Territoriality in the Gray Treefrog: *Hyla versicolor*

BIOS 569 - Practicum in Aquatic Biology

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1992

ABSTRACT

Various suggestions currently exist for the types of territoriality among different Anuran species. The definitions of territoriality for these species include individual spacing, clustering and orientation, and active defense of specific perch sites. This experiment was an attempt to determine if the amphibian species, *Hyla versicolor*, exhibits any form of territoriality. A mark-recapture experiment was the method of study. On nights with the appropriate environmental conditions, a specific area was searched for *H. versicolor* males and their sites were plotted on maps. Though little has been documented on this type of behavior by the *H. versicolor* males, Fellers (1979b) has indicated that this species exhibits an individual spacing form of territoriality. The data and observations from this study show that there is a short critical distance that two calling *H. versicolor* males maintain on a particular evening. In addition, the data and observations from this experiment do not show that there is maintenance and active defense of the same perch sites by the same frogs from night to night. Thus, from this experiment the *H. versicolor* appear to exhibit the individual distance form of territoriality described by Fellers.

INTRODUCTION

Ecologists and population biologists throughout the world seem to have solid anecdotal evidence that at least some of the world's 5130 amphibian species are declining at an alarming rate (Phillips 1990). Many scientists seem to believe that the destruction of natural amphibian habitats is a major cause of this decline, driving some of these animals to the brink of extinction. These scientists further suspect that amphibians may be particularly sensitive to subtle worldwide environmental changes. Environmental changes that may cause habitat destruction include the results of heavy metal and pesticide contamination, deforestation, predation, and acid precipitation (Beardsley 1991). To determine if there is a relationship between the decline of amphibians, the destruction of natural habitats, and significant environmental changes, scientists need additional data including systemic censuses of amphibian populations and analyses of the habitats in which these animals live (Phillips 1990, Beardsley 1991). In addition, it may be equally important to understand the behavior of amphibians, their reproductive behavior in particular, to understand how they perpetuate the species naturally in order to predict how they will behave in the midst of environmental changes.

The reproductive success of a species is dependent upon the reproductive strategies of males and females. "A mating strategy is defined here as a set of evolved characteristics (both morphological and behavioral) that function in obtaining sexual partners (Howard 1978)." In general, a male's reproductive success is maximized by increasing the number of mates and distributing his genes to as many offspring as possible. Conversely, a female's reproductive success is maximized by optimizing clutch size, egg size, mate quality, and offspring environment. Thus, these different strategies are the result of the two sexes responding to different environmental stimuli.

The reproductive behavior of Anuran amphibians is based on these sexually related mating strategies. In general, the reproductive behavior of Anurans is divided into two groups: prolonged breeders and explosive breeders. While both explosive and prolonged breeders vocalize to advertise breeding sites, the primary distinction between these two groups is the length of breeding time. Prolonged breeding usually covers a period of more than a month while explosive breeding varies from a period of a few days to a few weeks. This distinction is important because the length of breeding time necessarily contributes to the reproductive behavior (Wells 1977a).

Explosive breeders generally occupy habitats in the northern hemisphere. This type of breeding is characterized by aggregate clumping at oviposition sites, active search for mates by both sexes, and intense male to male competition. The behavior of the males in these aggregations is essentially trial-and-error. Because of the short period of breeding time, males attempt to increase the chances of passing their genes along by clasping almost every moving object within its immediate area (Wells 1977a). The selective pressure contributing to the reproductive success of explosive breeding therefore appears to be dominated by the maximization of mating by the males of the species.

Because of the longer breeding season, prolonged Anuran breeders exhibit a very different reproductive strategy. Instead of actively searching for females, the males of these species tend to call from the edges of temporary ponds, lakes, pools, and flooded ditches where they wait for females to come down, choose an individual, initiate amplexus, and move to an oviposition site (Resetarits & Wilbur 1991). Because of this behavior, male to male competition for females is rare. The competition in these species is indirect as males vocally compete for the attention of females and defend the territories around the calling sites (Wells 1977a). According to Darwin's theory of natural selection, it would seem that the ability of males to predict oviposition sites appealing to females would be favored (Resetarits & Wilbur 1991). It would thus seem favorable for males of prolonged breeders to acquire specific territories which would make them more attractive to gravid females.

Though territoriality has been extensively studied in certain species of fish, birds, lizards, and mammals, little is known about territoriality in frogs. The concept of territory has been observed in several hylids (Fellers 1979a, Whitney & Krebs 1975a), *Rana catesbeiana* (Emlen 1968), and *R. clamitans* (Wells 1977b). These Anurans are prolonged breeders and the presence of territories may indicate that there are specific qualities of these sites which are attractive to females and thus aid in increasing the reproductive success of the males defending the sites.

Most researchers conclude that the mating calls of prolonged breeding Anuran species are correlated with the maintenance of individual spaces (Fellers 1979a, Resetarits & Wilbur 1991, Robertson 1988, Emlen 1968, Whitney & Krebs 1975b, Wells 1977a). Whether or not these individual spaces are territories depends upon an individual's definition of territoriality. In its strictest sense, territoriality may be defined as "the tendency for an animal to restrict its activities to a specified area against other members of its species (Emlen 1968)." The implications of this definition are twofold. First, there is a tendency for animals to show a strong attachment to particular sites because of an important resource found at the site. Second, because the presence of a particular resource may increase the chance that a male occupying the territory will mate, the male will have the tendency to defend these sites (Wells 1977a).

This experiment was an attempt to study the social behavior, particularly the reproductive behavior of the species *Hyla versicolor.* The purpose of this study was to determine if *H. versicolor* exhibits territoriality and, if so, what the definition of territoriality is for this Anuran species. By using a mark and recapture study, an attempt was made to determine if the same frogs returned to the same perches night after night. If this behavior occurred, it would be probable that this species is territorial in the strictest sense of maintaining specific sites. If this behavior did not occur, it is essential to carefully analyze the data to determine if this species exhibits any other type of predictable reproductive behavior such as individual spacing or clustering.

MATERIALS AND METHODS

The experiment was conducted at the University of Notre Dame Environmental Research Center (UNDERC) between June and July of 1992. The specific site of the study was a 25 by 30 square meter plot of land across from Bog Pot Lake. A culvert running under the road transports water from Bog Pot to the site. The site was located about 60 meters from the road and was bordered on the north side by the forest. The plot was a fairly uniform vernal pond like area in which the water level fluctuated, depending on the amount of rainfall, from 52 to 110 centimeters. Various grasses and shrubs were distributed randomly throughout the area and the east, south, and west sides of the plot were boarded by this same uniform habitat. Before beginning the study, the boundaries of this area were marked with twine and colored plastic ribbon. Additionally, trees along the perimeter and inside were labelled to aid in locating the specific sites.

The experiment was essentially a mark-and-recapture study. Each day at dusk when the male frogs began calling I went to the mapped site with a group of 4-6 UNDERC volunteers. Because the frogs appeared to call only on warm nights, air and water temperatures of the area were recorded. Once we made it into the site, the area was searched for female, calling and noncalling male *Hyla versicolor* individuals. The volunteers were aided by flashlights covered with red plastic wrap; no change or effect on activity was observed in response to the light. Upon sighting a *H. versicolor*, the volunteers captured it by hand, placed it in a net weighing bag, marked the sight of capture with a uniquely numbered flag, and brought the frog to me to be processed. The frog was weighed to the nearest gram with a spring scale and marked by colored leg bands or toe clipping. The volunteer who found the frog then released the marked frog to the site of capture indicated by the marked flag. The volunteers and I continued to search, mark, and process the frogs for approximately one hour. The volunteers were also instructed to be alert and look for any examples of additional social behaviors such as amplexus, fighting, or predation. On the day following a night of study, I returned to the area and recorded the sites marked by flags on a scaled map.

RESULTS AND OBSERVATIONS

By the time we arrived on the UNDERC property on May 18, 1992 the male *Hyla versicolor* had begun calling. The experiment was started on June 4 during the peak of their breeding season. The reproductive behavior, indicated by the calling of the males, was irregular and appeared to dependent upon the air and water temperatures. Both the air and the water temperatures increased throughout the period of study as is shown in Table 1. It was observed that with these increased air and water temperatures, the average weight of the frogs decreased throughout the period of study (Figure 1).

Ten nights of mark-recapture study were completed during a period from June 4 to July 8. During this time, 59 different males were weighed and marked, 10 of which were later recaptured one or more times (Appendix 1). Following each night of study, the perches used by the frogs were plotted on maps of the study area (Appendix 2). When each of these individual maps are overlaid and compiled into one larger map, Figure 2, the perches used by the frogs on all nights of the season may be compared. This Figure shows that frogs were found calling in all areas of the plot but that a greater number of frogs were captured on the side closer to the forest than on the other side. The distribution of these frogs based on their distance from the forest may be seen in Figure 3. This figure shows that 40% of the frogs were found within 10 meters of the forest and that the majority of frogs, 34%, were found 10-15 meters from the forest. It was found that the small frogs (< or = to 13 g) called primarily from sites within 5 m of the forest, medium sized frogs (14-17 g) called from sites throughout the plot but most often from perches 20-25 m from the forest, and, large frogs (18+ g) called from the middle of the plot, 5-20 m from the forest. The breakdown of these perch distances from the forest based on the weight of the calling frogs is graphed in Figure 3.

In attempt to determine if there is a critical distance between two calling frogs to prevent acoustical interference, the distances between the closest neighbors were determined in Appendix 3. The average distance between two calling frogs on the same night was determined to be 3.7 m. In general, the data are consistent with this value with the exception of the 17 m distance between the two closest calling frogs on June 27. These distances are graphed in relation to this mean in Figure 5. The average distances that all of the frogs maintained on each particular night were determined in Appendix 4. It was found that on the average, the frogs appeared to maintain a distance of 6.47 meters from each other on each night. In general, the data for each night are consistent with this; however, on one night the average distance was 20 meters. If this value is discarded and the average is found again, the average of the other dates is equal to 4.78 meters, a value which is much closer to the actual distances. These distances are graphed along with these means in Figure 6.

The sites of each of the frogs that were recaptured one or more times are recorded on individual maps (Appendix 5). In attempt to determine if these recaptured frogs did in fact exhibit any sort of territoriality, the average distances between the sightings on different nights of these recaptured frogs were determined in Appendix 6. This data shows that three of the ten recaptured frogs were relocated within 1.5 m on different nights. These distances were considerably greater and much more variable (5.2-30.8 m) for the other seven frogs. These distances are graphed in relation to the average distance of 9.53 m in Figure 6.

DISCUSSION

Though there have been only a few studies of reproductive behavior in the *Hyla versicolor,* Fellers indicates that the males of this species maintain individual territories by calling and actively defending. In addition, Fellers indicates that *H. versicolor* rarely call from perches closer than 75 cm (Fellers, 1979b). In determining if the *H. versicolor* exhibited any spacing out behavior in this experiment it is necessary to study Figure 2 and Appendix 2. An important observation may be made from examining this figure. In this figure, the data show that for all 10 of the experimental nights of study, on only one, June 12, more than one frog was found calling at the site. Additionally, the data show that in general the frogs were found calling at different sites on different nights. Only in the bottom and in the top right do there seem to be areas in which more than one frog was found calling on different nights. From this we may interpret that the uniformity of the site made it no more beneficial for a frog to call from one spot to another.

In Figure 6, the data show the distances between the calling frogs on each night of study. For all 9 of the nights in which more than one frog was captured the average distance was 6.47 meters. However, on one of these nights, only three frogs were found each on a different side of the property giving a nightly average of 20 meters between the frogs. When this high number is discarded, the average appears to be more consistent with the data at a value of 4.78 meters. Though this value is greater than Emlen's value of 75 cm, it may be significant for this particular habitat.

When only the distance between the two closest calling frogs is determined for each night as in Figure 5, we may determine if there is a critical distance the frogs maintain to avoid acoustical interference. The average distance between the two closest calling frogs for each night was determined to be 3.7 meters. For all of the dates except June 27 however, the actual distance was lower than this average. On this date the shortest distance between two calling frogs was 17 meters. On the opposite end of the spectrum, on June 12 two frogs were found calling from the same branch only a few centimeters from each other. Because of this range it is difficult to determine if there is a minimal distance two frogs will maintain and if so, what this distance is. It would seem that the average distance of 3.7 meters should be the average critical distance between two calling frogs on a particular evening. However, since 8 of the 9 evenings had shorter distances ranging from 0 - 3.5 meters, it would seem that the critical distance should be lower. In fact, it may only be a few centimeters given that two calling frogs were found on the same branch on the same night. Given this information, the data show that there is only a very short critical distance, if any, that *Hyla versicolor* males maintain when calling. This may be more consistent with Fellers' 1979 determination of the 75 cm critical distance.

It appears that the *Hyla versicolor* exhibit a type of territoriality in which individual calling males space themselves out to prevent acoustical interference. To determine if these males are territorial night after night, returning to the same perch sites as described for the bullfrog, *Rana catesbeiana* (Emlen, 1968), frogs that had already been marked were recaptured when found. The plots of the perch sites for each of the recaptured frogs are seen in Appendix 5. It is apparent from looking at the plots that 3 of the 10 recaptures were found in the same area on different nights while the other 7 were not. It is important to note here that these plots may not be exact. When the volunteers were looking for frogs they may have captured them from areas away from the sites where they originally were calling from. The recorded sites of capture therefore depend upon where the volunteer placed the marked flag. The actual distances between the same recaptured frogs are graphed in Figure 7. The three frogs which appeared to be recaptured in the same area were found only 0.5 to 1.5 meters away from the first site. These distances may be low enough to account for the variability among the volunteers' placement of the flags and represent the same site. The other frogs however, were recaptured much further from their original sites at distances ranging from

5.2 to 30.8 meters. The average distance between each of the recaptured frogs is 9.53 meters. Though 4 of the 10 recaptured frogs were recaptured at distances very close to this average, these distances are most probably not due to discrepancies in the placement of the flags. These must therefore indicate that these frogs were found at different perch sites on different nights. It is difficult therefore to determine from this experiment whether *H. versicolor* return to the same perch sites to call night after night. Though this behavior was seen in three of the recaptured frogs, this experiment does not provide enough evidence to conclude such. In describing male reproductive behavior of the *H. versicolor*, it seems that males actively acquire perch sites which are located a minimal distance away from other perch sites but these perch sites are not always returned to night after night. Whitney and Krebs explain this sort of behavior by sexual selection. By spacing out, an individual male increases his chance of mating by reducing interference to approaching females by other males. In addition, spacing out facilitates location of individual males by females (Whitney & Krebs 1975b).

This experiment seems to be successful in determining a working definition of territorial behavior in the male *Hyla versicolor* frogs. During analysis of the data supporting this behavior, several additional observations were made. First, as is shown in Table 1, both the air and water temperatures increased throughout the study period. Additionally, though no behavioral changes were observed with these increases, the average weight of the frogs did in fact decrease throughout the period. This experiment cannot prove that there is any correlation between these two trends however, we can attempt to explain them. The increase in temperature may be attributed to the onset of summer with warmer days, nights, and precipitation. The decrease in body weight is more difficult to explain. One reason for the decrease may be that the larger males call and attract mates earlier in the summer while the smaller ones cannot compete until later in the season. Another reason may be that the *H. versicolor* males do not eat; instead they invest all of their time and energy in calling and mating. As a result of not eating while expending great amounts of energy, the males may lose body weight over the breeding season.

Another observation is that the behavior of the *Hyla versicolor* males is characterized by a relatively uneventful day spent resting up in the trees. After dusk the males come down out of the trees to the edges of the ponds where they are visited by females who choose an individual male, approach him, and initiate amplexus (Resetarits & Wilbur 1991). In looking at Figure 2 as noted above, it is evident that the male frogs were captured at perch sites throughout the study area. This is probably due to the uniformity of the site, a horizontal stretch of land with little vegetation, an area which is preferred by male *H. versicolor* because it does not interfere with sound propagation. When looking at this closer however, it seems as though more frogs were captured on the right side of the plot, the side adjacent to the north forest. A breakdown of the number of frogs captured at particular distances from the forest is shown in Figure 3. Indeed, this graph shows that nearly 3/4 of the captured frogs, 74%, were captured within 15 meters of the forest while only 26% were found further away. The frogs therefore appear to prefer to call from areas close to the forest.

It may be hypothesized that larger males may have the strength to travel further distances and thus be found further away from the forest. A graph of the plot showing the distribution of the frogs by weight is shown in Figure 4. An interpretation of this graph showing the distributions of six different weight ranges is shown in Figure 5. Two trends are evident from these graphs. First, the smaller the frog the more often it was found 0 - 5 meters from the forest. Fifty percent of the smallest frogs (< 10 g) while 0% of the largest frogs (18 g+) were captured here. Second, with the exception of the 18 g+ frogs, the larger the frog, the more often it was found 15 - 25 meters away from the forest. The largest frogs may be too slow to escape predation and travel far away from the forest. Additionally, as noted by Emlen, older and larger males strategically locate themselves in the centers of choruses (Emlen, 1968). Because the area beyond the south boundary was uniform with the habitat inside the area, the center of the chorus may not have been in the center of the plot but instead have been on the left side.

The overall conclusion that may be drawn from these results and observations is that the male *Hyla versicolor* behavior may be described as an individual distancing system. The males were found throughout the entire property though they were generally not found within several meters of each other. Some sites were occupied more than others in a relation which seemed to be dependent upon both distance to the forest and individual body weight. Additionally, particular perch sites were neither maintained nor defended by the individual males. Finally, there was no evidence to indicate that the *H. versicolor* exhibited any clustering or orientation behavior. It is this individual distancing system then, which must be studied more in depth by ecologists and population biologists in order to predict how the *H. versicolor* will respond to global changes. By determining this one aspect of this species' reproductive behavior we may attempt to understand the delicate relationship between amphibian behavior and population decline with detrimental environmental changes.

ACKNOWLEDGEMENTS

Many thanks to the Bernard J. Hank Family Endowment for the funding of the UNDERC program and providing the opportunity for me to take part in the 1992 UNDERC class. Thanks also to Dr. Sunny K. Boyd and Dr. Martin Berg for their advice, help, and guidance before, during, and after the experiment. Finally, a very warm thanks to all of the friends up on the UNDERC property during the 1992 summer who braved heat, rain, and multitudes of biting insects to assist me in the field during the experimental nights.

REFERENCES CITED

Beardsley, T. 1991. Murder mystery: ecologists seek better data on extinction. Scientific American 265: 29.

Emlen, S. T. 1968. Territoriality in the bullfrog, *Rana catesbeiana*. Copeia 2: 240-24.

Fellers, G. M. 1979a. Aggression, territoriality,and mating behavior in North American treefrogs. Animal Behavior 27: 107-19.

Fellers, G. M. 1979b. Mate selection in the gray treefrog, *Hyla versicolor*. Copeia 11: 286-90.

Howard, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution 32(4): 850-71.

Phillips, K. 1990. Where have all the frogs and toads gone? BioScience 40: 422-4.

Resetarits, V. J., and Wilbur, H. M. 1991. Calling site choice by *Hyla chrysoscelis*: effect of predators, competitors, and oviposition sites. Ecology 72(3): 778-86.

Robertson, J. G. M. 1988. Male territoriality, fighting, and assessment of fighting ability in the Australian frog, *Uperoleia rugosa*. Animal Behavior 36: 1247-49.

Wells, K. D. 1977a. The social behaviour of Anuran amphibians. Animal Behavior 25: 666-93.

Wells, K. D. 1977b. Territoriality and male mating success in the green frog (*Rana clamitans*). Ecology 58: 750-62.

Whitney, C. L., and Krebs, J. R. 1975a. Mate selection in Pacific treefrogs. Nature 255: 325-6.

Whitney, C. L., and Krebs, J. R. 1975b. Spacing and calling Pacific treefrogs, *Hyla regilla*. Canadian Journal of Zoology 53: 1519-1527.

Table 1: Air and Water Temperatures on Experimental Nights

Date	Air Temp (C°)	Water Temp (C°)
June 4	17.9	20.4
June 5	17.4	20.6
June 9	18.6	21.4
June 10	21.1	21.2
June 11	18.3	22.7
June 12	19.5	22.5
June 27	24.3	23.4
June 28	*	*
July 7	*	*
July 8	*	*

* = Thermometer broken, unable to measure temperatures.

Figure 1: Average weight of frogs captured on each night of study.

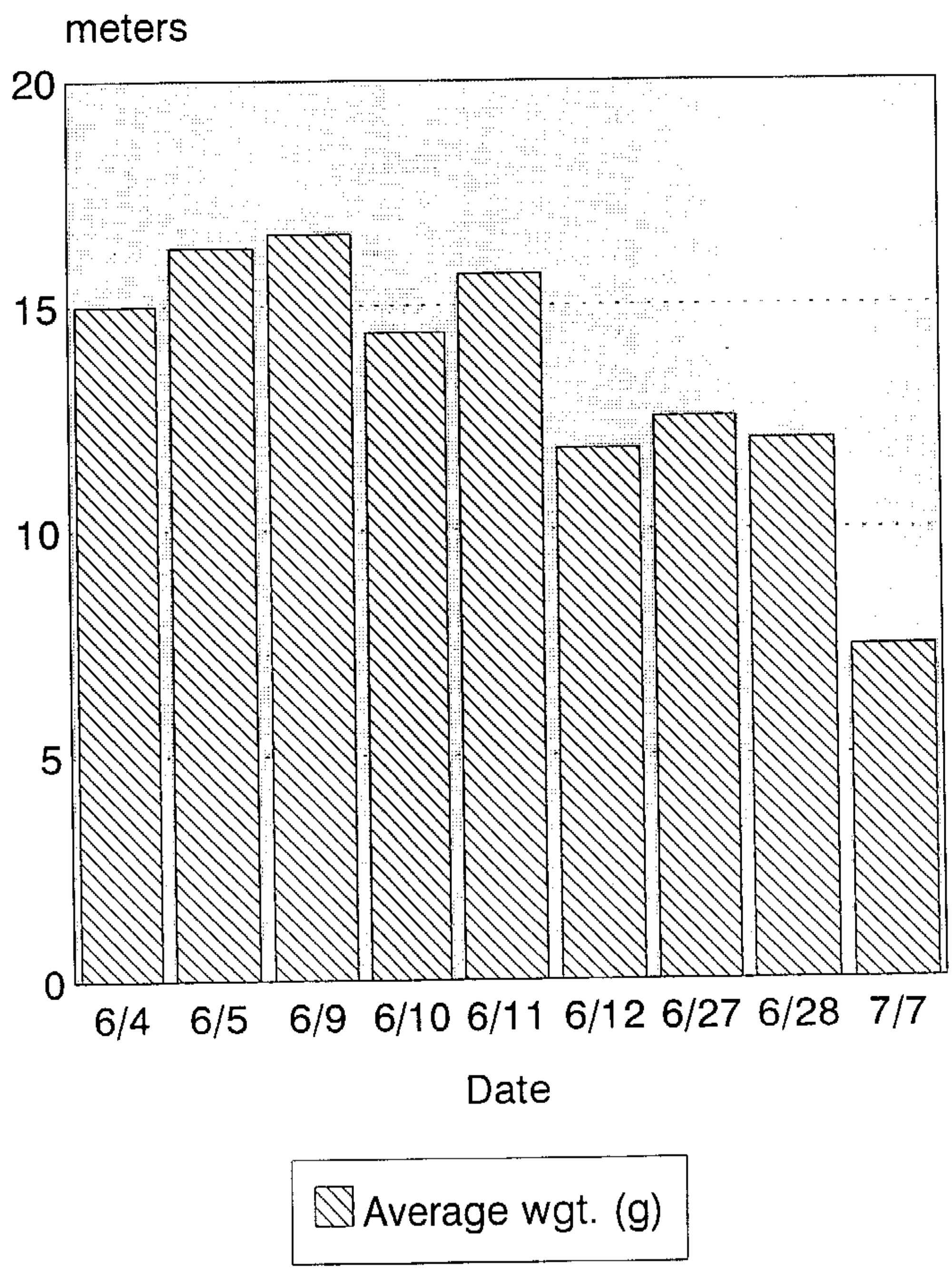


Figure 2: Distribution of all frogs captured throughout the study period.

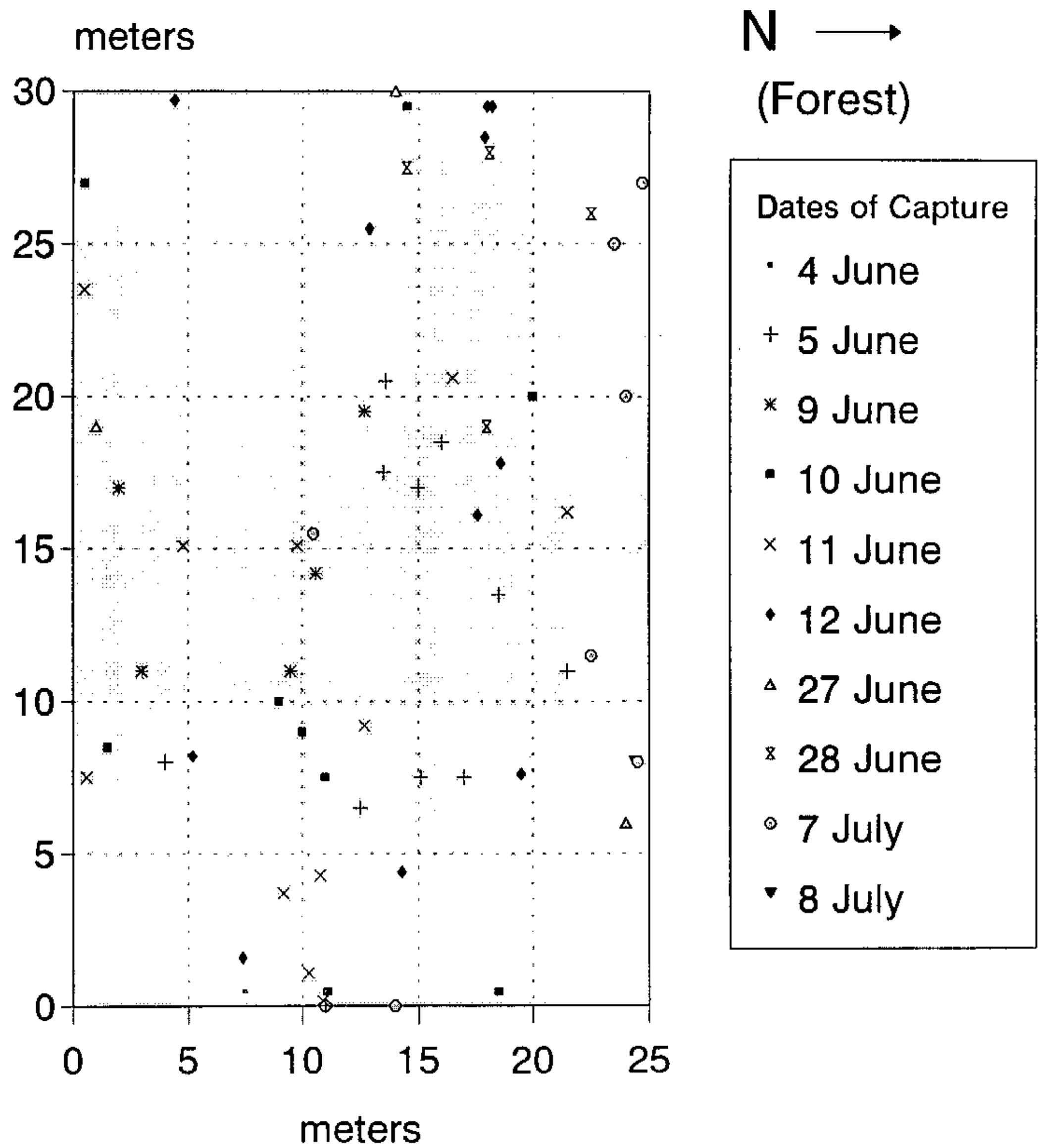


Figure 3: Location of frog calling sites in relation to the north forest.

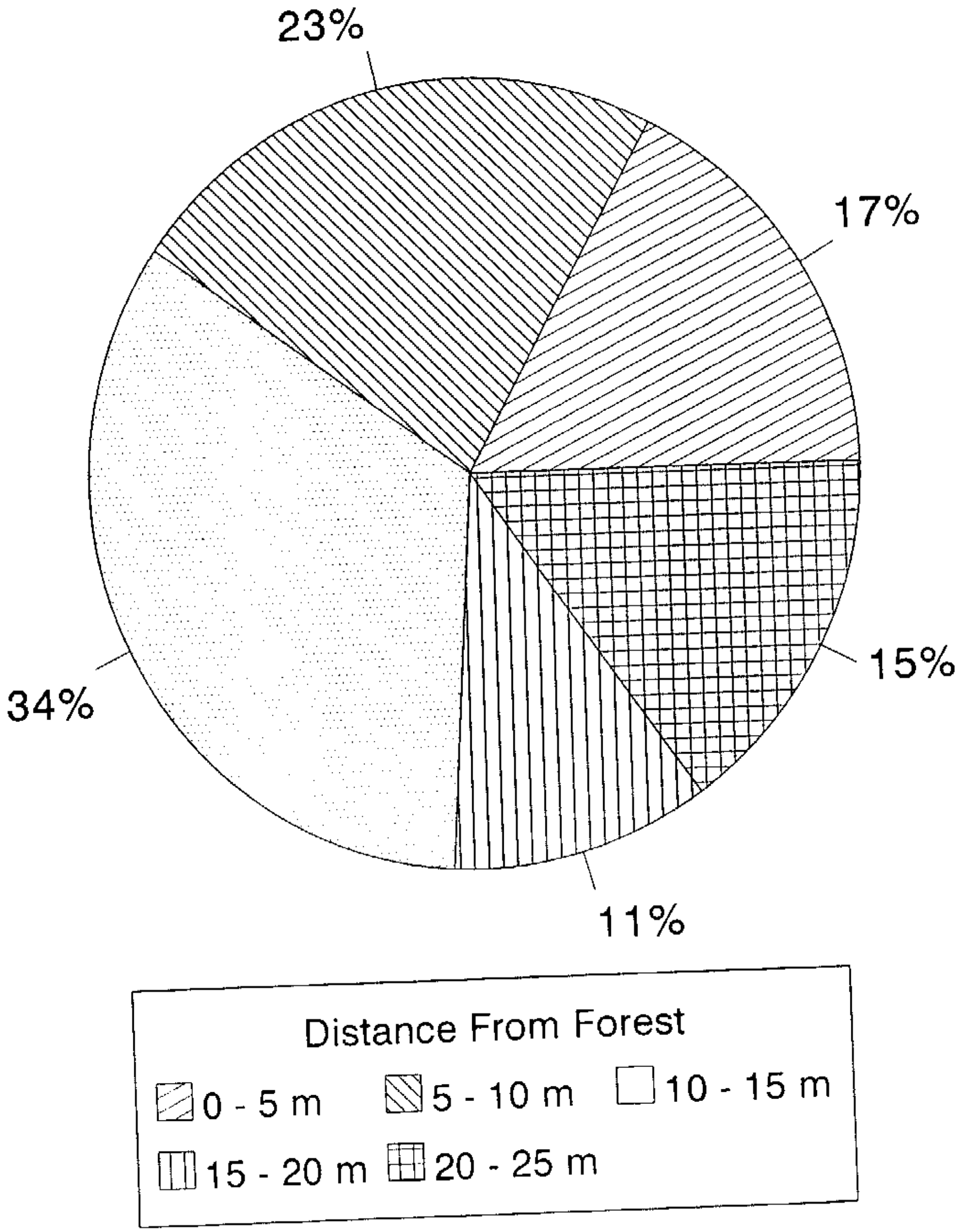


Figure 4: The distribution of the frogs by weight in relation to the forest.

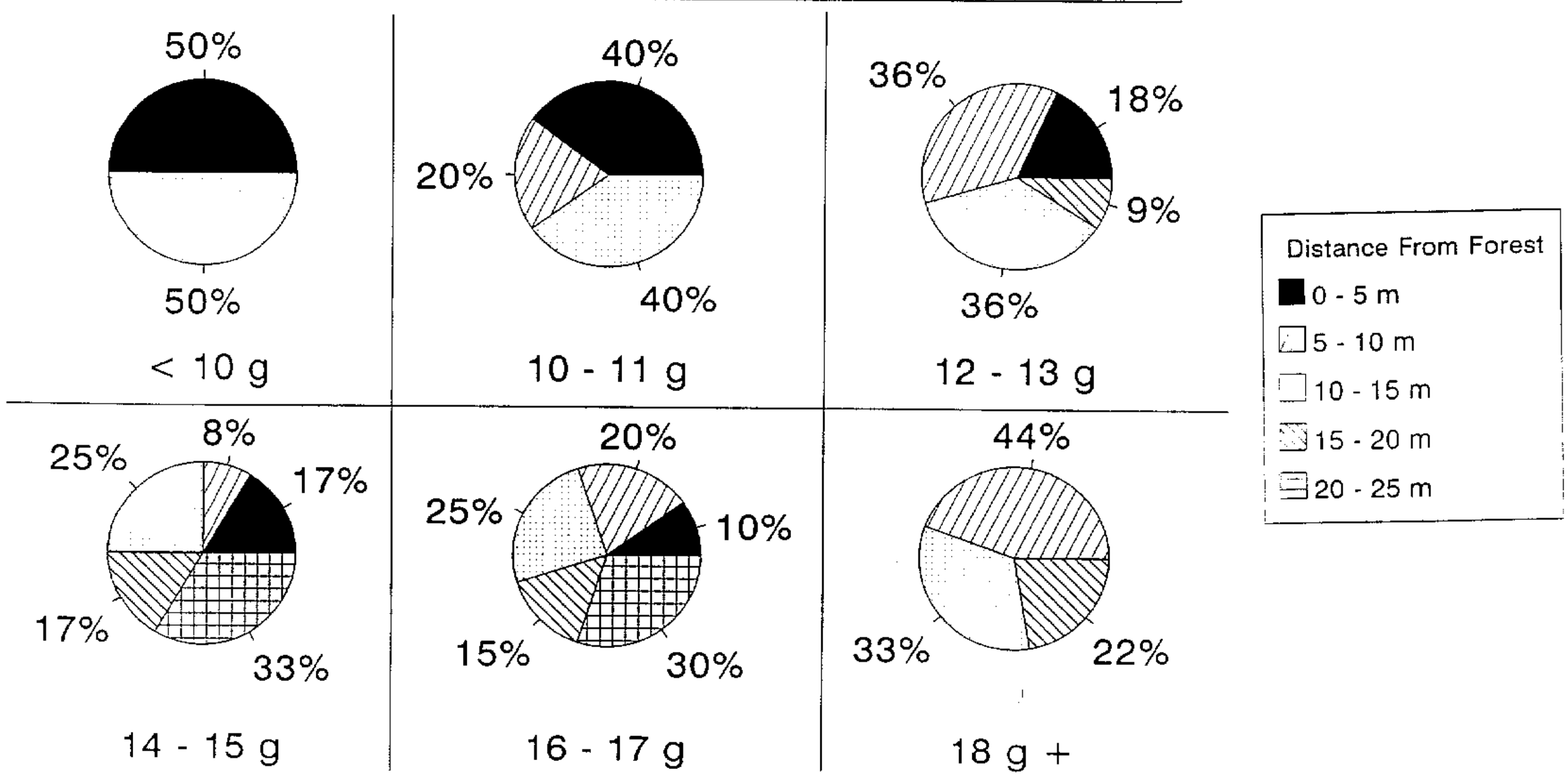
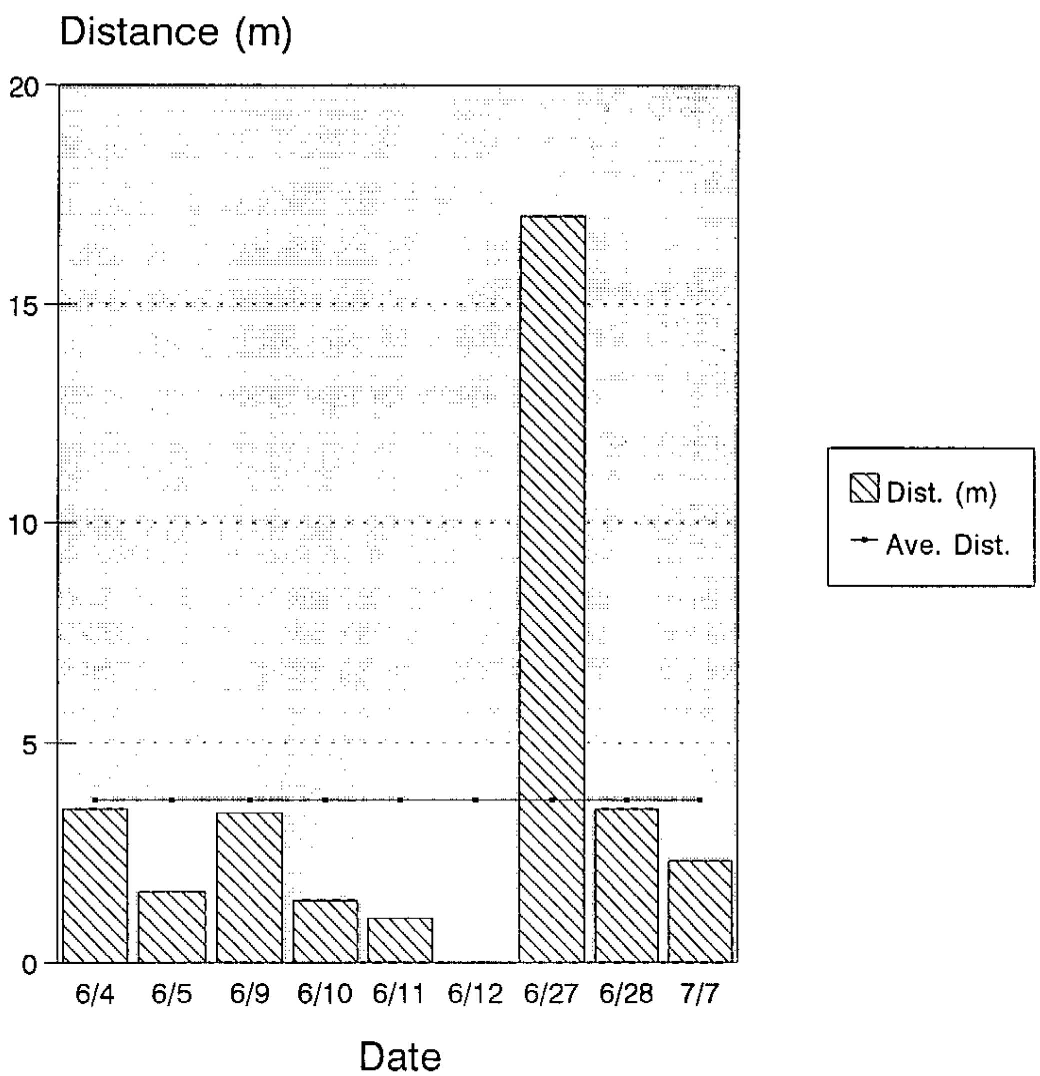
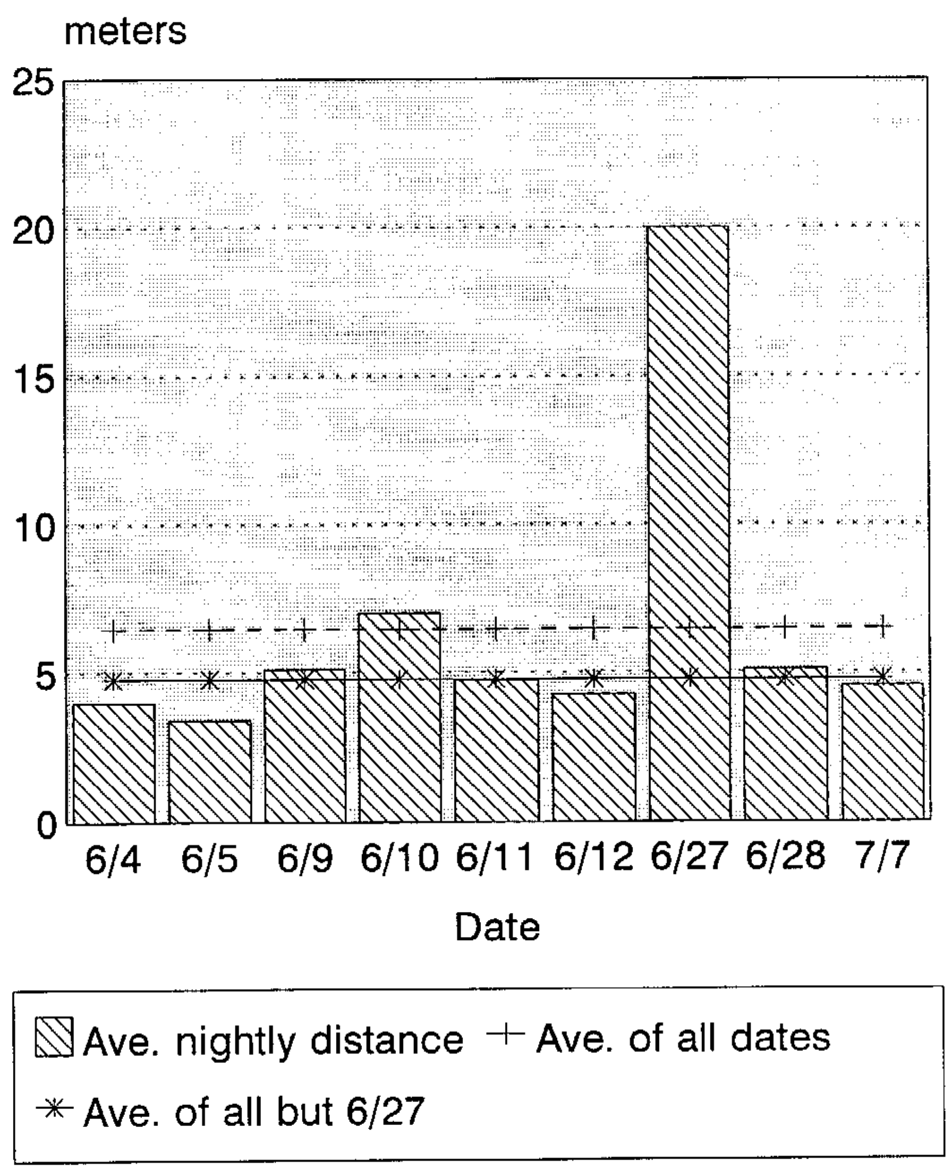


Figure 5: Distances between the two closest frogs for each night of study.



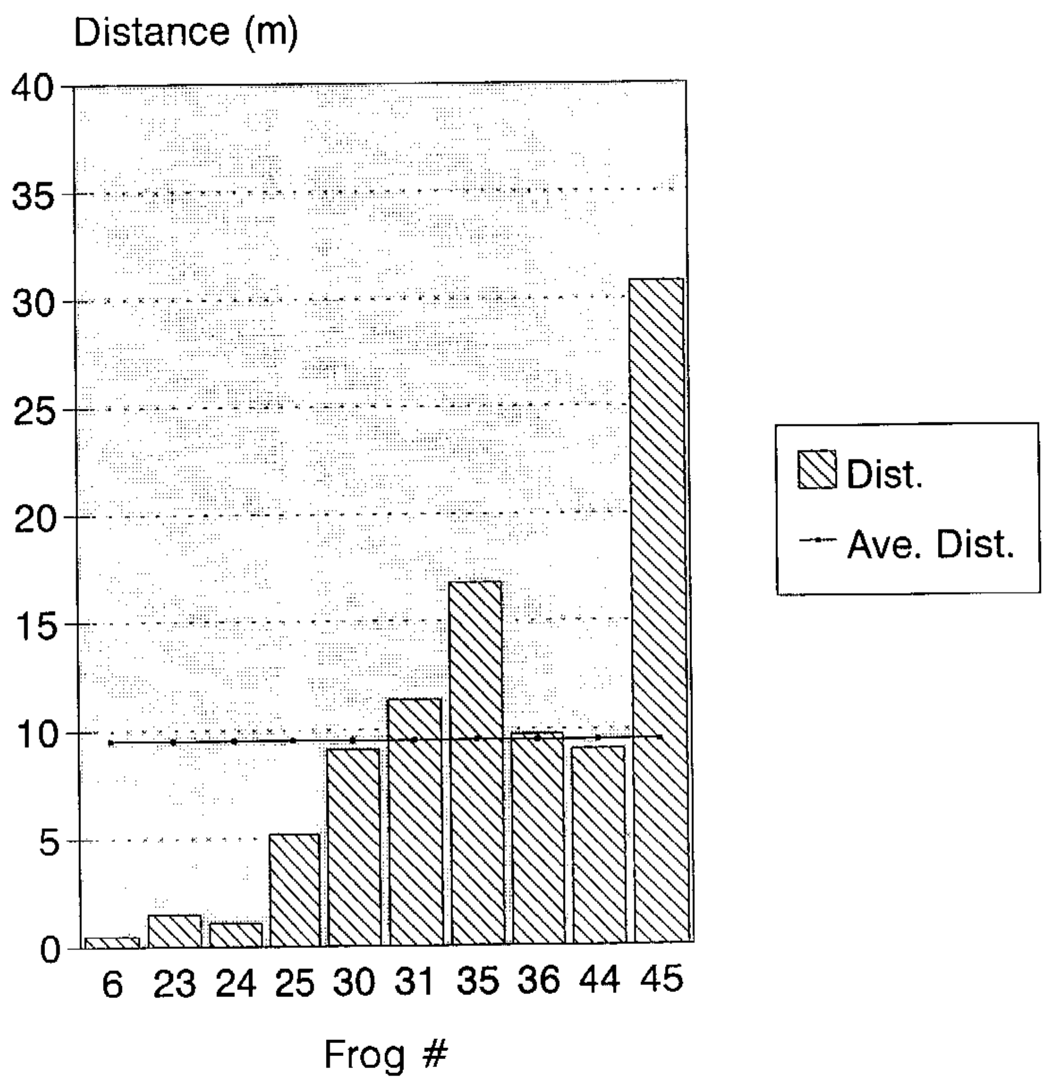
The striped bars represent the specific nightly distances while the line, equivalent to 3.7 meters, represents the average of these distancs.

Figure 6: Average distances between all frogs for each night of study.



The distances to the closest frog for each of the frogs captured on one night were averaged.
The average of all of these averages is equal to 6.47 meters and is represented by the dotted line.
The average of all but the data from 27 June is equal to 4.78 and represented by the solid line.

Figure 7: Distances between the closest sightings of each recaptured frog.



The striped bars represent distances between two sightings of each individual frog while the line, equivalent to 9.53 m, represents the average of these distances.

Appendix 1: Information from the nightly processing of the calling males.

Frog #	Marker	Weight (g)	Dates
1	green 22	14	6/4
2	yellow 34	13	6/4
3	pink 13	18	6/4
4	pink 12	?	6/4
5	red 3	14	6/5
6	red 4	13	6/5, 6/10
7	red 5	19	6/5
8	red 6	18	6/5
9	red 7	16	6/5
10	red 8	14	6/5
11	red 41	17	6/5
12	red 9	13	6/5
13	red 10	16	6/5, 6/10
14	yellow 35	18	6/5
15	yellow 36	17	6/5
16	orange 11	15	6/5
17	yellow 37	16	6/5
18	yellow 38	18	6/5
19	yellow 39	18	6/5

Appendix 1: Continued

Frog #	Marker	Weight (g)	Dates
20	orange 12	16	6/5
21	blue 41	18	6/5
22	blue 42	18	6/5
23	blue 43	16	6/5, 6/10, 6/12, 6/28, 7/7
24	pink 1	18	6/9, 6/10, 6/11
25	pink 2	16	6/9, 6/10
26	pink 3	17	6/9
27	pink 4	15	6/9
28	pink 6	17	6/9
29	orange 13	12	6/10
30	RH 1	13	6/10, 6/12
31	RH 2	12	6/10, 6/12, 7/7
32	orange 14	14	6/10
33	RH 3	14	6/10
34	RH 4	16	6/11
35	RH 5	16	6/11, 6/12
36	blue 46	15	6/11, 6/12
37	blue 47	17	6/11
38	LH 1	17	6/11

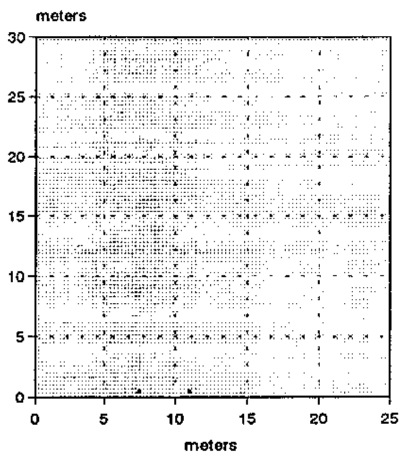
Appendix 1: Continued

Frog #	Marker	Weight (g)	Dates
39	pink 8	14	6/11
40	blue 48	16	6/11
41	LH 2	16	6/11
42	pink 10	15	6/11
43	pink 9	15	6/11
44	LH 3	13	6/12, 6/28
45	LH 4, LH 5	15	6/12, 6/27
46	LH 5	11	6/12
47	RH 2, LH 1	9	6/12
48	RH 2, LH 2	11	6/12
49	RH 2, LH 3	12	6/12
50	RH 2, LH 4	18	6/27
51	RH 2, LH 5	18	6/27
52	RH 1, LH 2	12	6/28
53	RH 3, LH 2	12	6/28
54	LH 2, RH 4	10	7/7, 7/8
55	LH 2, RH 5	7	7/7
56	RF 1	8	7/7
57	RF 2	11	7/7
58	RF 3	10	7/7
59	RF 4	6	7/7

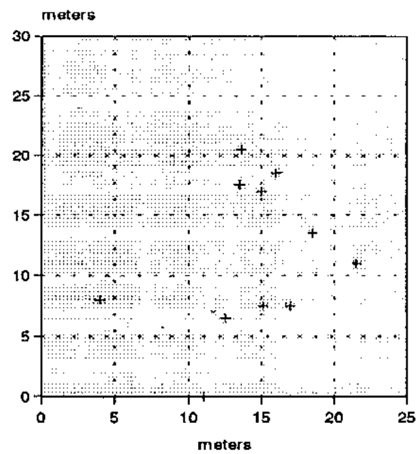
1. Not all frogs captured before 6/5 appear on the maps due to a change in the size of the area.
2. The colors and numbers on the markers indicate the identification band used.
3. RH=Right hind toe clipped. RF=Right front toe clipped. Same for LH and LF on the left side.

Appendix 2: Nightly distributions of frogs.

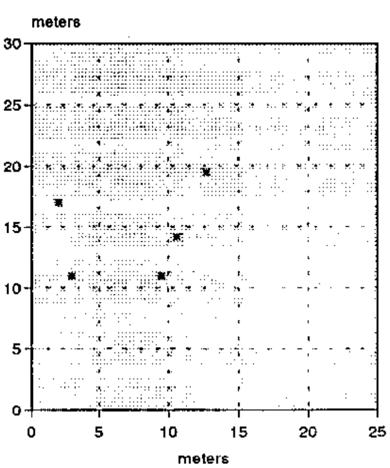
4 June 1992



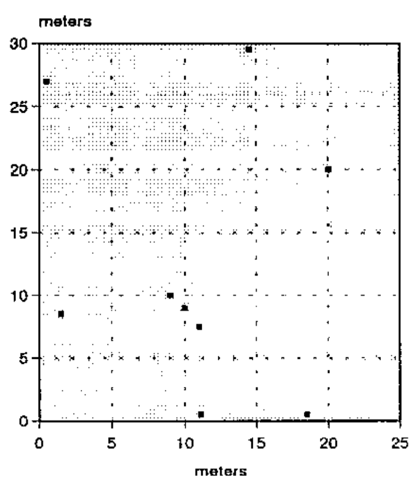
5 June 1992



9 June 1992

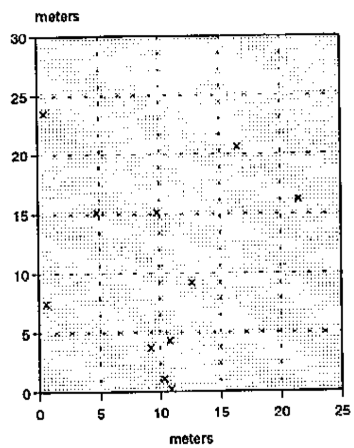


10 June 1992

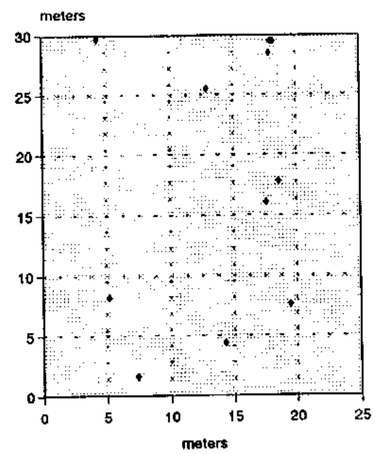


Appendix 2: Continued

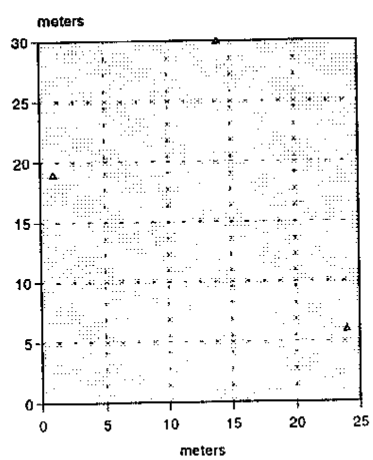
11 June 1992



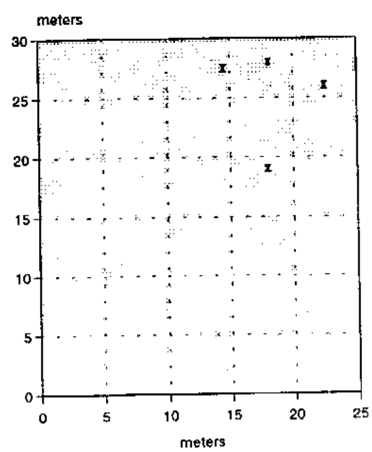
12 June 1992



27 June 1992

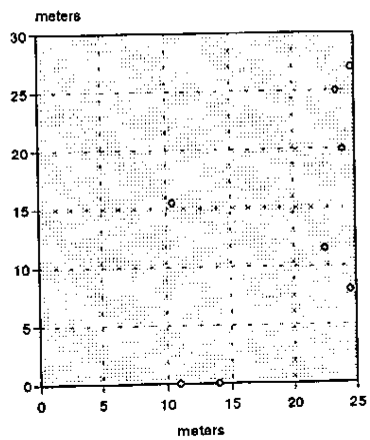


28 June 1992

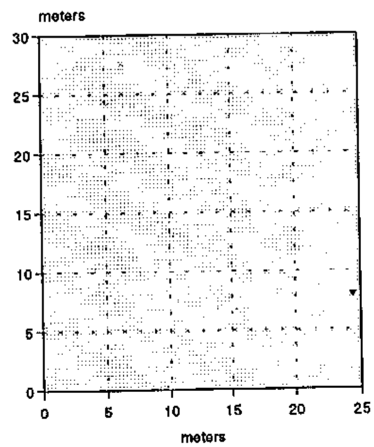


Appendix 2: Continued

7 July 1992



8 July 1992



Appendix 3: Distances between the two closest frogs for each night of study.

Date 1992	Distance Between the Two Closest Frogs (m)	Average Distance For All Frogs ($\bar{X}$)	Standard Deviation	Standard Error From the Mean (SEM)
June 4	3.5	3.7	5.2	1.73
June 5	1.6			
June 9	3.4			
June 10	1.4			
June 11	1.0			
June 12	0.0			
June 27	17.0			
June 28	3.5			
July 7	2.3			
$\bar{x} \pm SEM = 3.7 \pm 1.73$				

Appendix 4: Average distances between frogs for each experimental night of study.

Date	Number of frogs	Closest distance from one frog to another (m)	Average distance for each night (m)	Average distance for all nights (m)
June 4	2	4	4	6.47
		4		
June 5	11	2	3.43	
		2		
		2.69		
		3.91		
		1.58		
		1.58		
		3.91		
		1.8		
		3		
		6.67		
		8.63		
June 9	5	5.7	5.1	
		3.83		
		3.83		
		6.08		
		6.08		
June 10	9	11	7	
		11		
		7		
		7.5		
		1.41		

The distances between frogs was determined by using the Pythagorean theorem on the individual nightly plots (Appendix 2).

Appendix 4: Continued

Date	Number of frogs	Closest distance from one frog to another (m)	Average distance for each night (m)	Average distance for all nights (m)
June 10		1.41		6.47
(continued)		1.8		
		7.65		
		14.22		
June 11	11	5	4.75	
		5		
		1.71		
		1.71		
		1.08		
		1.08		
		8.68		
		9.44		
		5.26		
		6.66		
		6.66		
June 12	11	0	4.27	
		0		
		6.95		
		6.95		
		1.04		
		6.11		
		6.11		
		1.97		

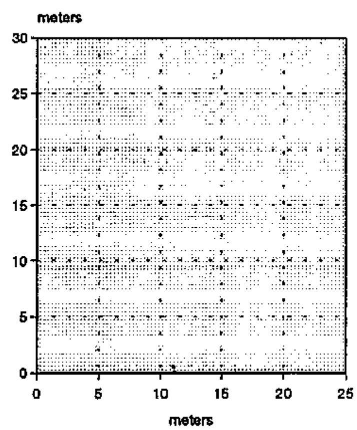
Appendix 4: Continued

Date	Number of frogs	Closest distance from one frog to another (m)	Average distance for each night (m)	Average distance for all nights (m)
June 12	11	1.97	4.27	6.47
(continued)		6.4		
		9.48		
June 27	3	17	20	
		17		
		26		
June 28	4	3.63	5.1	
		3.63		
		4.83		
		8.32		
July 7	8	3	4.55	
		3		
		2.33		
		2.33		
		5.02		
		4.03		
		4.03		
		12.65		

Appendix 5: Locations of the different perches occupied by each recaptured frog.

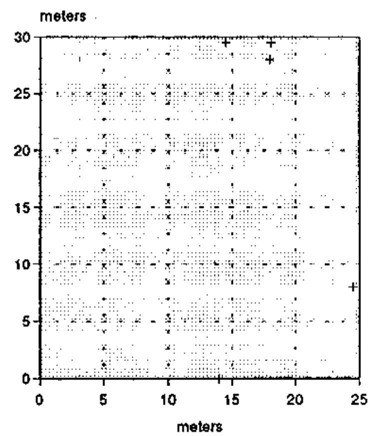
Frog #6

13 g



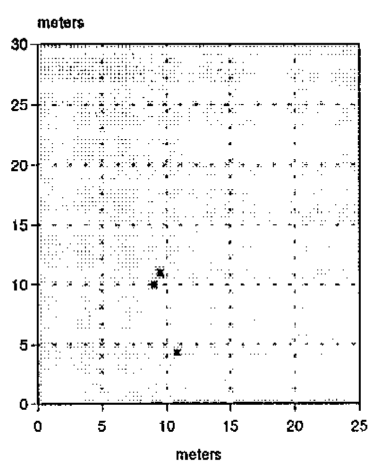
Frog #23

16 g



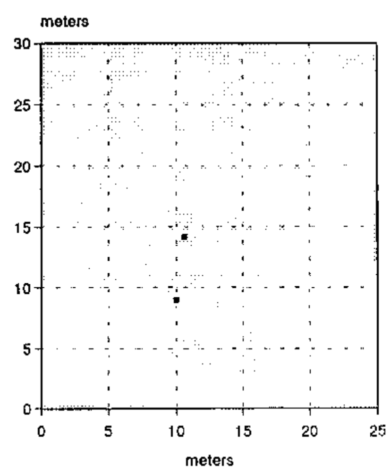
Frog #24

18 g



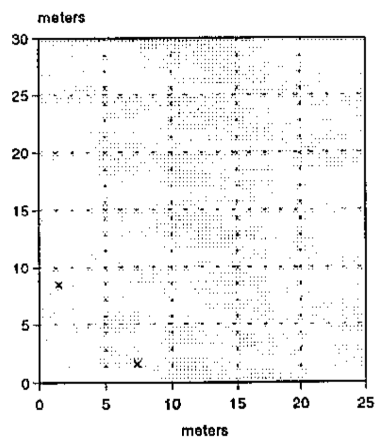
Frog #25

16 g

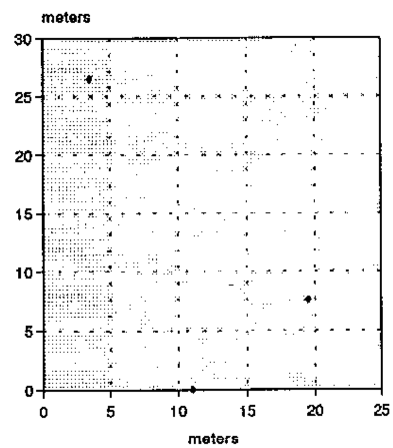


Appendix 5: Continued

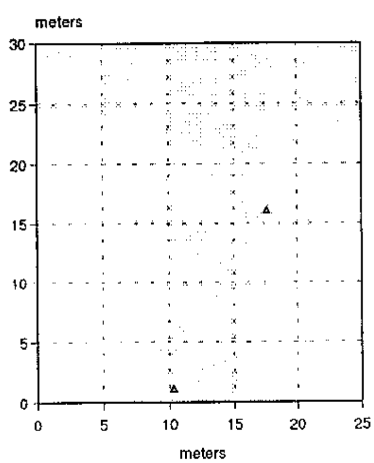
Frog #30
16 g



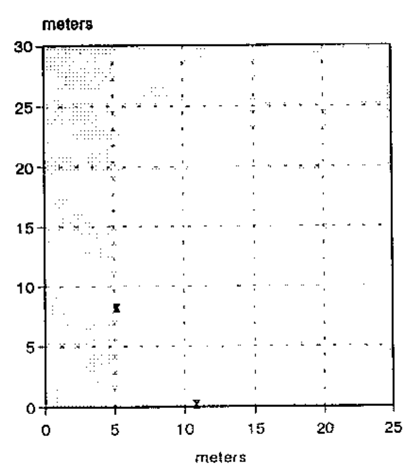
Frog #31
16 g



Frog #35
16 g

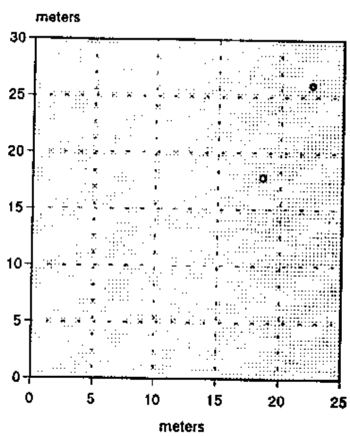


Frog #36
15 g

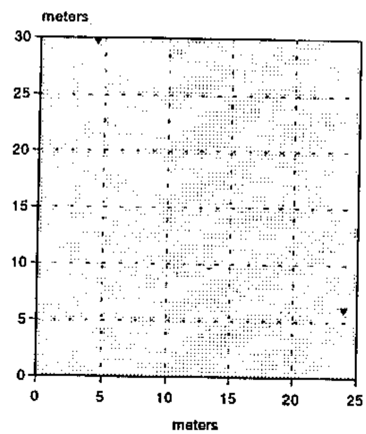


Appendix 5: Continued

Frog #44
13 g



Frog #45
15 g



Appendix 6: Distances between the closest sightings of each recaptured frog.

Frog #	Distance Between Sites of Frogs (m)	Average Distances For All Frogs ($\bar{x}$)	Average Standard Deviation	Standard Error From the Mean (SEM)
6	0.5	9.53	9.1	2.88
23	1.5			
24	1.1			
25	5.2			
30	9.1			
31	11.4			
35	16.8			
36	9.6			
44	9.1			
45	30.6			
$\bar{x}\pm SEM = 9.53\pm2.88$				