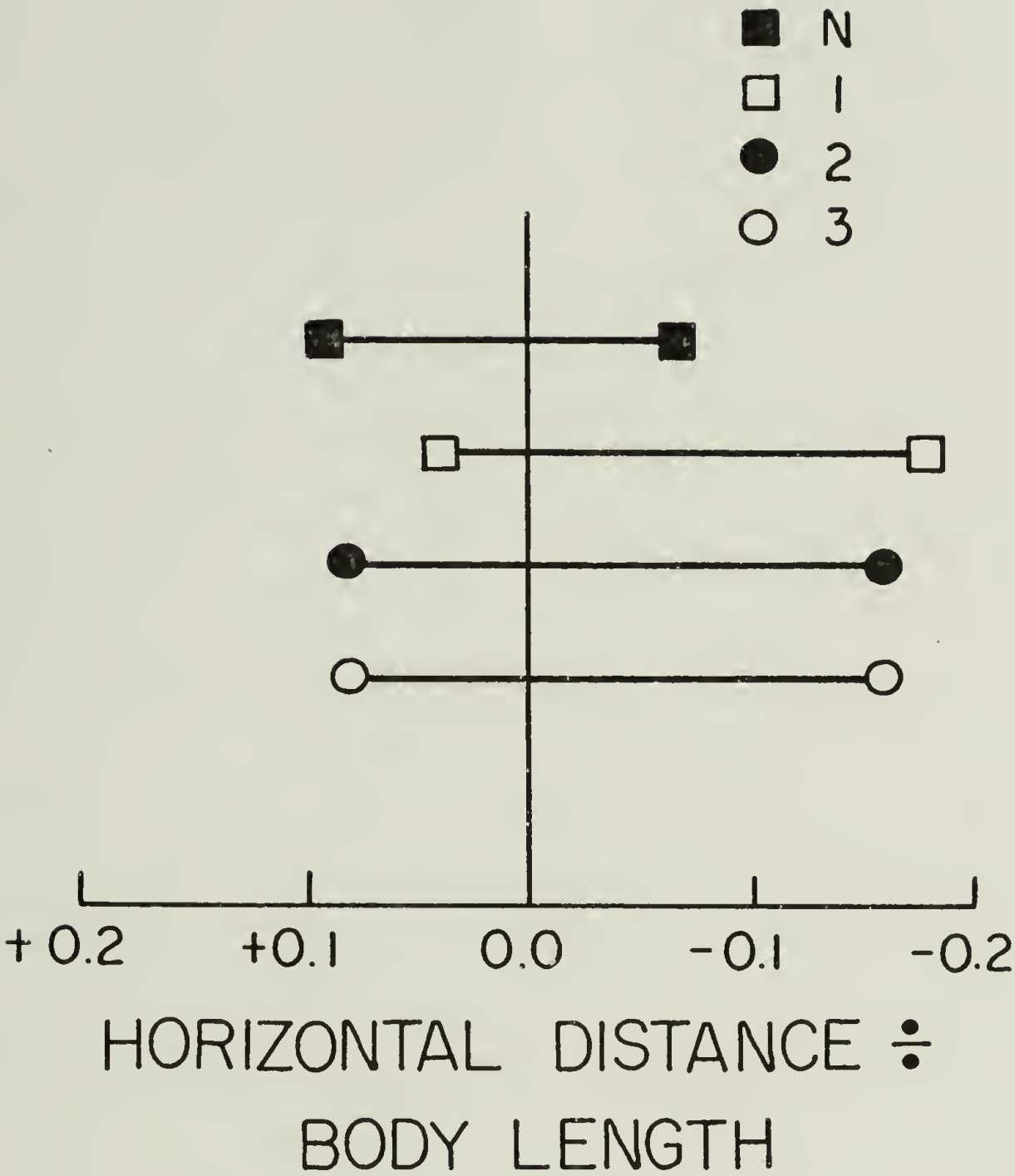


Figure 31

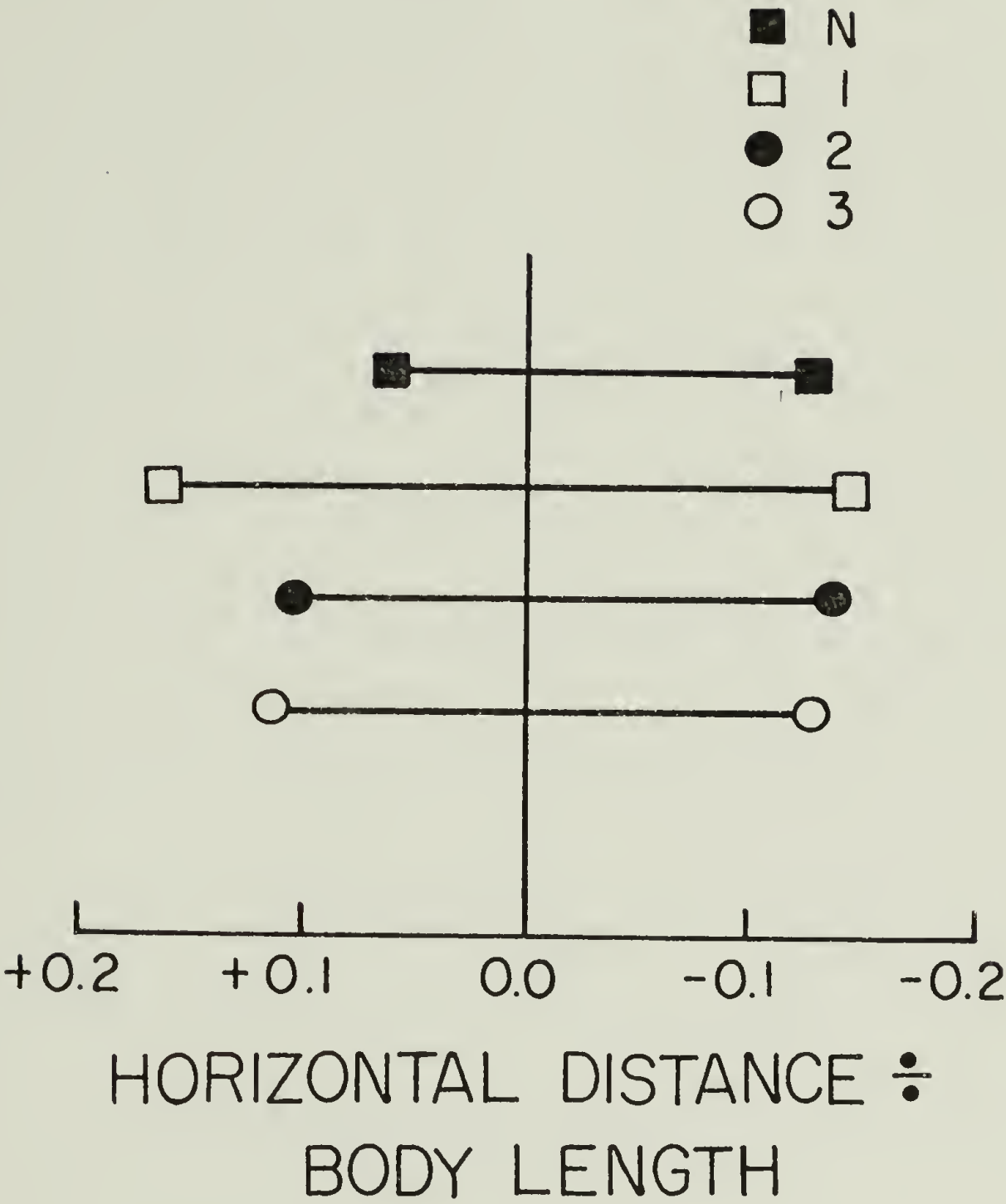


Figure 32

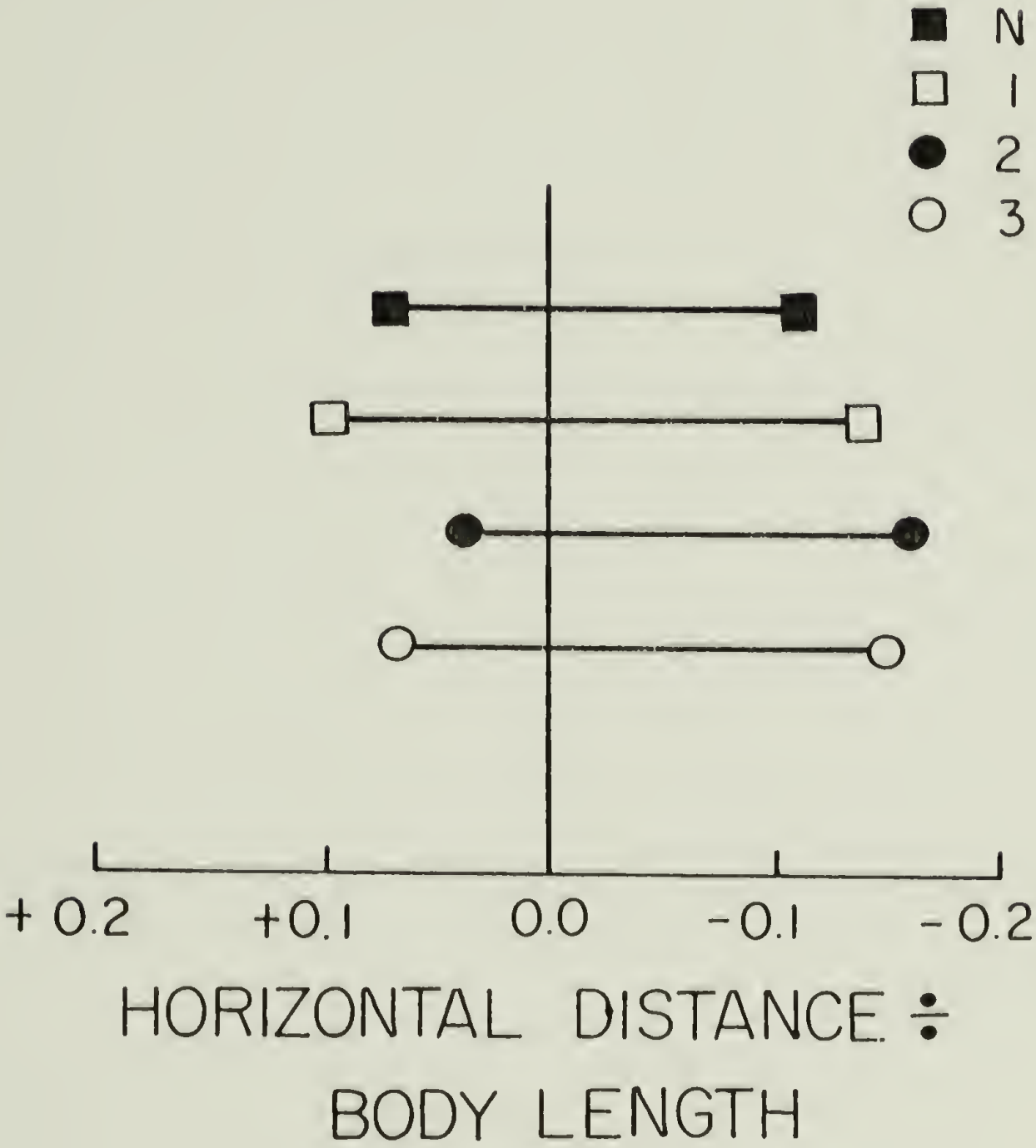


Figure 33

