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Variation in reproductive success within a natural population of the American toad (*Bufo americanus*)

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VARIATION IN REPRODUCTIVE SUCCESS WITHIN A NATURAL
POPULATION OF THE AMERICAN TOAD (*Bufo americanus*)

BY

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DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy

in

Zoology

September, 1997

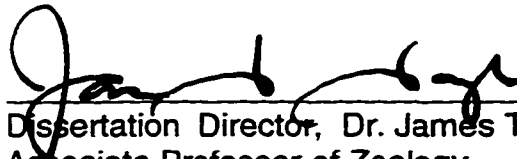
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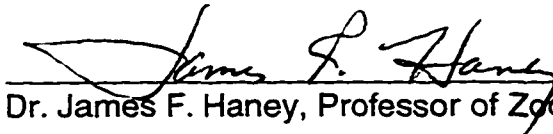
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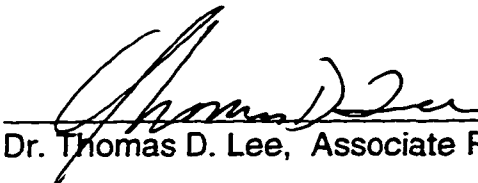
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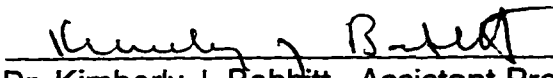
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ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. James T. Taylor, for his support, suggestions, and encouragement throughout the production of this dissertation. I am also grateful to my committee members, Dr. Kimberly Babbitt, Dr. James F. Haney, Dr. Larry G. Harris, and Dr. Thomas D. Lee for their constructive comments.

My deepest appreciation goes to my wife, Helena Matthews Cascon, for her support, suggestions and comments during the execution of this dissertation. I am very thankful to my sons Leandro and Pedro for help with love and patience throughout this changing process in our lives.

I am also grateful to my parents for their love and long time support, and to my parents-in-law for helping us with the problems resulted of our absence of Brazil.

I also wish to thank Sue Reidy for her support and friendship, and Many Hult, Diane Lavalliere and Barbara Millman for being always very helpful.

I thank Dr. Barry Keim, New Hampshire State Climatologist, for providing meteorological data.

I would like to acknowledge a grant from the Brazilian government agency "Conselho Nacional de Desenvolvimento

Científico e Tecnológico (CNPq)”, and the support of the
“Universidade Federal do Ceará”.

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ABSTRACT

VARIATION IN REPRODUCTIVE SUCCESS WITHIN A NATURAL POPULATION OF THE AMERICAN TOAD (*Bufo americanus*)

by

Paulo Cascon

University of New Hampshire, September, 1997

The purpose of this study was to investigate if mating success and clutch size are good estimates of reproductive success in a population of *Bufo americanus*, through the study of the contribution of life history parameters to the variation in individual reproductive success. A *B.americanus* population that breeds in a pond located in Madbury, NH was studied during the 1994, 1995 and 1996 mating seasons. In 1995 and 1996 clutches were also studied and the larvae were used in laboratory and field experiments. The following fitness parameters were investigated: mating success, clutch and egg size, growth rate and survivorship of the larvae, time to metamorphosis, proportion of larvae that

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completed metamorphosis, and body size at metamorphosis.

The results of this study suggest that male mating success was not size dependent in any of the three mating seasons studied. However, size assortative mating found in 1995 is an indication that male body size may represent an advantage in reproductive success, and consequently be subject to selection, because larger males may father a larger number of offspring due to the positive correlation between female body size and clutch size.

The influence of male and female body size on reproductive success was limited to effects on the number of eggs produced (females) or fertilized (males), as variation in the other fitness parameters could not be related to variation in the size of parents. Variation in the larvae in the fitness parameters studied was also not significantly related to variation in number of offspring or mean size of eggs in the clutches.

Experimental results suggest that variation in food and density levels affect larval growth and survival, as increase in food level and decrease in initial density had a positive effect on larvae size and survivorship, and on the percent of larvae that complete metamorphosis.

INTRODUCTION

Breeding success is the most important aspect of fitness of organisms. According to Clutton-Brock (1988a), breeding success has the following components: survival to breeding age; reproductive life span; fecundity; mating success; and offspring survival.

Differences in reproductive success can be caused by chance, by short-term individual variation or by genetically-based phenotypic variation (Clutton-Brock, 1988a), but only differences caused by the latter can lead to the occurrence of natural selection (McVey, 1988). Understanding the extent and distribution of individual differences in the number of offspring produced in natural populations is relevant to studies of both population dynamics and natural selection (Brown, 1988).

Mating success and clutch size have been used as measures of reproductive success in many studies. However, number of young surviving to breed or the number of grandchildren are more useful measures of parental fitness (Godfray *et al.*, 1991). Clutton-Brock (1988b), in an analysis of studies of lifetime reproductive success, concluded that "there appears to be a consistent tendency for estimates of standardized variance in female breeding success based on the number of zygotes produced to underestimate

variation in the number of offspring recruited into the breeding population, in some cases by as much as an order of magnitude”.

The reproductive success of each individual will, ultimately, be the result of several variables. In anurans these variables include mating success, number of ova produced (females) or fertilized (males), proportion of eggs that hatch, proportion of larvae that complete metamorphosis, and survival from metamorphosis to sexual maturity. Nevertheless, mortality during the larval period is the most important mechanism regulating amphibian populations (Savage, 1952; Wilbur, 1977; Heyer, 1979; Wilbur, 1980; Tejedo, 1993). In the natural environment several mortality agents can affect numbers and kinds of individuals recruited into the adult population, including temperature, ephemeral habitats, rainfall, disease, predation, competition, and chemical effects (Kaplan, 1980). Thus egg viability, hatching size, larval growth rate, length of larval period, and size at metamorphosis play critical roles in determining survivorship in amphibian larvae, and all are subject to persistent selection (Travis *et al.*, 1987). Anurans present several advantages as objects of studies on fitness, such as ease of capture, visibility, and suitability for field experimentation. However, their greatest advantage is their external mode of fertilization that allows unambiguous quantification of the initial reproductive success of

individuals (Howard, 1988a).

Non-random mating with respect to body size has been observed for most anuran populations that have been studied (reviews in Arak 1983, Howard and Kluge, 1985 and Andersson, 1994; but see Crump and Townsend, 1990). It may take two different forms: size dependent mating, in which large males have higher reproductive success than do smaller ones; or size assortative mating, where there is a significant correlation between the size of males and the size of females in mated pairs (Arak, 1983).

Size dependent mating is a result of sexual selection, which can operate through two different processes (Maynard-Smith, 1991): female choice (intersexual selection) in which females would mate preferentially with larger males; and/or male-male competition (intrasexual selection) where larger males would have superior ability in getting mates than smaller ones.

Size assortative mating could also be a result of sexual selection. In this case, females would select males of particular sizes relative to their own, and/or males would compete to mate with females of particular sizes (Howard, 1988b). Male-male competition would also produce assortative mating if only those males who were well matched with females would resist take-over attempts by other males (Arak, 1983; Halliday, 1983a).

Previous studies have suggested that body size represents an advantage in initial reproductive success in *Bufo americanus*, as clutch size is correlated with female body size (Howard, 1988b), and large males are more successful in mating (Gatz, 1981; Howard *et al.* 1994) or mate with larger females (Licht, 1976; but see Wilbur *et al.*, 1978; Kruse, 1981; Sullivan, 1992) than do small males.

The purpose of this study was to investigate if mating success and clutch size are good estimates of reproductive success in a population of *Bufo americanus*, through the study of the contribution of life history parameters to the variation in individual reproductive success. The following fitness parameters were investigated: mating success, clutch and egg size, growth rate and survivorship of the larvae, time to metamorphosis, proportion of larvae that complete metamorphosis, and body size at metamorphosis.

The following null hypotheses were tested: a) mating success is not related to body size; b) the number of zygotes produced or fertilized is not a predictor of reproductive success; c) egg size does not affect probability of metamorphosis or size at metamorphosis; and d) variation in food and density levels does not affect larvae growth and survival, or the correlations between them.

Density dependence has been widely demonstrated in

populations of amphibian larvae, where crowding has been shown to affect larval survivorship, growth rate, body size at metamorphosis, and length of the larval period (review in Smith, 1987). Crowded effects may be the result of reduced food ration, competition for limited food, social interactions, and psychological stress (references in Murray, 1990). The effects of density on *Bufo americanus* larvae were the subject of previous experimental studies (Brockelman 1969, Wilbur, 1977). In the present study, I investigated variation in growth and survival of the larvae, at different levels of food per individual, as well as at different densities. This allowed evaluation of the crowding effects independent of the effects of variation in food availability.

METHODS

Study Organism

Bufo americanus is one of the most common anurans in North America, with a distribution that includes most of the eastern half of the United States and southeast Canada (Conant and Collins, 1991). Populations of this species have a short breeding season, which often lasts less than three days (Howard, 1988b). They breed in a wide array of fresh-water habitats, including lake shores, ponds, temporary marshes and swamps (Brockelman, 1969). Males of *B. americanus* do not defend territories or provide any form of parental care (Howard *et al.*, 1994). The larval stage lasts only 2-3 months, and the metamorphs undergo rapid post-metamorphic growth and development (Pough and Kamel, 1984).

Study Site

The study was conducted in a permanent artificial pond, known as the Forestry Pond, located at the Kingman Farm, Madbury, NH. This facility is an agricultural experiment station of the University of New Hampshire.

The Forestry Pond is a oval mass of water, with an area of 0.13 ha, 139 m of shoreline, and a maximum distance between opposite margins of 57 m (Duerring, 1982). Duerring (1982) gives a

complete description of this pond. For analysis of spatial location of the animals in the pond, 28 numbered wooden sticks were laid along the margins of the pond at intervals of approximately 5 meters, prior to the beginning of the mating seasons. Other anuran species in this pond are *Pseudacris crucifer*, *Rana catesbeiana* and *Rana clamitans*.

Observation, Capture, and Marking Techniques

Field work in 1994 was limited to 4 nights in the middle of the *Bufo americanus* mating season. In 1995 and 1996 the pond was visited nightly from early April, before the beginning of the mating season, until the end of all reproductive activity in May. Individuals of *B. americanus* were captured manually with the aid of hand held flash lights and head lamps, after determination of behavior and location in the pond.

At first capture, all individuals were sexed, measured and marked by clipping a unique combination of the toes (Waichman, 1992). The thumbs were not clipped, as they are used in reproduction. Body weight was measured to the nearest gram with a 200 g Pesola scale. Snout-vent length (SVL) (distance from anterior margin of snout to posterior margin of vent); head width (HEW); radio-ulna length (RUL) (distance from insertion of digit one to elbow); thumb length (TML) (minimum distance from medial edge of palmar tubercle to tip of digit one); and tarsus length (TSL),

were measured to the nearest millimeter with a ruler fitted with a right-angle stop at one end (SVL) or a plastic caliper (the other measures).

Pairs found in amplexus, but not yet laying eggs, were put in plastic bags with some pond water and transported to the laboratory. There they were placed in 15 l buckets with 1 l of aged tap or well water. After oviposition the parents were measured, marked, and returned to the source pond as soon as possible. In 1996 a series of 30 pairs already laying eggs were collected and the toads measured and marked as above.

Air temperature and precipitation data collected in 1995 and 1996 at the UNH Campus in Durham (approximately 3.8 km from the study pond) were provided by Dr. Barry Keim, New Hampshire State Climatologist.

Clutch and Egg Size

Each egg mass laid in the 15 l buckets was transferred to white pans and photographed. The number of eggs was later counted from a projected 35 mm slide. Samples of 20 eggs were haphazardly selected from each clutch, in 5 segments with 4 eggs each, taken from different parts of the clutch. These eggs were immediately measured with an ocular micrometer fitted to a dissecting microscope, and then preserved in 10% formalin. Egg size was recorded to the nearest 0.01 mm, as the average of two

diameter measures taken perpendicular to each other.

Hatching Success

From each clutch laid in the laboratory, three (1995) or four (1996) samples of 100 eggs were randomly selected and kept separately in 34 x 27 x 11 cm plastic containers containing 8 L of water, under identical laboratory conditions. The rest of the eggs were returned, as soon as possible, to the source pond. The number of eggs that hatched into live tadpoles was noted. Samples of 20 tadpoles randomly selected from each clutch were fixed in 10% formalin, 8 (1995) or 4 (1996) days after hatching. Later, these larvae were measured to the nearest 0.1 mm, with a caliper observed through a dissecting microscope.

Larval Survival, Growth and Development Rates

Laboratory Experiment

The larvae hatched in the laboratory, when in stage 25 of Gosner (1960), were used in a factorial experiment in which two levels of density and food availability were combined in 4 different treatments in a completely randomized design (Table 1). The treatments with high and low density started with 20 and 10 individuals, respectively. Treatments with high food levels received twice the amount of food per individual than those with low food level. The purpose of this experiment was to investigate variation in survival and in growth and development rates, among the

different clutches, as a function of density and food availability.

This experiment was performed in 1995 and again in 1996, with larvae from 10 randomly selected ovipositions. In one of the treatments (D=low density/high food), it was performed with larvae from all 34 (1995) and 28 (1996) clutches collected. Each treatment had three (1995) or four (1996) replicates from each egg mass.

The larvae were kept in 19 x 14.5 x 5 cm plastic containers containing 1.4 L of aged tap water or well water that was completely or partially changed before each addition of food. The food used in these experiments was a mixture of PURINA rabbit chow and TETRA-MIN fish flakes, mixed in a 3:1 ratio by mass and ground (Alford, 1986). The amount of food added to each container during the experiments is presented in Table 2. Based on the observation of the amount of food remaining in the containers, the food ration per individual was determined such that there was always food available in the high food treatments, whereas in the low food treatments there were periods of food shortage before the next addition of food.

Mortality caused a reduction in the number of larvae in the containers, especially in the treatments that received less food. In 1996 the experiment was allowed to run to completion without interference, but in 1995 an attempt was made to keep densities in

each treatment relatively constant by reducing the number of larvae in each container, and by moving tadpoles from one replicate to another. This led to elimination of one of the replicates. The two treatments with low food levels (A and C), were eliminated after the first 53 days of the 1995 experiment, as most of the tadpoles had died by that time. The changes in the number of individuals in each replicate and in the number of replicates in the 1995 experiment are presented in Table 3.

During the 1995 experiment, total length of each surviving larva was measured on day 27 and on day 52 of the larval period. On day 27, all tadpoles from one replicate of each clutch were measured. On day 52, all surviving tadpoles were measured. The exception to this was Treatment D (High food / low density) in which larvae from all ovipositions were measured on day 27, and from 10 selected ovipositions on day 52. The measurement was made to the nearest 0.1 mm, with a caliper observed through a dissecting microscope. This experiment was interrupted on day 60, due to mass mortality resulting from the use of contaminated water.

In 1996, the lengths of the larvae remaining on day 40 were measured by video taping the larvae inside a water container with a 10 mm scale in the bottom. The sizes of the larvae were then estimated by comparing the larva with the scale as projected

on a TV monitor. The number of larvae that completed metamorphosis, and the duration of the larval period (beginning of the experiment to complete metamorphosis) of each individual were noted.

Field Experiment

The purpose of this experiment was to investigate variation in survival and in growth and development rates among the different clutches in the natural environment. Fifty 1 l plastic containers were modified with screens in the sides and in the top, to allow circulation of water, and with three Styrofoam balls linked at the sides close to the top, to provide flotation. Fifty larvae from each of ten egg masses were divided into sets of 10, and each set placed in a container. The containers were then floated in the pond, linked one to the other by a rope, in a line in which their sequence was randomly established. On day 50 of the larval period, the larvae remaining in each container were temporarily transferred to a container with a 10 mm scale in the bottom, and video taped. The sizes of the larvae were later estimated by comparing the larvae with the scale projected on a TV monitor. The containers were checked weekly, and all individuals with 4 fully developed limbs were transferred to the laboratory inside plastic bags for further measurements.

Size at Metamorphosis

The metamorphosed animals from the field and laboratory experiments of 1996 were measured immediately after complete loss of the tail (stage 46; Gosner, 1960). The measurements were made by video taping them over a 10 mm scale, and later comparing the animal with the scale as projected on a TV monitor.

Data Analysis

Statistical analyses were performed using INSTAT version 2.01 (GraphPad Software) and SYSTAT version 5.0 (Systat Inc., Evanston, IL.), both for Macintosh. Means were compared with unpaired t tests, when data showed approximate equality of variance, and Mann-Whitney tests when variances were not equal. Two-way ANOVAs were used to estimate the effects of variation in food and density levels in the laboratory experiments. Variance proportions (R^2) were used to estimate associations among life history parameters. Analyses of Covariance were used to estimate associations, while adjusting for a third variable. To estimate the association between female body weight and number of eggs, with effect of body length removed, residuals from the regression of number of eggs on body length were correlated with body weight.

When necessary, data were log transformed to meet assumptions of normality or homogeneity of variances.

RESULTS

Mating Pattern

Although in both 1995 and 1996, individuals of *Bufo americanus* first arrived at the study pond on exactly the same day (April 19), the two mating seasons differed in many aspects. In 1995, reproductive activity started 12 days after arrival, whereas in 1996 it started 3 days later. In 1995 vocalization and amplexus lasted respectively 13 and 9 days, whereas in 1996 they lasted 4 and 6 days. These seasonal differences may be related to the fact that in 1995 the early spring was colder and had much less precipitation than in 1996 (Figure 1).

A total of 516 individuals was marked during this study: 65 in 1994, 236 in 1995, and 215 in 1996. During the 1995 and 1996 mating seasons, respectively, 7 and 8 individuals marked in the previous year were recaptured. Sixty one individuals were recaptured in the same year they were marked; analysis of distance moved between recaptures (Figure 2) shows that males moved an average of 0.49 m/day between recaptures. Thus, males did not remain in the same places in the pond during the mating season.

The sex ratio was male-biased (5:1 males/female in 1994; 4.9:1 in 1995; and 3.03:1 in 1996). This bias may have been a

consequence of longer activity period by males.

The total numbers of pairs of *B. americanus* collected in amplexus were 13 in 1994, 41 in 1995, and 64 in 1996.

Ovipositions of the 1994 amplexed females were not studied. Eggs were laid in the laboratory by 34 of the 1995 amplexed females. In 1996, 30 females were already laying eggs when found; among the 34 others, 28 laid eggs in the laboratory.

The daily mean size of the males found in vocalization, amplexus, and not performing any reproductive activity, and of females found in amplexus is shown in Figure 3. There were no significant differences in size through time during the 1995 and 1996 mating seasons.

Males found in vocalization were larger than males found in amplexus in 1994, 1995 and 1996, with a statistically significant difference in 1994 and 1996 (Tables 4 and 5). When the size of males found in different periods of the 1995 and 1996 mating seasons were compared, males in vocalization were larger than males in amplexus in the beginning, middle and end of both seasons, with a statistically significant difference in the end of the 1996 mating season (Figure 4). The size of the males found in vocalization and in amplexus had a unimodal distribution (Figure 5). These results suggest that larger size did not represent an advantage for males in the process of getting mates in those

mating seasons.

Males found in vocalization were also significantly larger than males found not performing any reproductive activity in 1996 (Tables 4 and 5). In 1995, on the other hand, the only significant size difference among males was the larger size of males not performing any reproductive activity, in relation to the males in amplexus (Tables 4 and 5). In 1996, males in vocalization also had greater head width, tarsus length, and weight than males in amplexus (Figure 6). When adjusted for differences in body size, males in vocalization were relatively heavier than males in amplexus in all three years (Table 6), but this might be due to the fact that the males in amplexus were weighed after they released sperm for egg fertilization.

The mean size of the males observed trying to displace amplexed males in 1996 was not significantly different than that of males found in vocalization, amplexed with females not laying eggs, amplexed with females laying eggs, or not performing any reproductive activity (Tables 4 and 5).

Mean size of males found in amplexus with females laying eggs in 1996 was not significantly different than that of the males found in amplexus with females not yet laying eggs (Tables 4 and 5). This indicates that if displacement of amplexed males by larger males happens, it was not frequent enough to

change the mean size of the amplexed males.

Females were significantly larger than the males with which they were amplexed in all three years (Table 7). Snout-vent length, head width, radio-ulna, thumb and tarsus length, and weight in males were positively correlated with those measures in females with which they were amplexed in 1995 (Figures 7 and 8), suggesting a size assortative mating in this year. However, there were no significant correlations among the pairs collected in 1994 or 1996, with the exception of a positive correlation in tarsus length in 1994 (Figures 7 and 8).

When adjusted for body size in an analysis of covariance, there were almost significant trends in amplexed couples for males to have relatively larger tarsus than females in 1994 ($P=0.052$) and for females to have relatively larger thumbs than males in 1995 ($P=0.056$) and 1996 ($P=0.03$).

Clutch and Egg Size

The number of eggs per clutch averaged $5,497 \pm 2,153$ SD (range 1,494 - 11,322, $n=31$) in 1995 and $5,271 \pm 2,255$ SD (range 831 - 9,639, $N=26$) in 1996. Clutch size was positively related to the snout-vent length of both parents in 1995 and of the mother in 1996 (Figure 9). The positive relationship between clutch size and female size was probably a consequence of a higher egg production capacity by larger females. On the other hand, the

positive relation between clutch size and male size in 1995 was a consequence of the positive size assortment in mated pairs observed in this year. When corrected for body length, number of eggs was also positively correlated with female body weight in 1995 ($P < 0.01$, $R^2 = 0.32$) and in 1996 ($P < 0.01$, $R^2 = 0.53$).

The mean size of the eggs in each clutch averaged 1.86 ± 0.10 SD mm (range 1.67 - 2.10 mm, $N=20$) in 1995, and 1.92 ± 0.07 SD mm (range 1.78 - 2.04 mm, $N=27$) in 1996. The size of the eggs had a unimodal distribution in both years (Figure 10). Egg size was positively related to the mother's but not to the father's snout-vent length in 1995, and not related to the length of either parent in 1996 (Figure 9). When corrected for mother's body length, egg size was positively correlated to female weight in 1995 ($P=0.02$, $R^2=0.25$), but not in 1996 ($P=0.13$, $R^2= 0.09$).

There was no correlation between number and size of the eggs in either 1995 or 1996 mating seasons (Figure 11). However, when controlling for female size, egg size was inversely correlated with clutch size in 1995 ($P < 0.01$).

Hatching Success

The percent of hatchings from each egg mass was negatively correlated with egg size in 1996, but not in 1995 (Figure 12). This may have been a consequence of deficient oxygenation of

the water where the eggs were kept in 1996. Large eggs might be susceptible to higher mortality than small ones in poorly oxygenated water, because they have smaller surface area to volume ratio.

The percent hatching was not related to the number of eggs, nor to parent's snout-vent length in either of the mating seasons (Figure 12).

Larval Experiments: Survival and Growth Rate

Larval size immediately after hatching, an indicator of initial development rate, showed a trend toward a positive relationship with egg size in 1996, when the measurement was made just four days after oviposition, but not in 1995, when the larvae were measured eight days after oviposition (Figure 13). On the other hand, larval size immediately after hatching was not related to the number of eggs (Figure 13), or to the snout-vent length of either parent (Figure 14).

Higher mortality in the two experimental treatments with higher initial density led to disappearance of the difference in the number of tadpoles among the four treatments after 60 days of the experiment in 1996 (Figure 15). Consequently, in this year, density effects could only have existed in the initial period of larval development.

The mean length of the tadpoles in each of the

treatments of the 1995 and 1996 laboratory experiments, and in the 1996 field experiment, and the results of 2-way ANOVA on the laboratory data, are presented in Table 8. Increase in food level and decrease in initial density had a positive effect on larvae size in 1996.

Following initial development, size of the tadpoles was not related to the snout-vent length of the mother in any of the treatments of the 1995 and 1996 experiments (Figures 16 and 17). In general there were no paternal effects on larval size either (Figures 16 and 17).

Larval size after initial development was not correlated with either clutch or egg size in 1995 (Figure 18) nor in 1996 (Figure 17).

The size of tadpoles at day 50 of the larval period in the 1996 field experiment was not correlated with size of either parent, nor with the number or size of the eggs (Figure 19).

Larval Survivorship

The mean percent of larval survival in each of the treatments of the 1995 and 1996 laboratory experiments, and the results of the 2-way ANOVA of those data are presented in Tables 9 and 10. The results indicate that decrease in the amount of food and increase in density had a significant negative effect on larval survival in both experiments (Tables 9 and 10). Food was more

important that density early in the larval life, but later density became more important than food (Tables 9 and 10).

The survival of the tadpoles in general was not significantly related to the number or size of the eggs in any of the treatments of the 1995 or 1996 laboratory experiments (Figures 20, 21, 22 and 23). These results suggest that energetic reserves from the egg are only marginally important for survival, and only when food is scarce.

The only significant relationship between larval survival and larvae length found in the 1995 and 1996 laboratory experiments was a negative one observed between day 28 and day 52 of the larval period, in the high food / high density treatment of the 1995 experiment (Figure 24). This result suggests that smaller larvae can on occasion have a survival advantage over larger ones in conditions of intense competition.

Metamorphic Success

The mean percent of larvae that completed metamorphosis in each of the treatments of the 1996 laboratory experiments, and in the field experiment, and the results of a 2-way ANOVA of the laboratory data, are presented in Table 11. The mean percent of larvae that successfully completed metamorphosis was higher in the field experiment than in any of the treatments of the laboratory experiment (Table 12).

The percentage of larvae that successfully completed metamorphosis was not significantly related to the snout-vent length or weight of either parent, to the number or size of the eggs, or to the length of the larvae, in any experimental situation (Figures 25, 26, 27 and 28).

Time to Metamorphosis

The mean time to metamorphosis in each of the treatments of the laboratory experiment, and in the field experiment, and the results of a 2-way ANOVA of the laboratory data are presented in Table 13. The results indicate that neither food nor density levels had a significant effect on the length of the larval period. Mean time to metamorphosis in the field experiment was significantly shorter ($p < 0.001$) than in each one of the treatments of the laboratory experiment (Table 14).

Time to metamorphosis was not significantly related to the size of either parent, to the clutch or egg size, nor to the larval length, in any of the treatments of the 1996 laboratory experiment (Figures 29 and 30) or in the field experiment (Figure 31).

Size at metamorphosis

The mean body length at metamorphosis of the larvae raised in each one of the treatments of the 1996 laboratory experiment, and in the 1996 field experiment, and the results of a 2-

way ANOVA of the laboratory data, are presented in Table 15. The results showed that neither food nor initial density level had a significant effect on size at metamorphosis in the laboratory experiment. The mean size of the metamorphs from the field experiment was significantly larger than those from both low initial density treatments in the laboratory experiment ($p=0.02$, $p<0.001$). The size of the metamorphs from both experiments had a unimodal distribution (Figure 32).

Body length of metamorphs from the 1996 laboratory experiment, and from the field experiment, was not related to the snout-vent length and weight of either parent (Figures 33 and 34), or to clutch or egg size (Figure 34 and 35).

Metamorph body length was not related to larval length in any of the treatments of the laboratory experiment, nor in the field experiment (Figure 36). There was a negative correlation between body length of the metamorphs and time to metamorphosis as well as percent of larvae that successfully completed metamorphosis in the field experiment (Figures 37 and 38). This result was not seen in the laboratory experiment (Figures 37 and 38).

DISCUSSION

Mating Pattern

The *Bufo americanus* population studied here showed yearly variation in mating pattern: size assortative mating in 1995 and random size mating in 1994 and 1996. Previous studies on *Bufo americanus* have also presented conflicting results with respect to the nature of mating in this species. Random mating with respect to male body size in *B. americanus* was found in three studies (Wilbur *et al.* 1978; Kruse, 1981; and Sullivan, 1992). On the other hand, three other studies demonstrated non-random mating: Licht (1976) reported significant size-assortative mating, but no size-dependent mating among males; Gatz (1981) found no size-assortative mating but demonstrated size-dependent mating success among males; and Howard *et al.* (1994), in a long-term investigation, found size-dependent mating success in 5 of the 8 years studied.

Female choice is expected to have a major role in the reproductive behavior of anurans with a relatively long breeding season, but not in anurans with a short mating season (explosive breeders), such as *Bufo americanus* (Wells, 1977a). Nevertheless, Licht (1976), Gatz (1981) and Howard (1988b) suggested that the

non-random mating pattern observed in *B. americanus* populations was, at least in part, a product of sexual selection operating by the mechanism of female choice.

Licht (1976) based his conclusions on observations that “females moved directly to particular calling males and passed by others on their way to those with which they finally achieved amplexus”, and that “females waited for males to resume calling before they resumed swimming and moved directly towards them”. Gatz (1981) suggested that the occurrence of female choice in his study was indicated by the male behaviors of calling, remaining stationary during a single night, and attempting amplexus with any approaching toad. Finally, Howard *et al.* (1994) concluded that mate choice occurs in this species, based on the fact that females initiated 48 ± 28 % of the observed pairings each year, and that of the 56 observed pairings during this 8 year study that were initiated by females, larger than average males were chosen 38 times.

Mate choice may have played a role in the assortative mating found in the study population in the 1995 mating season. However, during all three mating seasons, males formed dense aggregations in which they actively searched and scrambled for the possession of females, a pattern typical of explosive breeders (Wells, 1977a; Arak, 1983). There was also a strongly male-biased sex ratio in all three seasons. Such conditions would reduce the

chances for females of the *Bufo americanus* population to exercise choice. Nevertheless, Halliday (1983a) stressed that studies on Elephant Seals have shown that intense competition among members of one sex does not preclude the expression of mate choice by the other sex.

Anurans are acoustically oriented organisms, and the major component of anuran courtship is the production of advertisement calls by males (Duellman and Trueb, 1986). Female choice would possibly be based on the variation in call parameters such as rate (number of calls/min), duration, pulse rate, or dominant frequency. Consequently, the production of a non-random mating pattern with relation to male size by the mechanism of female choice would depend on the correlation of one or more call parameters with male body size, and on the ability of females to discriminate variation in call parameters.

The way in which female preferences evolve remains a controversial issue in the theory of sexual selection (Andersson, 1994; Andersson and Iwasa, 1996). In anurans, mate preference may provide immediate effects on the female's reproductive success, such as better oviposition sites and/or paternal care (Ryan, 1991), or higher fertilization success or reduced chances of contracting a disease or parasite from a mate (Howard *et al.*, 1994). Nonetheless, *Bufo americanus* is not territorial and does not

provide paternal care. Moreover, a correlation between fertilization efficiency and male body size or degree of body size difference between mated pairs was not found in this study or by Kruse (1981). On the other hand, the possibility that females selected males to avoid contamination by parasites was not investigated for this species.

There are two major classes of models that try to explain how selection maintains mating preferences for species in which they do not provide immediate benefits for the female: the “good-genes” and the “correlated responses” or “runaway selection” models (Balmford and Read, 1991; Howard *et al.*, 1994). The good gene hypothesis suggests that females should select traits that are indicative of heritable variation in viability (Arnold, 1983). As larger males are either older or have grown faster than smaller males, females may gain by mating with a large male because the benefits of rapid growth and/or high survival will be passed on to offspring (Arak, 1983). Moreover, male size may also be correlated with other traits that enhance an offspring fitness component (Howard *et al.*, 1994).

The runaway selection model suggests that female mating preference is essentially arbitrary, and that it may evolve as a correlated response to the selection pressure that is exerted on preferred male sexual characters. In this case mate choice would be

nonadaptative, because discriminating females would have the same survivorship and fecundity as nondiscriminating females (Howard *et al.*, 1994).

Mate choice also may not be a result of active choice, but simply a result of the attraction to mates emitting more conspicuous or intense signals (Forrest and Raspet, 1994; Gibson and Langen, 1996). As call intensity, as measured by sound pressure levels, was positively correlated with body size in a population of *Bufo americanus* studied by Gerhardt (1975), the non-random mating observed in this study may have been a consequence of a higher attractiveness of large males, instead of a active choice by the females.

Mate choice is only one of the factors that may determine the distribution of mating among individuals in a breeding population; the other is mating competition. Mate choice and mating competition will often occur together and interact within a single mating system (Halliday, 1983a).

Male-male competition in anurans takes the form of territorial defense, scramble competition, or calling in choruses (Arak, 1983). Although the defense of favorable reproductive habitat by large males may produce a male size advantage in mating, as in *Rana catesbeiana* (Howard, 1978) and *Rana clamitans* (Wells, 1977b), territorial behavior is more typical of species with

a long mating season. Moreover, the spatial location of calling males observed in this study, where on several occasions they were found calling less than 20 cm apart, along with the movement of the males from night to night, suggests that the non-random mating pattern in this species was not the result of territorial behavior.

In explosive breeders, large males have been shown to have advantage over small ones in aggressive encounters during mate search (Davies and Halliday, 1979) and in interactions between unpaired males and paired males (Berven, 1981, Davies and Halliday, 1977, Wells, 1979). Such a size advantage may occur because larger males are stronger than smaller males and/or because some correlate of male body size influences competitive ability.

Male arm length has been cited as one body size correlate that could influence competitive ability, as males with longer arms may possess an advantage in remaining clasped to females when challenged by other males (Howard and Kluge, 1985). In fact, Lee (1986) found that in 4 of the 5 species of explosive breeders he tested, amplexant males had longer forelimbs than non-amplexant males at any body length. Moreover, males with longer arms than females with the same body length, a result of sexual selection operating on males, was found for the explosive breeder *Rana sylvatica* (Howard and Kluge, 1985).

In this study, amplexant males did not have longer arms than non-amplexant males, nor did males have relatively longer arms than females. These results suggest that displacement of amplexant males by other males is not frequent in this population.

Displacement of amplexed males by other males has been observed in *Bufo bufo* and *Rana temporaria*. In these species some males congregate around the spawn-site and attempt to dislodge paired males from females (Arak, 1983) whereas others search for females away from the spawning site, often at the edges of the pond where unpaired females are arriving. Although these alternative strategies are not rigidly fixed in particular males, with individuals moving around the pond and switching between searching and struggling, Arak (1983) found that those males searching at the spawning site are significantly larger than those away from it.

In this study, the size of the males found trying to displace amplexed males in the communal spawn-site was not significantly different from the size of the males found in other areas of the pond. This also suggests that displacement of amplexed males by other males is not common in this population.

Gatz (1981) and Howard (1988b) suggested that male-male competition played a role in the non-random mating by body size that they observed in *Bufo americanus*. Gatz (1981) stated

that the displacement of amplexed males by other males happened at least once in his study, although he did not believe that this form of male-male competition contributed significantly to the size-dependent mating he found. The capture of a female twice in an interval of two days, each time amplexed with different males, led him to conclude that the original male was displaced by a larger one. However, such an observation is not a strong indication of male displacement, as the second male could have amplexed the female just after her release by the first male, following a successful mating. In the present study, females returned to the pond after having laid eggs in the laboratory were found amplexed to other males days later, in which cases there was no oviposition.

Howard (1988b) considered males to be successful in mating only after egg deposition was observed. He considered that pair formation alone was not a sufficient measure of mating success because of the chance that a paired male could be separated from his mate prior to fertilization.

The frequency with which males try to displace amplexed males seems to be subject to variation among *Bufo americanus* populations. Whereas this behavior was observed many times in the present study, it was observed just once by Gatz (1981), who studied two breeding populations of this species, one of them in two different breeding seasons. Arak (1983) stressed that the presence

or absence of male displacement is not necessarily a species attribute. Indeed, male reproductive tactics are expected to vary with the operational sex ratio, and the density of individuals.

Non-random mating with relation to male body size may also be a result of forms of male-male competition that do not involve direct interaction between males, but rather are a result of variation in some other behavioral patterns.

Number of nights spent by the male in the pond could be one of these behavioral patterns, as an increase in this number would improve the chances of mating. Gatz (1981) found that large *Bufo americanus* males were captured on significantly more nights at the pond than small ones, and considered that this was one of the factors that produced the non-random mating by size observed. Arak (1988) found that number of nights that males spent at the pond influenced the seasonal mating success in a population of *Bufo calamita*. However, Christein and Taylor (1978) found that breeding and non breeding male *B.americanus* spent the same amount of time in the pond area.

An early arrival at the breeding pond would also improve the chances of mating success especially if the reproductive females also arrive in the pond at the beginning of the mating season. Gatz (1981) did not cite early arrival as one of the factors that produced the non-random mating by size he observed, although

he found that large *Bufo americanus* males tended to arrive at the pond earlier than small males and that one of the factors that produced the non-random mating with relation to size was that larger males spent more days in the pond than smaller ones. Moreover, it seems reasonable to believe that there is a positive correlation between early arrival in the pond and number of days spent there. Consequently, the early arrival of larger males in Gatz's study could have been one of the factors responsible for the non-random mating observed. In the present study the mean size of the males and females seemed to decrease during the mating season in 1995, and this may have been one of the factors responsible for the occurrence of the size assortative mating observed in this year. Larger animals could arrive earlier than smaller ones as a result of accumulated experience, as large animals could be older than smaller ones, or by being faster in movement to the pond than smaller ones. Larger males would also arrive earlier in the pond if the distances from their overwintering shelter to the pond were shorter than those of smaller males.

Patterns of movement in the pond could also affect mating success, as more active males could have more chances to find a female. Gatz (1981) did not find any difference in the patterns of movement between successful and unsuccessful *Bufo americanus* males. However, in the study of Christein and Taylor

(1978), although breeding and non breeding *B. americanus* males spent the same amount of time in the pond area, the breeding males were more active than their non breeding counterparts. On the other hand, Wells and Taigen (1984), studying the reproductive behavior of male *B. americanus*, did not find significant correlation between body mass and distance moved, amount of calling, or number of clasping attempts.

Amount of time spent by the males calling is another factor that could affect mating success, especially if females respond to calls by moving in the direction of the caller (Gatz, 1981). Gatz (1981) compared the percentage of successful and unsuccessful males captured while calling, and concluded that time spent calling was one of the factors that determined male mating success.

Ability to intercept females in the entry points of the pond would also increase mating success. Christein and Taylor (1978) found that in some populations of *Bufo americanus* individuals enter and leave a breeding pond in the same compass direction. If individual *B. americanus* used the same route from year to year, as found for other amphibians such as *Ambystoma maculatum* (Shoop, 1965), older males could learn the favored females's routes and outcompete younger males.

Although on one occasion a couple was observed arriving

in the pond already in amplexus, the data obtained in the present study indicated that pairing occurs primarily at the pond. Gatz (1981) stated that the pattern of movements of males and the variation in areas of amplexus in different years rule out this mechanism as the one responsible for non-random mating.

Size assortative mating was found for populations of some anuran species such as *Bufo bufo* (Davies and Halliday, 1977), *Rana pretiosa* (Licht, 1975), *Rana sylvatica* (Howard and Kluge, 1985) and *Uperoleia laevigata* (Robertson, 1990). Arak (1983) suggested that size assortative mating could be a result of female choice with or without male-male competition. When amplexed by desirable males, females would swim away from other males to reduce male-male competition. If, however, they were amplexed by an undesirable male, they could swim to where there were other males to incite take-over attempts. However, the same author considered it unlikely that such a form of behavior would be selected for in females, as it would expose the females to drowning at the center of a ball of struggling males. Consequently, Arak (1983) agreed with Wells (1979) that size-assortative mating is most likely a mechanical consequence of the fact that only pairs well matched for size can resist takeovers by other males.

According to Crespi (1989), "assortative mating by size . . . may be explained by three hypotheses: (1) mate choice, whereby

large males, large females or large individuals of both sexes choose large mates because they benefit reproductively and are differentially capable of exercising choice; (2) mate availability, whereby large females or large individuals of both sexes are differentially available for mating because of size-differential variation in mating probability or timing that is unrelated to mate choice; and (3) mating constraints, whereby relative size differences between males and females cause physical or energetic difficulties with courtship, pairing or mating". There is no evidence that suggests the existence of physical constraints that could play a role in the size assortative mating observed in the study population. On the other hand, the male biased sex ratio probably prevented mate choice by the males. However, a combination of female choice of large males, larger male advantage in male-male competition, and early initiation of breeding by large males and females could explain the size assortative mating observed. The three hypotheses that have been invoked to explain assortative mating need not be mutually exclusive (Crespi, 1989). Howard and Palmer (1995) found that in discriminatory experiments, older *B. americanus* females appear to make mating decisions faster than younger females. This tendency could also account for the assortative mating in the present study.

It may be advantageous for a female to mate with a male

of about the same size, as fertilization success might be greatest in those pairs which are well matched for size, because this would facilitate the apposition of the cloacas of the pair (Davies and Halliday, 1977; Halliday, 1983b). However, such an advantage was not detected for *Bufo americanus* in the present study or by Kruse (1981), nor for *Rana catesbeiana* (Howard, 1978). On the other hand, Gibbons and McCarthy (1986) observed, in laboratory mating experiments with *Rana temporaria*, that egg fertility was positively correlated with absolute male length and with relative male/female length in amplexus. Robertson (1990) found that size assortative mating increases fertilization success in *Uperoleia laevigata*, but not due to facilitation in the apposition of the cloacas, as this species uses inguinal amplexus, and the smallest males can reach the cloaca of the largest female. He considered that assortative mating increased fertilization because small males may have insufficient sperm to fertilize the whole clutch, and large males are difficult to carry and may drown the female.

The yearly variation in the mating pattern found in this study is an indication that the conflicting results presented by previous studies may be related to difference in some environmental variable, rather than genetic differences among populations. Mating systems are a consequence of the way in which individuals interact in response to various ecological and social

pressures, and, as stated by Arak (1983) "it is the collective behavior of individuals which determines the mating system and not the other way round".

Density of males and operational sex ratio at the breeding site are two environmental variables that can affect the mating pattern of the population (Arak, 1983). Both could affect mate choice and / or male-male competition.

The chances of a female mating with a target male would increase with a decrease in male density in the pond, and with a decrease in the degree to which the sex ratio is male-biased. On the other hand, an increase in these parameters would make struggles between males and pairs more frequent, and many takeovers probably would occur. Consequently, an increase in the male density and / or in male bias of sex ratio would increase the probability of occurrence of non-random mating if the mechanism responsible is male-male competition. On the other hand, it would decrease the probability if the mechanism responsible is mate choice.

According to Kvarnemo and Ahnesjö (1996), the operational sex ratio may be affected by differences between the sexes in age at maturity, reproductive longevity, migration schedules, spatial distribution, and mortality during the reproductive season.

In the present study, the occurrence of non-random mating in 1995 but not in 1994 and 1996, may be the consequence of different male densities or male/female ratio. Nevertheless, non-random mating was not found in 1996, even in the first days of the mating season, when the density of males in the pond was low.

Differences in the frequency distribution of male size among the seasons could also have contributed to the yearly variation in mating pattern. Nevertheless, the unimodal distribution presented by size of the males found in vocalization and in amplexus in all three years did not support this explanation.

The larger mean size of males found in vocalization in comparison with that of males found in amplexus in 1994 and 1996 may have been a result of a longer time spent by larger males vocalizing, which would increase their probability of being found in this activity. According to Arak (1983), an increase in male density may lead to an increase in the mean size of the calling males; when the density is low it pays for most males to call because there is not much vocal competition for the available females. However, as density increases small males may do better by ceasing to call and attempting to intercept females approaching calling males (satellite male behaviour).

Variation in environmental factors such as temperature could also play a role in the yearly variation in mating patterns

observed in the studied population. Lower temperatures could alter the occurrence of female choice, as the discriminatory ability of females may change with temperature. For example, females of *Hyla cinerea* are able to discriminate between calls from conspecific males and calls from males that belong to the sympatric species *Hyla gratiosa* at high temperature range. However, at low temperature range females of *H. cinerea* occasionally mate with males of *H. gratiosa* (Gerhardt and Mudry, 1980).

Sullivan (1992) found that pulse rate and duration of the advertisement call were significantly correlated with temperature in a *B. americanus* population. In the present study the air temperature was lower on average during the 1995 mating season, when a nonrandom mating was found, than during the 1994 and 1996 mating seasons, when the mating was not significantly different from random with relation to body size. Those results indicate that variation in temperature among mating seasons was not related to the yearly variation in mating pattern found in this study.

Clutch and Egg Size

Variation in clutch parameters, such as egg size and clutch size among females, may simply be random; the result of the abiotic and biotic conditions experienced by individuals (e.g. Kaplan, 1987); or the result of selective pressures on adults or offspring (Williamson and Bull, 1995). The correlation between clutch size

and female size found in this study is common among both ectothermic vertebrates and invertebrates (Clutton-Brock, 1988b), and has been found for other anurans such as *Bufo calamita* (Tejedo and Reques, 1992), *Hyla crucifer* (Crump, 1984), *Rana catesbeiana* (Howard, 1978) and *Ranidella signifera* (Williamson & Bull, 1995). Such correlation makes it advantageous for males to mate with larger females, as they would have a chance to fertilize a larger number of eggs. Consequently, the size assortative mating found in 1995 means that in this year there was a size advantage for males in the number of fertilized eggs.

Egg size is a variable that may also be subject to natural selection, as selection ultimately maximizes expected offspring quality and not number of offspring (Brockelman, 1975). Egg size may also have influence on life history parameters such as larval size, growth and development rate. Egg size reflects female investment per offspring, and an increase in parental investment per offspring is expected to be related to offspring survival.

One of the assumptions of life history theory is the existence of a trade-off between size and number of offspring, due to limited energy available for reproduction (Smith and Fretwell, 1974; Kaplan, 1987; Bernardo, 1996). Selection should favor the production of many small offspring when environmental conditions are fluctuating or unpredictable, and mortality is expected to be

largely density-independent. Alternatively, under more constant and predictable environments, where mortality is expected to be largely density-dependent, the production of fewer larger offspring should confer greater fitness (Crump, 1984). Variation in offspring size within clutches has been proposed as a "strategy" whereby a female breeding in an environment that changes unpredictably may increase fitness (Williamson and Bull, 1995). However, the unimodal distribution in the size of the eggs suggests that this strategy is not present in the study population.

Inverse correlations between clutch and egg size were found for *Rana sylvatica* (Berven, 1988), *Rana temporaria* (Cummins, 1986), and *Ranidella signifera* (Williamson and Bull, 1995) after correction for female body size. In this study, egg size was also inversely related to clutch size when corrected for female size in 1995, but not in 1996, suggesting that the occurrence of this trade-off may depend on the amount of resources available for the female during the production of the eggs.

Hatching Success

A size advantage for males in egg fertilization efficiency could result from a positive correlation between body size and amount of sperm produced. Similarity between body size of the male and female could also improve fertilization, and consequently, hatching success, by allowing the juxtaposition of the

cloacas during amplexus. Although in the present study larger males and pairs well matched for size did not have greater hatching success, one must consider that the laboratory conditions under which the eggs were laid are very different from those found in the natural environment, where males frequently try to displace amplexed males during fertilization and several different males are sometimes found clasped to the same female.

Larval Growth Rate

The period from fertilization to feeding stages is probably when the embryos are most vulnerable to physical and biological hazards, such as desiccation due to falling water levels, freezing in surface ice, attack by egg predators, or infection by fungi. Moreover, the faster the embryos can develop to independent feeding, the sooner they can start exploiting the food resources in their environment (Williamson & Bull, 1989). Therefore, development rate from fertilization through to hatching and feeding stages is a component of fitness. Consequently, the production of larger eggs by *Bufo americanus* females could represent an adaptive advantage, as the results of the laboratory experiment suggested that larger eggs had a faster development rate in the first days after fertilization.

Among other amphibians, a positive relationship between egg size and initial tadpole size was found within clutches, for

Ranidella signifera (Williamson and Bull, 1989) and *Hyla crucifer* (Crump, 1984), and between clutches for *Ambystoma* (Kaplan, 1980; Walls and Altig, 1986) and *Bufo calamita* (Tejedo and Reques, 1992).

Savage (1952) stated that food is often limiting in natural populations of anuran larvae and maximum growth rates are rarely obtained. Savage (1961, in Brockelman, 1969) noted that differences in growth rate among several populations of *Rana temporaria* tadpoles seemed to be inversely related to density, and Smith (1987) observed that competition among tadpoles reduced developmental rates in *Pseudacris triseriata*.

Brockelman (1969) and Wilbur (1977) also found that growth rate was a density-dependent factor in their experiments with *Bufo americanus* larvae. The significant effects that variation on both food and density levels had on larval size in this study suggested that competition for food may not be the only factor responsible for the density affects on growth rate. In fact, it has been demonstrated that tadpoles also compete by interference, either by conditioning the water (Richards, 1958; 1962; Rose, 1959, Licht, 1967), or by behavioral interactions (Savage, 1952; Gromko *et al.* 1973, John and Fenster, 1975).

A body size advantage in amphibian larvae has been considered an influence in competitive interactions, by enabling

larger individuals to use greater proportions of the available resources and to interfere behaviorally or through habitat modifications with resource use by smaller individuals, particularly at high densities (Wilbur and Collins, 1973). However, Kaplan (1985) found that larvae of the salamander *Taricha torosa* that had a larger initial size took longer to metamorphose than smaller larvae when food was in short supply.

A high growth rate could also represent an adaptive response against predation, as larger larvae have been shown to be less prone to capture by gape-limited predators in several amphibian species (review in Tejedo, 1993). However, Tejedo (1993) argued that the hypothesis that larger, faster growing tadpoles may acquire an advantage against size-limited predators may only apply for larger species of tadpoles that exhibit a great range of sizes. In fact, several studies failed to demonstrate a size advantage against predators in amphibian larvae: Tejedo (1993) found that in predation experiments large tadpoles of *Bufo calamita* were preferentially selected by beetle larvae, and that the average number of strikes to grasp a small tadpole was higher than for large tadpoles; Alford (1986) showed that the initial size of tadpoles in *Hyla chrysocelis* was not a predictor of their ability to escape predators. Larger tadpoles may also metamorphose at a larger size (Kaplan and Cooper, 1984), and body size may be an important

component of fitness.

Larval Survival

Brockleman (1969) studied growth and survivorship of a population of *Bufo americanus* tadpoles, and concluded that mortality was density-dependent, and mediated by the supply of food. On the other hand, Wilbur (1977) found that mortality was a density-independent factor in his experiments with *Bufo americanus* larvae, although he found that growth rate was density-dependent. Wilbur (1977) found that larger larvae monopolized the largest leaf fragments and prevented access of smaller larvae to food by vigorous swimming movements. In his experiments this behavioral pattern produced a density-dependent growth rate but not density-dependent mortality. The production of density-dependent mortality in this study could be a result of a supply of food more limited than in Wilbur experiments (1977).

In the Wilbur experiments (1977), the amount of food remained constant over treatments with different densities. His results showed that density influenced mortality, independent of the amount of food available for each individual. However, this also could have been a result of competition for food, due to the monopolizing feeding behavior of larger tadpoles.

Tadpoles also compete by interference, and other factors besides competition for food could also produce density-dependent

mortality. As the larvae in this study were kept in containers with the same amount of water in all four treatments, those in higher initial density were exposed to an environment with a higher concentration of metabolites and food residuals, and to increased behavioral stress than those in lower initial density.

Competition among tadpoles also reduced larval survivorship in *Pseudacris triseriata* (Smith, 1987), but Calef (1973) observed that the percentage of *Rana aurora* tadpoles surviving in experimental enclosures with no predators was independent of density, and concluded that food is not limiting to these tadpoles at their normal densities.

The importance of competition in the control of a population, is demonstrated by the fact that predation may have a positive effect on the abundance of a particular larval prey by reducing competition. Van Buskirk (1988) found that the relative abundance of *Bufo americanus* larvae increased in the presence of predators, as two hylid species larvae decreased.

Metamorphic Success

Although Wilbur (1977) found that survival during the larval period was independent of population density, he also observed that the proportion of the population that successfully metamorphosed was a negative exponential function of density. Dash and Hota (1980) found similar results in experiments with *Rana*

tigrina : larval survival was independent of initial population density, while the proportion of the population that successfully completed metamorphosis was a negative exponential function of density. The explanation for this apparent paradox is that metamorphosis will be initiated only after a lower size threshold has been exceeded (Wilbur and Collins, 1973). As growth rate is density-dependent, fewer individuals will be able to reach this threshold before mortality in high density treatments. Consequently, the number of individuals that metamorphose will be a result of density-dependent growth rates rather than density-independent survival rates (Wilbur, 1977).

The positive effects that decrease in density and increase in the amount of food had on the proportion of larvae that completed metamorphosis were a consequence of the positive effects that both had on larvae size and survival.

Time to Metamorphosis

The duration of the larval period in amphibians was directly correlated to egg size in *Ranidella signifera* (Williamson and Bull, 1989), and *Ambystoma* (Kaplan, 1980, Walls and Altig, 1986). However, bufonids produce relatively small eggs, and egg size would not probably affect variables such as duration of the larval period in populations of bufonids.

Bufo americanus tadpoles increase development rate

and metamorphose earlier and at a lower body size in the presence of predatory odonate naiads (Van Buskirk, 1988; Wilbur and Fauth, 1990; Skelly and Werner, 1990).

Brockelman (1969) found, in field experiments with *B. americanus* larvae, that time of metamorphosis was directly related to initial tadpole density. The fact that variation in initial density and in amount of food available did not affect duration of the larval period in the present study was possibly due to the high mortality of the larvae in the laboratory experiment.

Size at Metamorphosis

Size at metamorphosis is considered a critical life history attribute of amphibians (Skelly and Werner, 1990), and has long been known to be a phenotypically plastic character that changes with resource levels or growth rates in the larval stage (Wilbur and Collins, 1973; Semlitsch *et al.*, 1988). Theories of amphibian metamorphosis predict that size at metamorphosis should depend on the relation between growth opportunities and risk of mortality in the larval and adult habitats (Skelly and Werner, 1990). Reduction in size at metamorphosis can happen through an increase of the development rate and consequent shortening of the larval period, and/or through a decrease in the growth rate unrelated to development rate.

Larger size at metamorphosis could represent a

protection against size-limited predators. Moreover, the growth rate of many organisms depends on their size (Stearns, 1992), and a size advantage at metamorphosis that persists throughout the terrestrial phase of the life cycle could positively affect reproductive success by directly affecting adult life history traits or by indirectly affecting other fitness-related characteristics. Studies have correlated increase in size at metamorphosis in amphibians with reduced time to maturity (Smith 1987, Semlitsch *et al.* 1988), increased survival to maturity (Berven and Gill, 1983), and increased size at maturity (Berven and Gill, 1983; Smith, 1987; Semlitsch *et al.* 1988). This latter attribute was correlated with physical performance and resistance to starvation (Goater, 1994), larger clutch size and egg size in females, and increased male breeding success.

Increases in metamorphic size with increases in food level or decreased density have been reported in many amphibian species (reviewed in Wilbur, 1980; 1984; Smith, 1987; Goater, 1994; Barandun and Reyer, 1997). The presence of predators has been shown to increase development rate, causing the larvae to metamorphose earlier and at lower body size among amphibians, including *Bufo americanus* (Van Buskirk, 1988; Wilbur and Fauth, 1990; Skelly and Werner, 1990).

Although in the present study, size at metamorphosis

was not influenced by either food or initial density levels. Skelly and Werner (1990) found a decrease in size at metamorphosis in *B. americanus* as a consequence of decrease in food availability. Brockelman (1969) found that size at metamorphosis was inversely related to initial tadpole density. Wilbur (1977), in experiments where the amount of food did not vary among treatments, found that at low densities of one to twenty individuals, body size increased with population density as a result of an Allee effect. However, at higher densities, where food became limiting, body size was negatively related to density. Wilbur noted that the Allee effect may have been a consequence of the butting behavior observed by him and by Beiswenger (1975) in aggregations of *B. americanus* larvae. This behavior could facilitate feeding because the substrate is stirred up, suspending food that larvae can filter from the water (Beiswenger, 1975; Wilbur, 1977).

The fact that food and initial density levels did not affect size at metamorphosis, although they did affect growth rate, is intriguing. One possible explanation would be that the slow growing tadpoles, although taking longer to metamorphose, would do so at about the same size as the fast growing tadpoles. However, length of the larval period was not affected by density or food levels. Another explanation would be that the higher larval mortality in lower food and / or high density treatments was size

dependent, and therefore metamorphosis was restricted to the larger surviving larvae. The inverse correlation between percent of metamorphosed larvae and metamorph body length in the field experiment supports this explanation.

The inverse correlation between percent of metamorphosed larvae and body length at metamorphosis also suggests a trade-off between the percent of larvae that successfully metamorphosed and the quality of the resulting metamorphs. A possible explanation for this trade-off would be that larvae that eventually reached metamorphosis in the containers with higher mortality were confronted with less competition for food than the larvae from containers that had higher initial metamorphosis success.

A negative correlation between length of the larval period and size at metamorphosis in the field experiment was also observed by Reques and Tejedo (1995) for *Bufo calamita*. One possible explanation for this trend would be a seasonal increase in water temperature, as higher temperature accelerates development relatively faster than growth, promoting smaller size at metamorphosis (Reques and Tejedo, 1995).

The results of this study suggest that the first null hypothesis tested, "mating success is not related to body size", should not be rejected, as male mating success was not size

dependent in any of the three mating seasons. However, the size assortative mating found in 1995 is an indication that male body size may represent an advantage in reproductive success, and consequently be subject to selection, because larger males may father a larger number of offspring due to the positive correlation between female body size and clutch size.

Female preference for males with about the same size of their own may have played a role in the size assortative mating found in 1995, although the observed male behavior of active search and scramble for the possession of females and the male-biased sex ratio, would reduce the chances of the females to exercise choice. The form of male-male competition where males try to displace amplexed males, observed on several occasions during this study, could also produce size assortative mating if just the pairs well matched for size would be able to resist these takeover attempts. Nevertheless, the absence of a sexual dimorphism in the size of the forearm in the population, suggests that these attacks are not frequently successful in the population. One other factor that could have contributed to the assortative mating of 1995, was the earlier initiation of breeding by large males and females suggested by the data.

The yearly variation in mating pattern could have been a consequence of differences in male density in the pond, sex

ratio, size distribution frequency of the animals, or environmental variables such as temperature and precipitation. However, the data were not conclusive with respect to any of these explanations.

The influence of male and female body size in the reproductive success, was limited to effects on the number of eggs produced (females) or fertilized (males), as variation in the other fitness parameters could not be related to variation in the size of parents.

Variation in the larvae in the fitness parameters studied was also not significantly related to variation in number of offspring or mean size of eggs in the clutches. These results suggest that the second null hypothesis: "the number of zygotes produced or fertilized is not a predictor of reproductive success", should be rejected, and that the third null hypothesis: "egg size does not affect probability of metamorphosis or size at metamorphosis", should not be rejected. The absence of a trade-off between number and size of the eggs in 1996, suggests that variation in these parameters is, at least in part, related to variation in the amount of resources available to the females during the production of the eggs.

Finally, the results suggest that the null hypothesis: "variation in food and density levels does not affect larvae growth and survival, or the correlations between them", should be rejected, as increase in food level and decrease in initial density had a

positive effect on larvae size and survivorship, and on the percent of larvae that completed metamorphosis. The absence of initial density and food effects on the duration of the larval period and on the size at metamorphosis may have been a consequence of the high mortality of the larvae during the experiments. Another explanation would be that the higher larva mortality in lower food and / or high density treatments was size dependent, and therefore metamorphosis was restricted to the larger surviving larvae. The inverse correlation between percent of metamorphosed larvae and metamorph body length in the field experiment supports this explanation.

Table 1. Design of a factorial experiment with *Bufo americanus* larvae, with two levels of food and density combined in 4 treatments.

Treatment	Food	Density
A	low	high
B	high	high
C	low	low
D	high	low

Table 2. Amount of food per individual (g) added to the containers in each one of the treatments, during the 1995 and 1996 laboratory experiments with *Bufo americanus* larvae.

DATA	TREATMENTS			
	A	B	C	D
1995				
May 19	0.002	0.002	0.002	0.002
May 26		0.002		0.002
Jun 06	0.004	0.004	0.004	0.004
Jun 12		0.005		0.005
Jun 24	0.010	0.010	0.010	0.010
Jul 04		0.010		0.010
1996				
May 07	0.001	0.002	0.001	0.002
May 13	0.001	0.002	0.001	0.002
May 17	0.002	0.004	0.002	0.004
Jun 01	0.002	0.004	0.002	0.004
Jun 12	0.002	0.004	0.002	0.004
Jun 20	0.002	0.004	0.002	0.004
Jun 28	0.008	0.016	0.008	0.016
Jul 08	0.008	0.016	0.008	0.016
Jul 19	0.008	0.016	0.008	0.016
Jul 31	0.016	0.032	0.016	0.032
Agu 14	0.032	0.064	0.032	0.064
Sep 18	0.032	0.064	0.032	0.064

Table 3. Average number of individuals per replicate, and average number of replicates in each of the treatments, during the 1995 laboratory experiment with *Bufo americanus* larvae.

treatment	Period				
	May 17 to June 14	June 14 to June 28	June 28 to July 09	July 09 to July 17	July 17 to July 23
A	20 - 3	11 - 2.6	6 - 2.4	XXXXX	XXXXX
B	20 - 3	15 - 2.9	12 - 2.7	10.5 - 2.6	7.9 - 2.4
C	10 - 3	6 - 2.7	4 - 2.4	XXXXX	XXXXX
D	10 - 3	8 - 3	7 - 3	6.6 - 2.9	4.9 - 2.9

Table 4. Snout-vent length (mm) of the individuals of *Bufo americanus* collected in the Forestry Pond, Kingman Farm, Madbury, NH, during the 1994, 1995 and 1996 mating seasons.

	N	RANGE	MEAN	SD
1994				
Males in vocalization	33	51-68	60.30	4.39
Males amplexed with females not laying eggs	13	49-65	56.53	4.20
Females	13	58-72	64.05	4.60
1995				
Male in vocalization	71	53-72	61.79	4.23
Males amplexed with females not laying eggs	41	51-73	60.83	4.69
Males not performing any reproductive activity	124	35-73	62.60	5.02
Females	41	59-90	72.90	7.92
1996				
Males in vocalization	27	54-72	64.37	4.69
Males amplexed with females not laying eggs	34	54-68	62.06	3.67
Males amplexed with females laying eggs	30	55-67	61.47	3.43
Males not performing any reproductive activity	47	52-73	61.49	5.20
Males trying to displace amplexant males	11	56-71	61.91	4.37
Females	64	61-87	72.47	6.90

Table 5. Results of F-tests comparing snout-vent length of different classes of *Bufo americanus* males during the 1994, 1995, and 1996 mating seasons (vocalizing = males in vocalization; amplexed - no eggs = males amplexed with females not laying eggs; amplexed - eggs = males amplexed with females laying eggs; resting = males apparently not performing any activity; disturbing pairs = males trying to displace amplexant males).

Comparison	DF	F-RATIO	R2	P
1994				
vocalizing X amplexed - no eggs	1, 44	7.03	0.138	0.01
1995				
vocalizing X amplexed - no eggs	1, 110	1.06	0.01	0.31
vocalizing X resting	1, 193	1.57	0.008	0.21
amplexed - no eggs X resting	1, 163	3.97	0.024	0.05
1996				
vocalizing X amplexed - no eggs	1, 59	4.67	0.073	0.03
vocalizing X amplexed - eggs	1, 55	7.21	0.116	0.01
vocalizing X resting	1, 71	6.51	0.084	0.01
vocalizing X disturbing pairs	1, 36	1.76	0.047	0.19
amplexed - no eggs X amplexed - egg	1, 62	0.44	0.007	0.51
amplexed - no eggs X resting	1, 78	0.54	0.007	0.47
amplexed - no eggs X disturbing pair	1, 44	<0.01	0	0.93
amplexed - eggs X resting	1, 74	0.02	0	0.88
amplexed - eggs X disturbing pairs	1, 40	0.31	0.008	0.59
resting X disturbing pairs	1, 56	0.29	0.005	0.59

Table 6. Results of ANCOVA comparing weight of *Bufo americanus* males found in amplexus and in vocalization, after adjusting for body length.

1994		R2= 0.759			
	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
Behavior	0.01	1	0.01	4.47	0.04
Log. SV Length	0.29	1	0.29	96.98	<0.001
ERROR	0.13	44	0.003		

1995		R2= 0.757			
	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
Behavior	0.01	1	0.01	3.92	0.05
Log. SV Length	0.8	1	0.8	325.4	<0.001
ERROR	0.27	109	0.002		

1996		R2= 0.779			
	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
Behavior	0.01	1	0.01	5.42	0.02
Log. SV Length	0.54	1	0.54	255.13	<0.001
ERROR	0.18	85	0.002		

Table 7. Results of F-tests comparing the snout-vent length of males and females *Bufo americanus* found in amplexus.

	DF	F-RATIO	R²	P
1994	1, 24	18.61	0.437	< 0.01
1995	1, 80	70.44	0.47	< 0.01
1996	1, 126	121.49	0.49	< 0.01

Table 8. Mean *Bufo americanus* larvae length (mm) in each of the treatments of the 1995 and 1996 laboratory experiments, and in the 1996 field experiment, and the results of the 2-way ANOVA of the lab data.

	mean	SD	min	max	
1995 day 30					
A (low food / high density)	12.75	0.35	12.23	13	
B (high food / high density)	12.73	0.61	11.83	13.12	
C (low food / low density)	11.52	0.6	10.65	12.45	
D (high food / low density)	17.42	0.65	16.48	18.56	
1995 day 50					
A (low food / high density)	17.78	0.82	16.69	18.96	
B (high food / high density)	17.87	1.27	17.01	21.4	
C (low food / low density)	17.42	0.65	16.48	18.56	
D (high food / low density)	19.14	0.54	18.24	19.82	
1996 day 40					
A (low food / high density)	12.2	0.53	11.52	13.4	
B (high food / high density)	13.26	0.5	12.48	13.84	
C (low food / low density)	12.54	0.52	11.64	13.24	
D (high food / low density)	14.19	0.53	12.88	15	
field 1996 day 50	18.17	1.73	16.28	21.11	
ANOVA 1995 day 30 R2= 0.452					
	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
FOOD	1.15	1	1.15	5.8	0.02
DENSITY	3.9	1	3.9	19.77	<0.001
FOOD*DENSITY	1.23	1	1.23	6.22	0.016
ERROR	9.48	48	0.2		
ANOVA 1995 day 50 R2= 0.39					
	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
FOOD	8	1	8	10.62	0.002
DENSITY	2	1	2	2.66	0.112
FOOD*DENSITY	6.48	1	6.48	8.59	0.006
ERROR	26.39	35	0.75		
ANOVA 1996 day 40 R2= 0.728					
	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
FOOD	21.79	1	21.8	79.56	<0.001
DENSITY	4.75	1	4.75	17.34	<0.001
FOOD*DENSITY	0.99	1	0.99	3.63	0.062
ERROR	14.24	52	0.27		

Table 9. Mean percent of *Bufo americanus* larvae survivorship in 3 different time intervals, in each one of the treatments of the 1995 lab experiment, and results of the ANOVA of the data.

	Mean	SD	Min	Max
day 1 to day 27				
A (low food / high density)	58.39	15.17	30	80
B (high food / high density)	84.8	9.33	65	95
C (low food / low density)	64.3	18.81	30	80
D (high food / low density)	90.28	8.78	70	100

day 23 to day 52				
A (low food / high density)	79.78	6.18	72.65	91
B (high food / high density)	86.38	7.03	69.5	93.1
C (low food / low density)	83.08	5.78	71.5	90.3
D (high food / low density)	91.63	5.76	74.4	100

day 53 to day 66				
B (high food / high density)	82.88	4.3	77.3	89.7
D (high food / low density)	86.55	6.61	71.45	97.5

ANOVA day 1 to day 27 R2= 0.556

	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
FOOD	8040.14	1	8040.14	56.34	<0.001
DENSITY	380.18	1	380.18	2.66	0.108
FOOD*DENSITY	0.54	1	0.54	<0.01	0.951
ERROR	8277.4	58	142.71		

ANOVA day 23 to day 52 R2= 0.382

	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
FOOD	672.32	1	672.32	18.48	<0.001
DENSITY	214.65	1	214.65	5.9	0.018
FOOD*DENSITY	11.09	1	11.09	0.3	0.583
ERROR	2110.21	58	36.38		

ANOVA day 53 to day 66 R2= 0.062

	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DENSITY	103.43	1	103.43	2.71	0.12
ERROR	1562.88	41	38.12		

Table 10. Mean percent of *Bufo americanus* larvae survival at the 32, 52, and 69 th days of the larval period, in each one of the treatments of the 1996 lab experiment, and results of the 2-way ANOVA.

	Mean	SD	Min	Max	
day 32					
A (low food / high density)	77.62	11.39	61.25	95	
B (high food / high density)	90.88	7.88	76.25	100	
C (low food / low density)	86.8	10.3	70	97.5	
D (high food / low density)	93.8	4.7	80	100	
day 52					
A (low food / high density)	35.88	10.1	21.25	57.5	
B (high food / high density)	50.38	12.36	38.75	73.75	
C (low food / low density)	54	12.4	40	70	
D (high food / low density)	68.5	9.1	52.5	85	
day 69					
A (low food / high density)	18	3.13	12.5	23.75	
B (high food / high density)	20.62	4.46	13.75	30	
C (low food / low density)	39.2	3.3	35	45	
D (high food / low density)	45	9.16	30	62.5	
ANOVA day 32 R2= 0.379					
	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
FOOD	1223.08	1	1223.08	19.54	<0.001
DENSITY	432.3	1	432.3	6.91	0.011
FOOD*DENSITY	111.89	1	111.89	1.79	0.19
ERROR	3255.07	52	62.6		
ANOVA day 52 R2= 0.594					
	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
FOOD	2478.19	1	2478.19	22.42	<0.001
DENSITY	3874.22	1	3874.22	35.05	<0.001
FOOD*DENSITY	<0.01	1	<0.01	<0.01	0.995
ERROR	5747.52	52	110.53		
ANOVA day 69 R2= 0.758					
	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
FOOD	207.23	1	207.23	4.37	0.042
DENSITY	6150.3	1	6150.3	129.6	<0.001
FOOD*DENSITY	28.85	1	28.85	0.61	0.439
ERROR	2467.66	52	47.45		

Table 11. Mean percent of *Bufo americanus* larvae that successfully completed metamorphosis in each one of the treatments of the 1996 lab experiment, and in the 1996 field experiment, and results of a 2-way ANOVA of the laboratory data.

	Mean	SD	Min	Max
Lab				
A (low food / high density)	6	2.02	2.5	10
B (high food / high density)	11.4	1.92	8.75	13.8
C (low food / low density)	11.5	2.42	7.5	15
D (high food / low density)	20.87	5.87	12.5	35
Field	44.6	18.52	8	64

ANOVA LAB EXPERIMENT		R2= 0.667			
	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
FOOD	621.65	1	621.65	32.84	<0.001
DENSITY	684.9	1	684.9	36.18	<0.001
FOOD*DENSITY	52.75	1	52.75	2.79	0.101
ERROR	984.35	52	18.93		

Table 12. Results of F-tests comparing the percentage of *Bufo americanus* larvae that successfully completed metamorphosis in the field experiment and in each of the treatments of the laboratory experiment.

	DF	F-RATIO	P
FIELD X LAB. A	1, 18	6.55	<0.0001
FIELD X LAB. B	1, 18	5.68	<0.0001
FIELD X LAB. C	1, 18	5.6	<0.0001
FIELD X LAB. D	1, 34	5.92	<0.0001

Table 13. Mean time to metamorphosis (days) of *Bufo americanus* larvae, in each one of the treatments of the 1996 lab experiment, and in the field experiment, and the results of a 2-way ANOVA of the laboratory data.

	Mean	SD	Min	Max
Lab				
A (low food / high density)	101.03	8.7	90.75	119
B (high food / high density)	99.41	3.48	95.87	106.62
C (low food / low density)	98.02	4.78	91.33	107.17
D (high food / low density)	97.95	4.88	89.2	108
Field	60.7	5.52	50	66.18

ANOVA LAB EXPERIMENT		R2= 0.047			
	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
FOOD	8.54	1	8.54	0.28	0.6
DENSITY	59.14	1	59.14	1.93	0.17
FOOD*DENSITY	7.06	1	7.06	0.23	0.63
ERROR	1590.9	52	30.59		

Table 14. Results of F-tests comparing the time to metamorphosis of *Bufo americanus* larvae in the field experiment and in each of the treatments of the laboratory experiment.

	DF	F-RATIO	P
FIELD X LAB. A	1, 18	4.41	<0.0001
FIELD X LAB. B	1, 18	4.41	<0.0001
FIELD X LAB. C	1, 18	4.41	<0.0001
FIELD X LAB. D	1, 34	4.13	<0.0001

Table 15. Mean body length (mm) at metamorphosis of the *Bufo americanus* larvae raised in each one of the treatments of the 1996 lab experiment, and in the 1996 field experiment, and results of a 2-way ANOVA on the lab data.

	Mean	SD	Min	Max
Lab Experiment				
A (low food / high density)	7.83	0.55	6.9	8.58
B (high food / high density)	8.01	0.3	7.55	8.54
C (low food / low density)	7.75	0.46	7.1	8.77
D (high food / low density)	7.72	0.34	6.74	8.31
Field Experiment	8.25	0.44	7.75	9.25

ANOVA LAB EXPERIMENT		R2= 0.0073			
	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
FOOD	0.06	1	0.06	0.39	0.535
DENSITY	0.41	1	0.41	2.54	0.12
FOOD*DENSITY	0.14	1	0.14	0.89	0.35
ERROR	8.44	52	0.16		

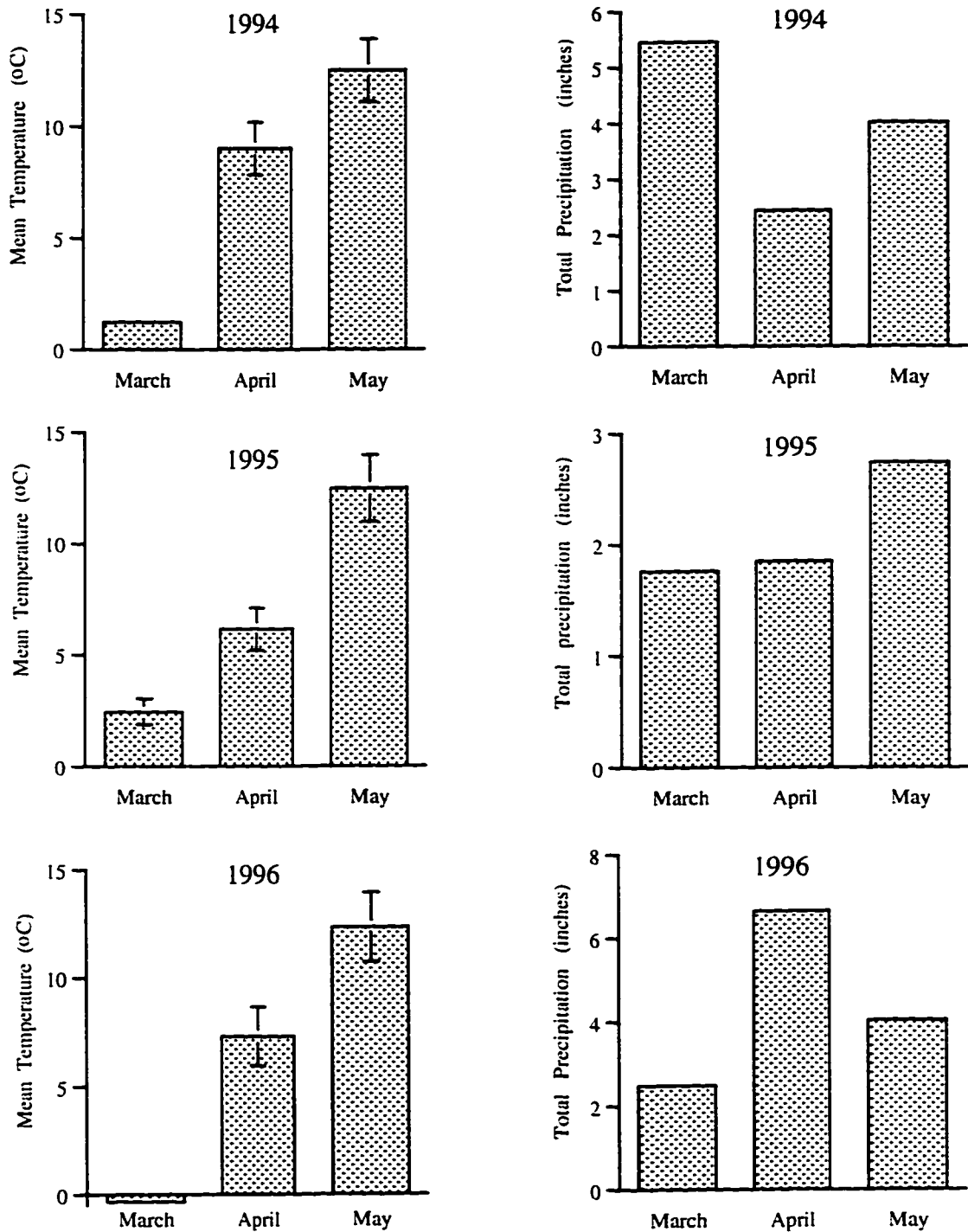


Figure 1. Total precipitation and mean temperature in March, April and May of 1995 and 1996 (data collected at the UNH Campus in Durham, NH, approximately 3.8 km from the study pond).

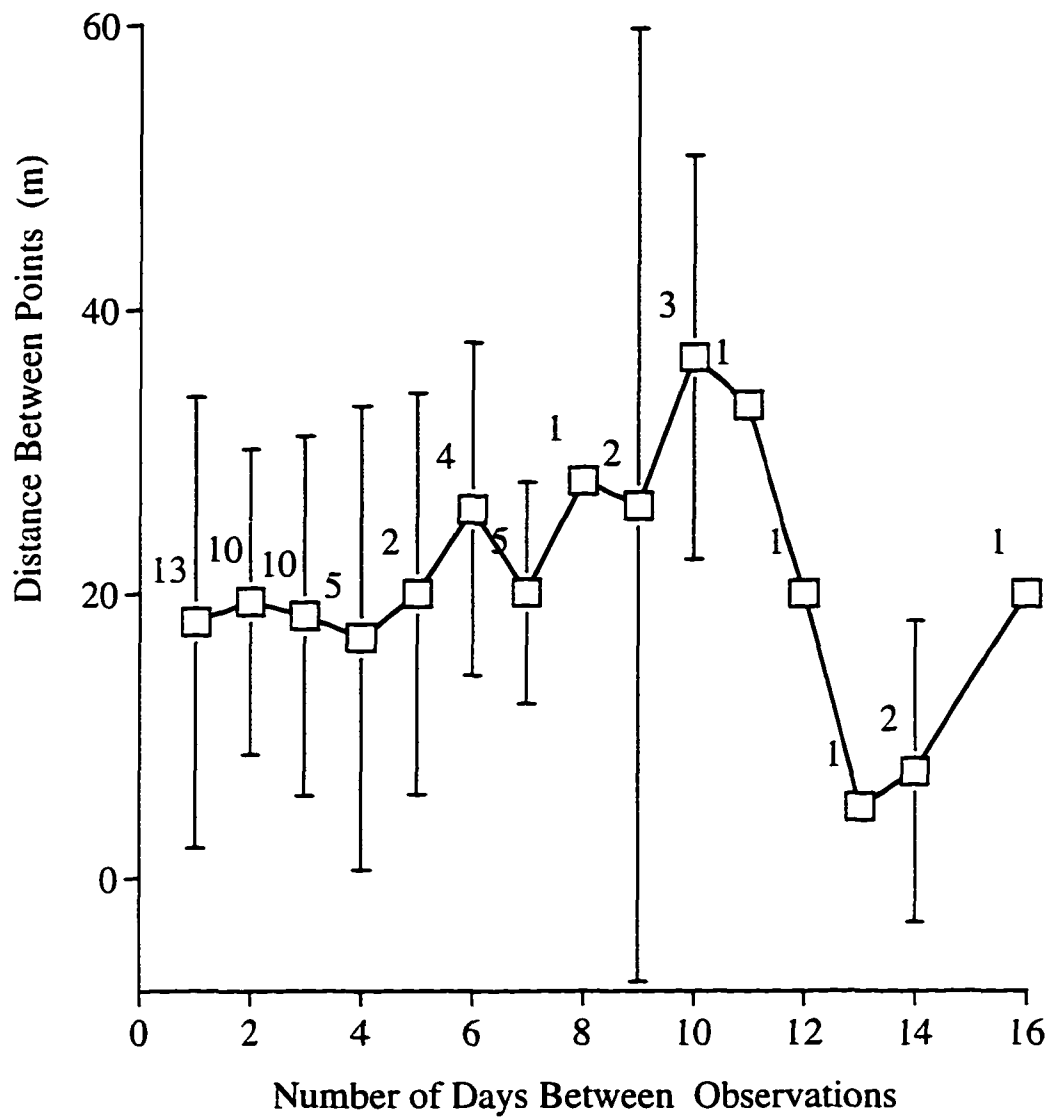


Figure 2. Relationship between the mean distance separating the points where the same individuals of *Bufo americanus* were found in different days, and number of days between observations (value labels represent the number of observations).

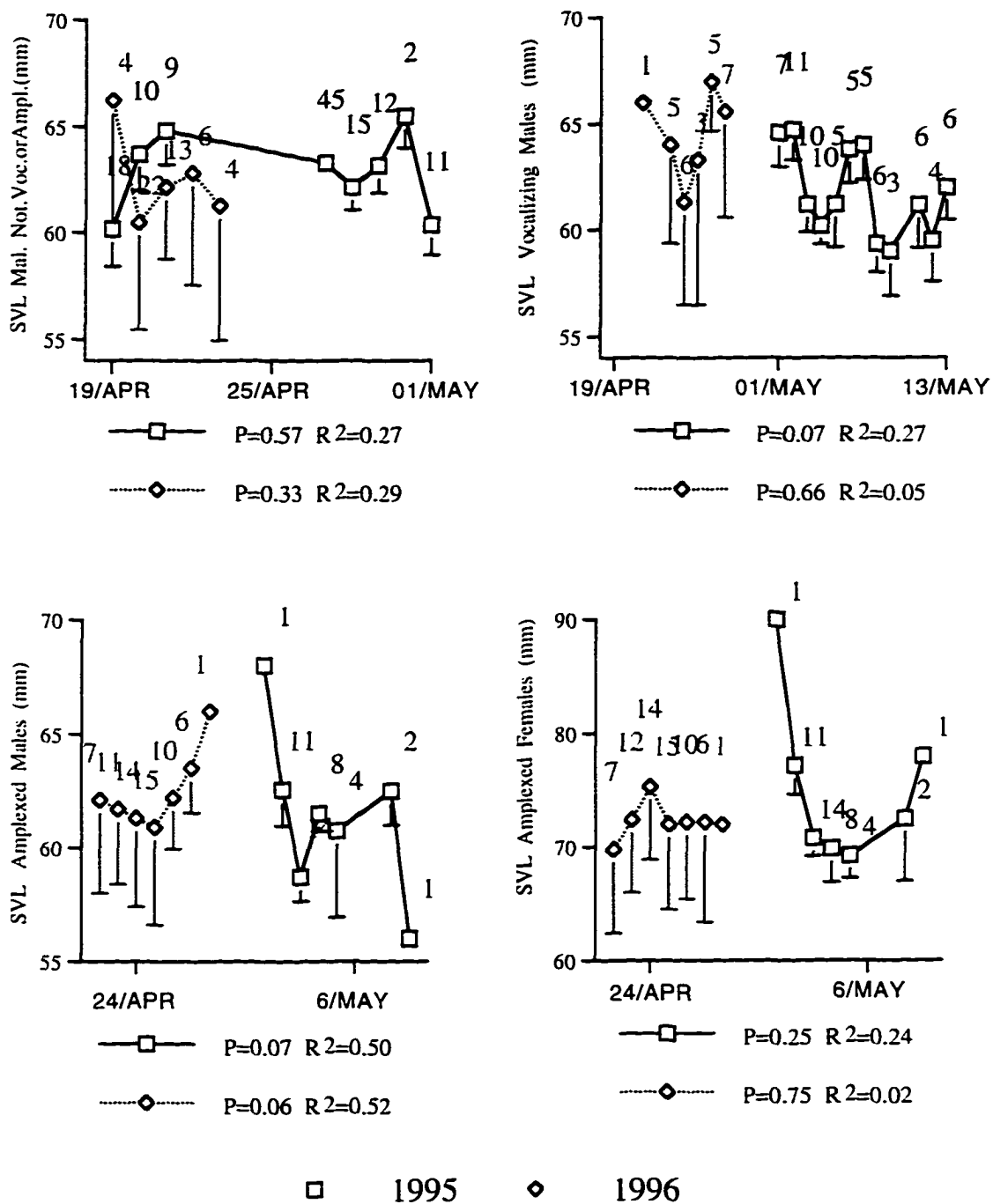


Figure 3. Variation in the daily mean snout-vent length (SVL) of *Bufo americanus* males found in vocalization, amplexus, and not in vocalization or amplexus, and of females found in amplexus (value labels represent the sample size).

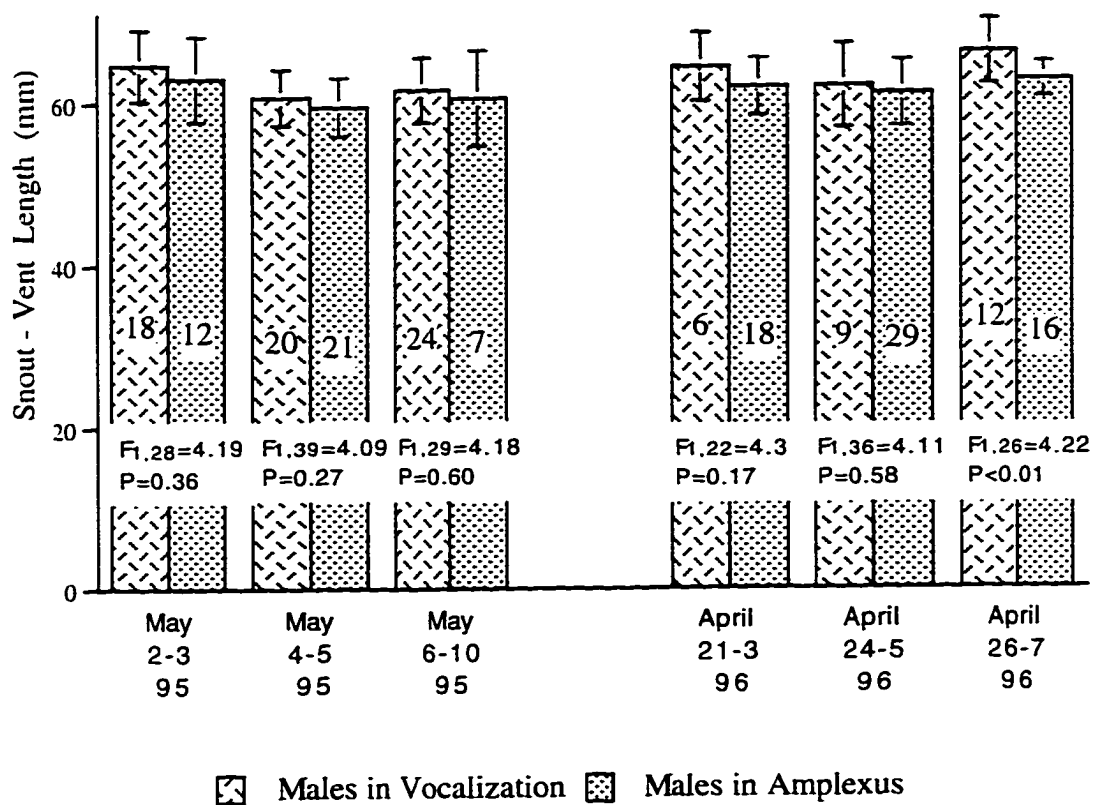


Figure 4. Mean snout-vent length of the males of *Bufo americanus* found in vocalization and in amplexus in the beginning, middle and end of the 1995 and 1996 mating seasons (value labels represent the sample's size).

Bufo

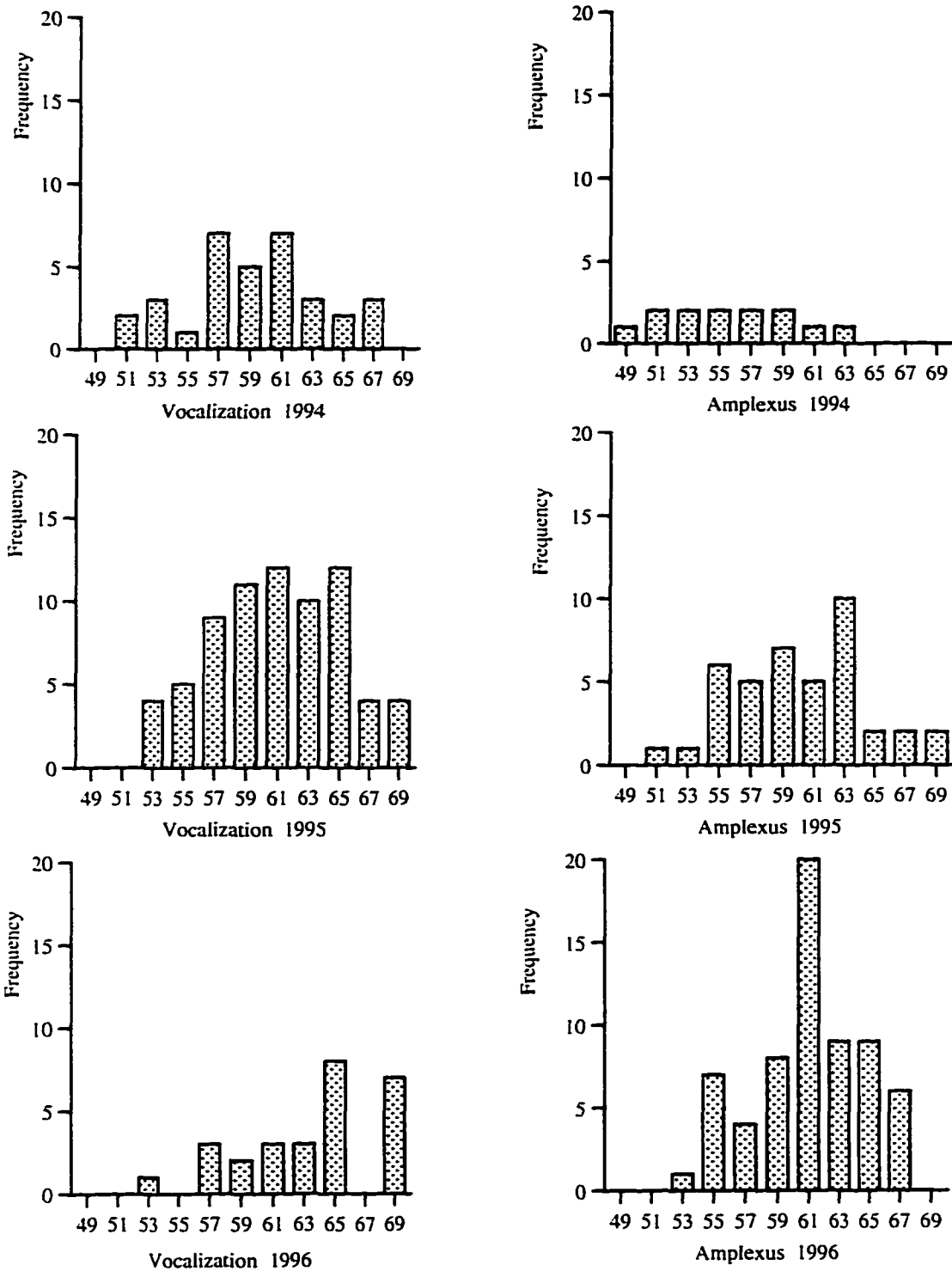


Figure 5. Histogram of frequency distribution of the snout-vent length (mm) of males of *Bufo americanus* found in vocalization and in amplexus in 1994, 1995 and 1996.

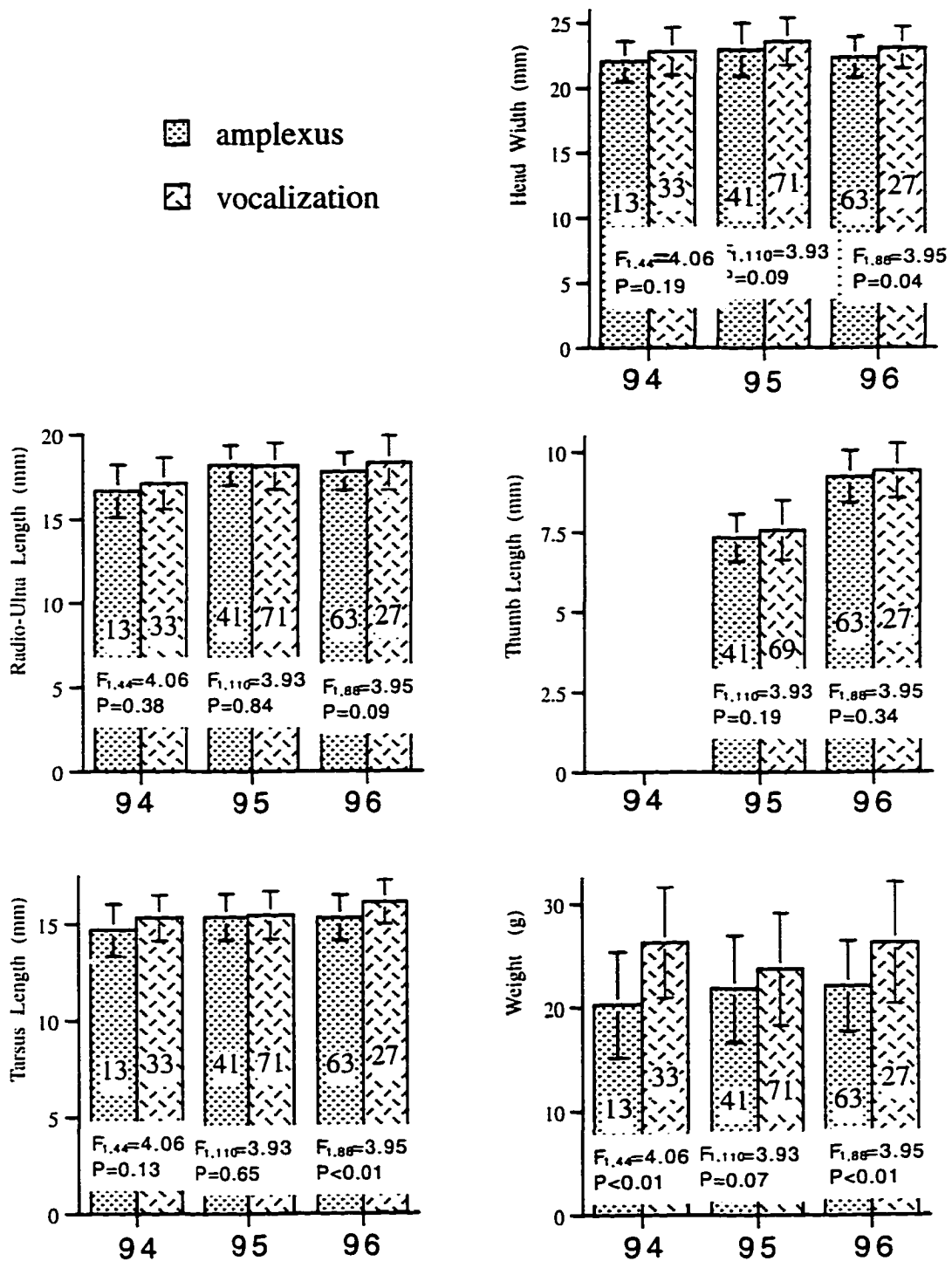


Figure 6. Mean head width, radio-ulna, thumb, and tarsus length, and weight in males of *Bufo americanus* found in amplexus and in vocalization (value labels represent the sample's size).

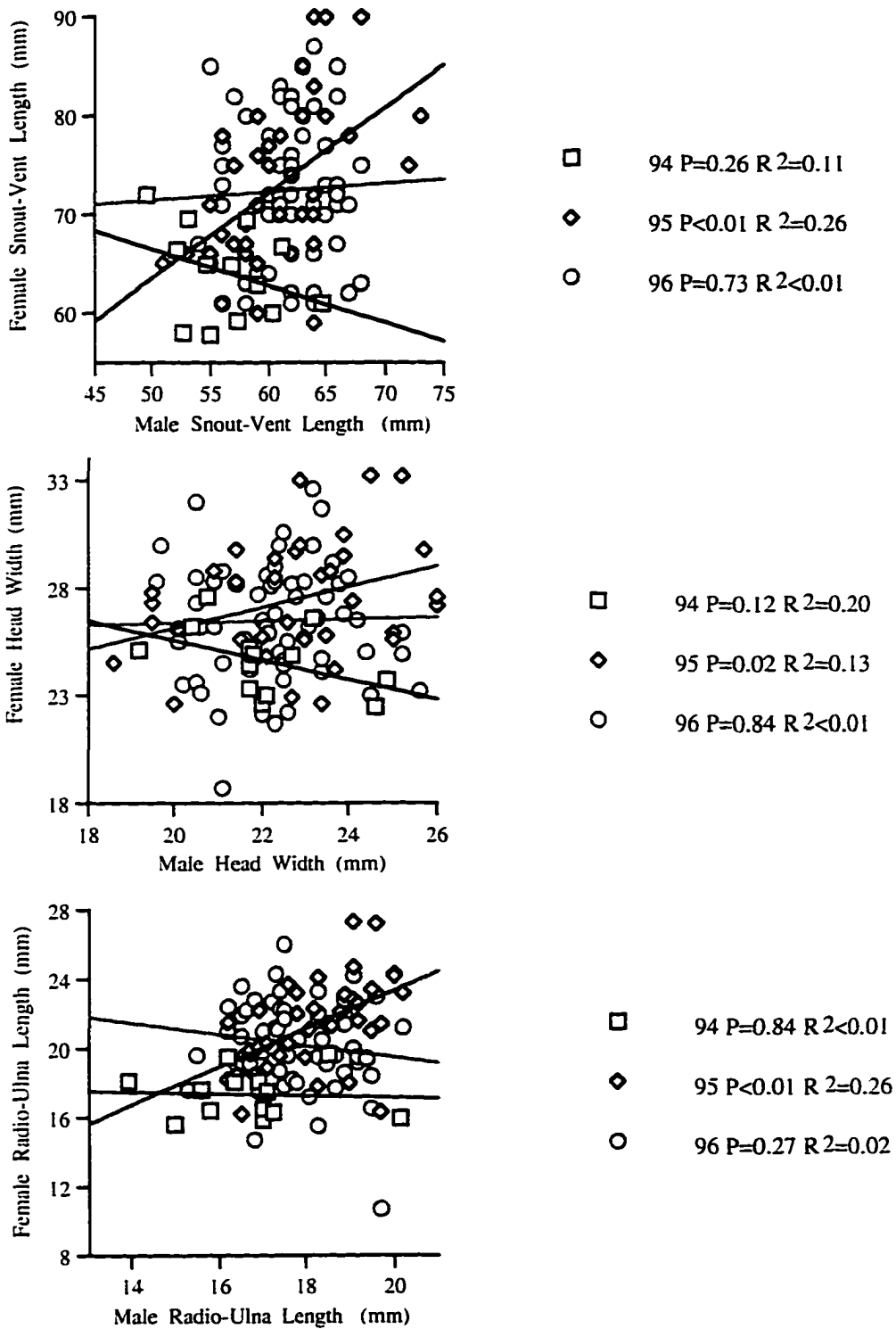


Figure 7. Relationships between male and female snout-vent length, head width, and radio-ulna in each one of the pairs of *Bufo americanus* found in amplexus.

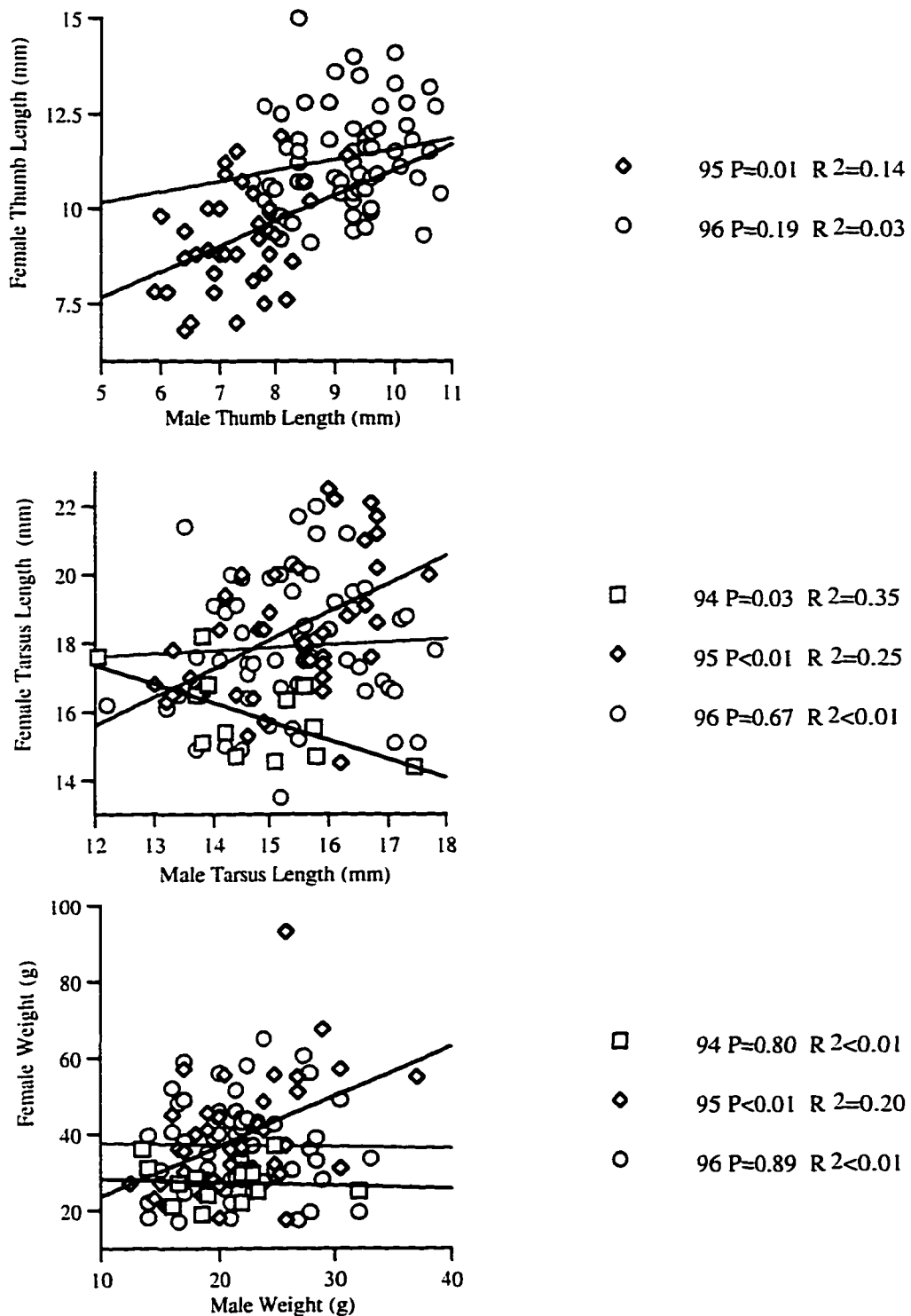


Figure 8. Relationships between male and female thumb and tarsus length, and body weight in each one of the pairs of *Bufo americanus* found in amplexus.

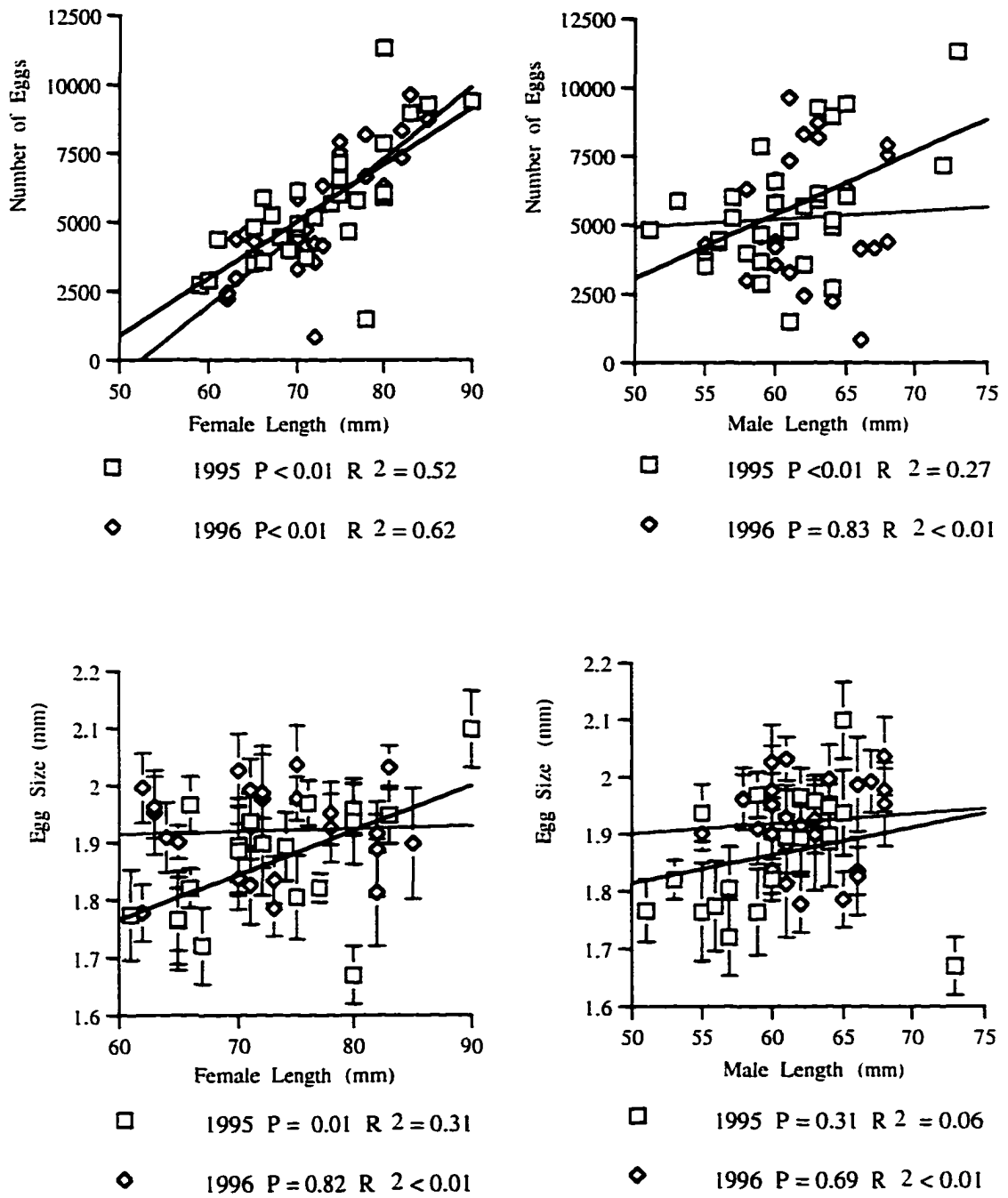


Figure 9. Relationships between *Bufo americanus* clutch and egg size, and snout-vent length of both parents.

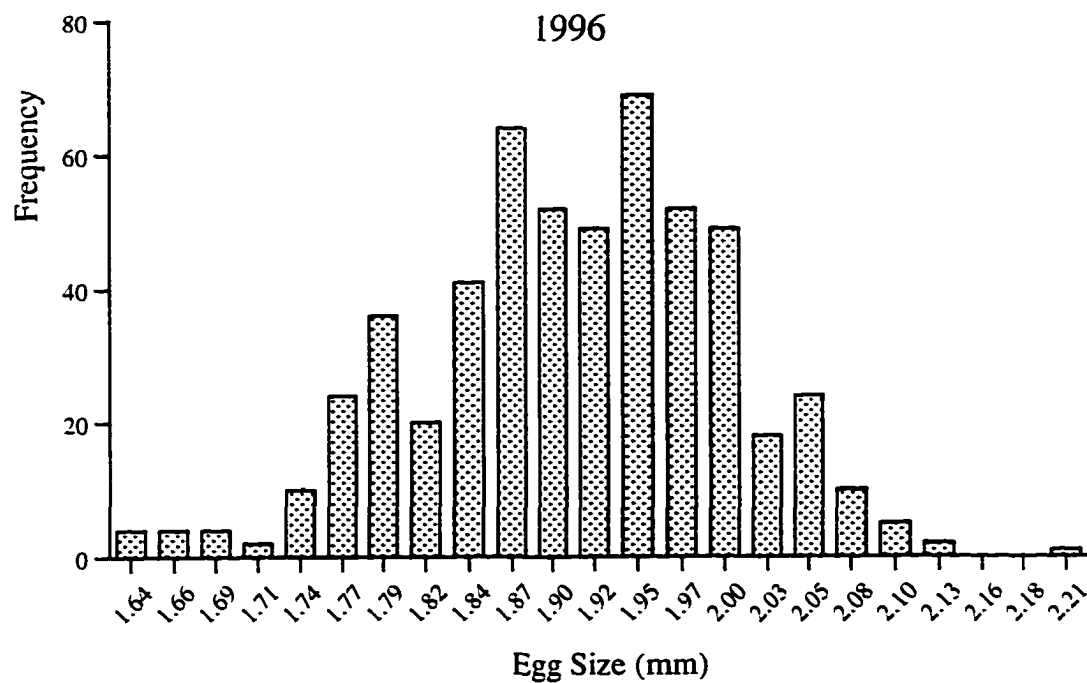
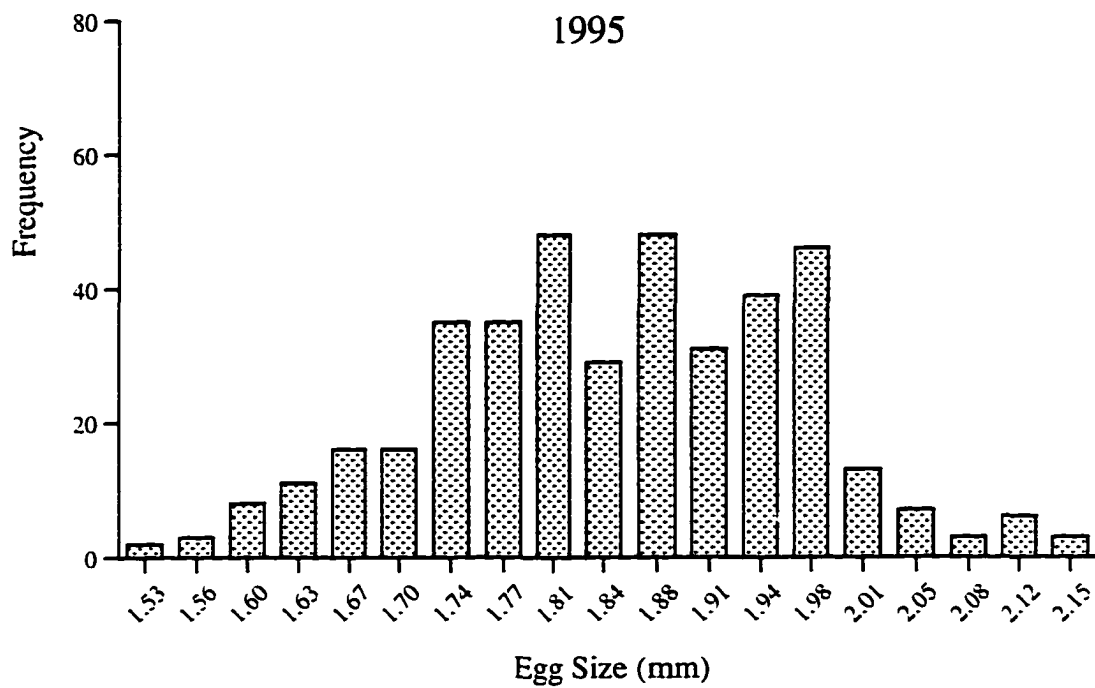


Figure 10. Histogram of frequency distribution of size of *Bufo americanus* eggs

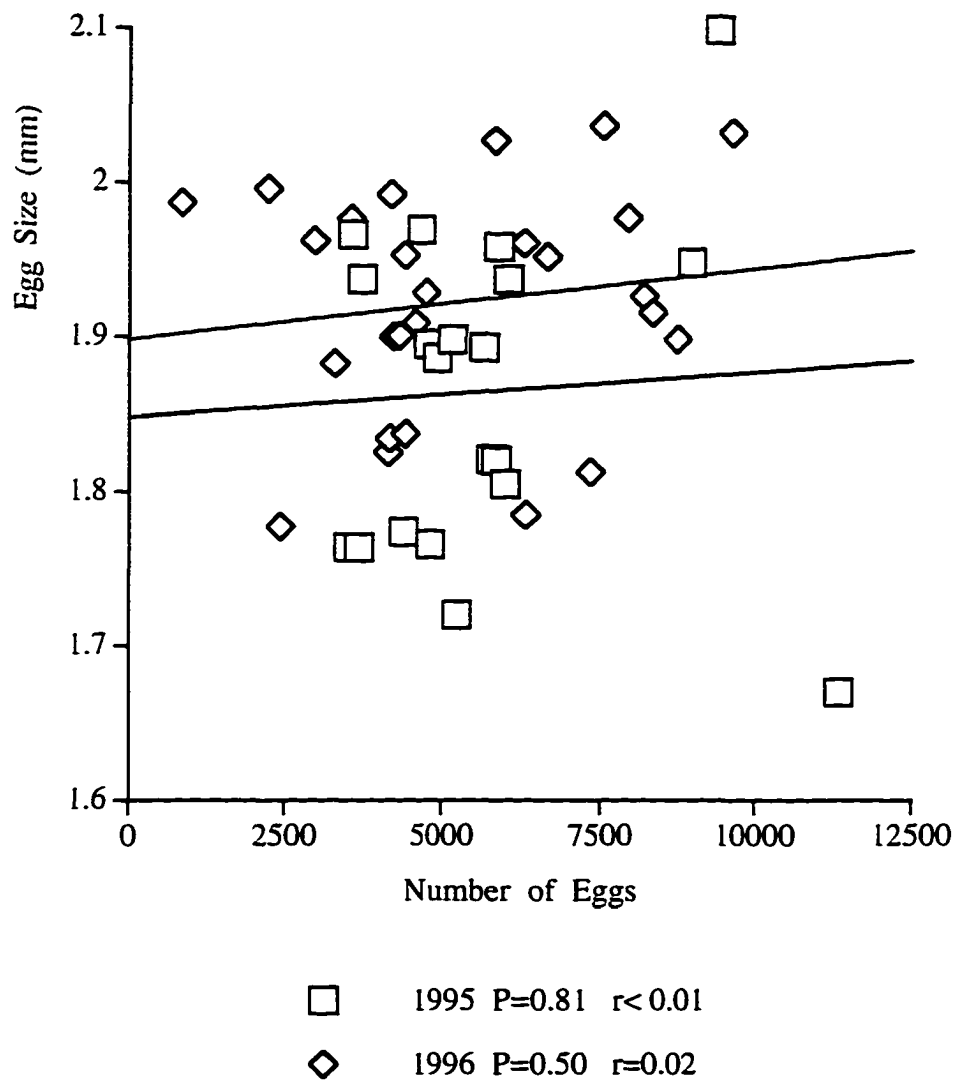


Figure 11. Relationship between clutch and egg size in *Bufo americanus* ovipositions.

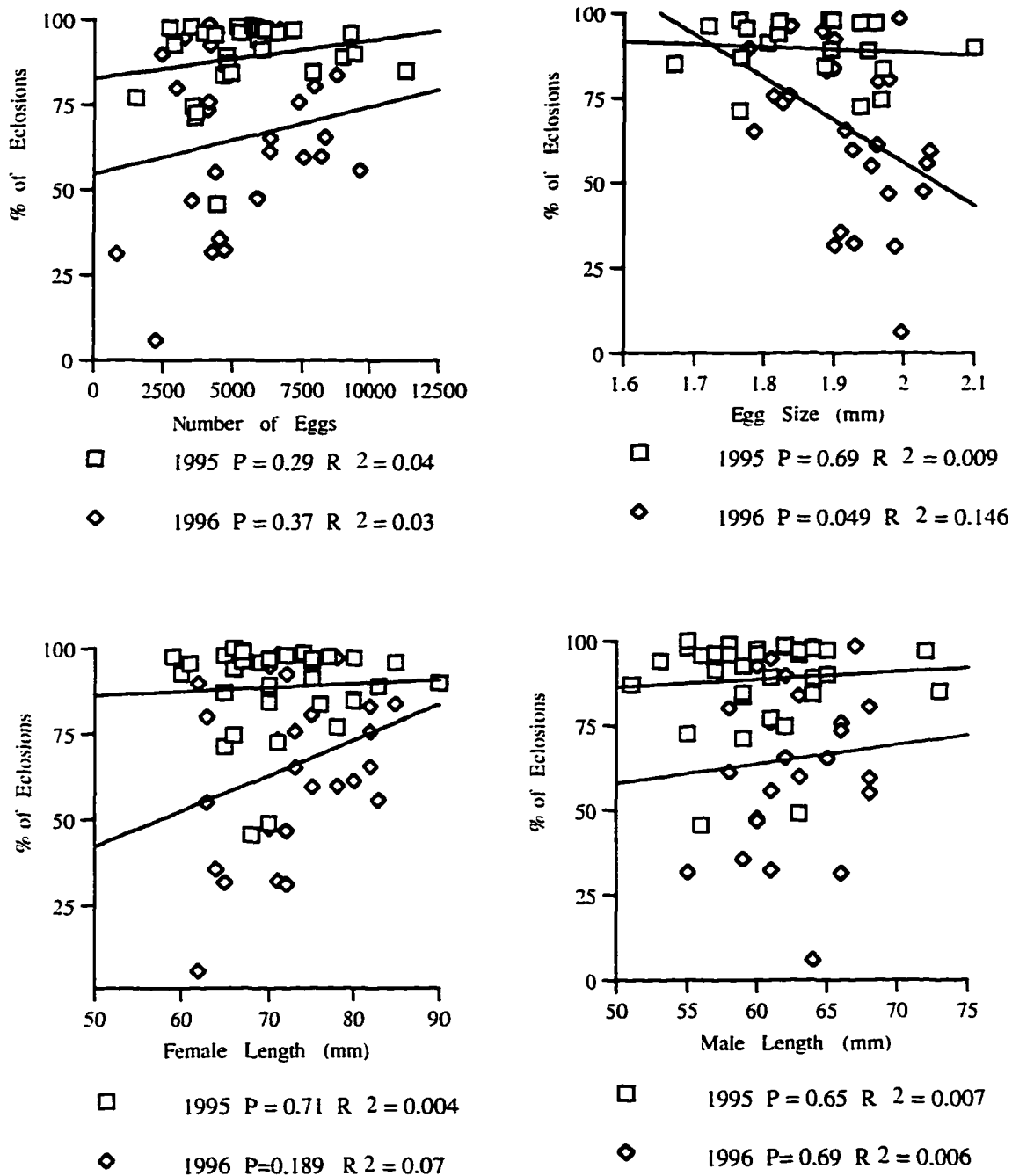


Figure 12. Relationships between percent of successful eclosions and clutch and egg size, snout-vent length of both parents in *Bufo americanus*.

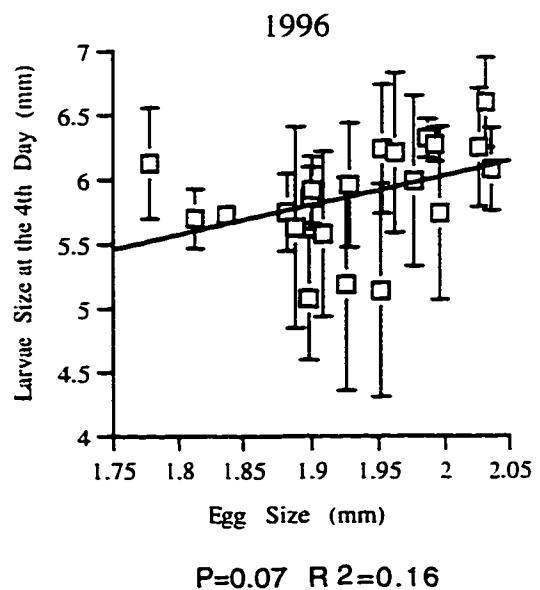
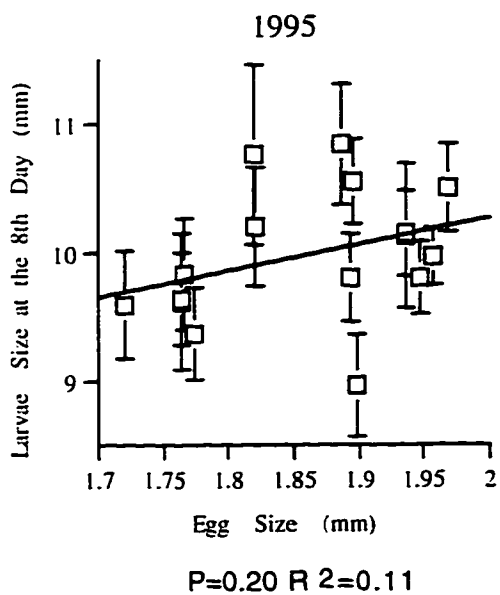
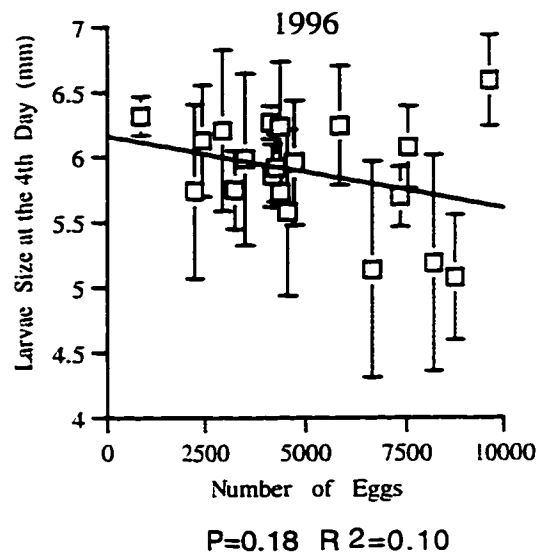
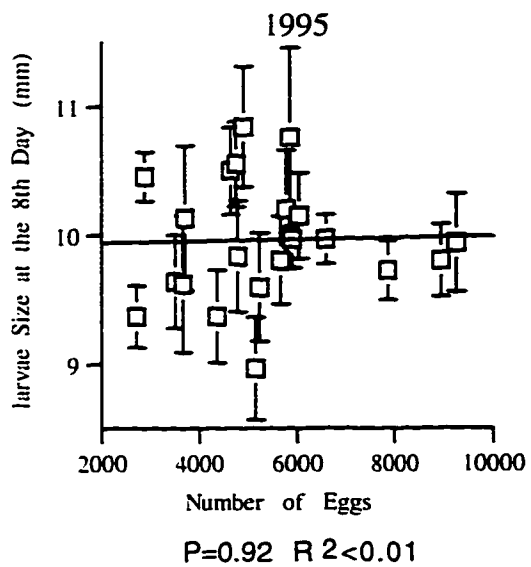


Figure 13. Relationships between length of *Bufo americanus* larvae at the day 8 (1995) and the day 4 (1996), and clutch and egg size.

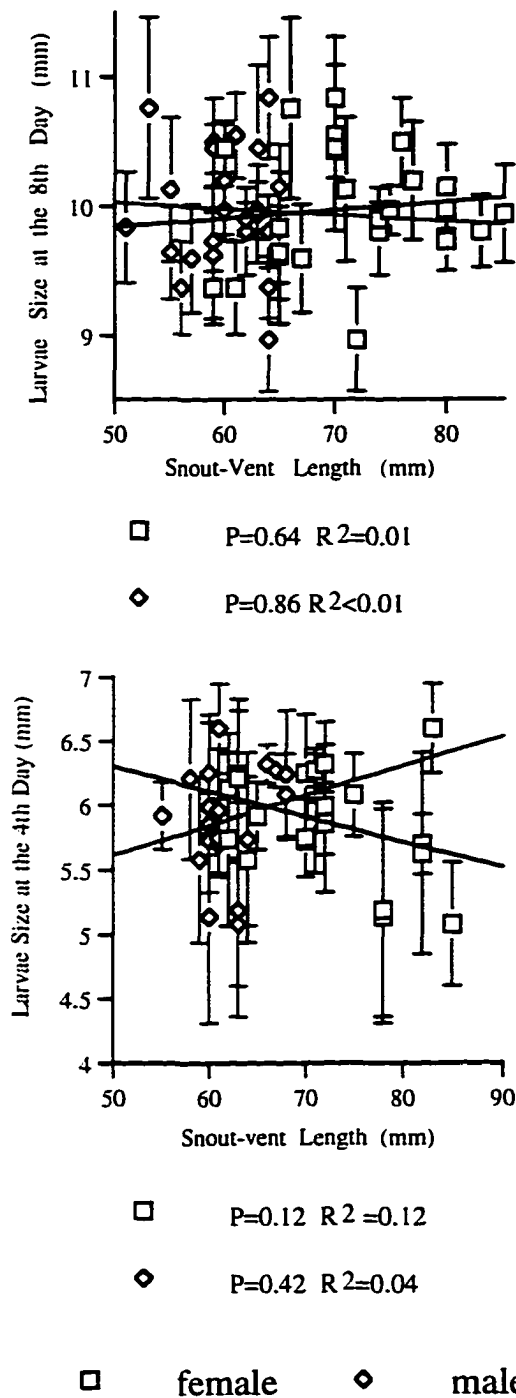


Figure 14. Relationships between length of *Bufo americanus* larvae at the day 8 (1995) and the day 4 (1996) after eclosion, and snout-vent length of both parents.

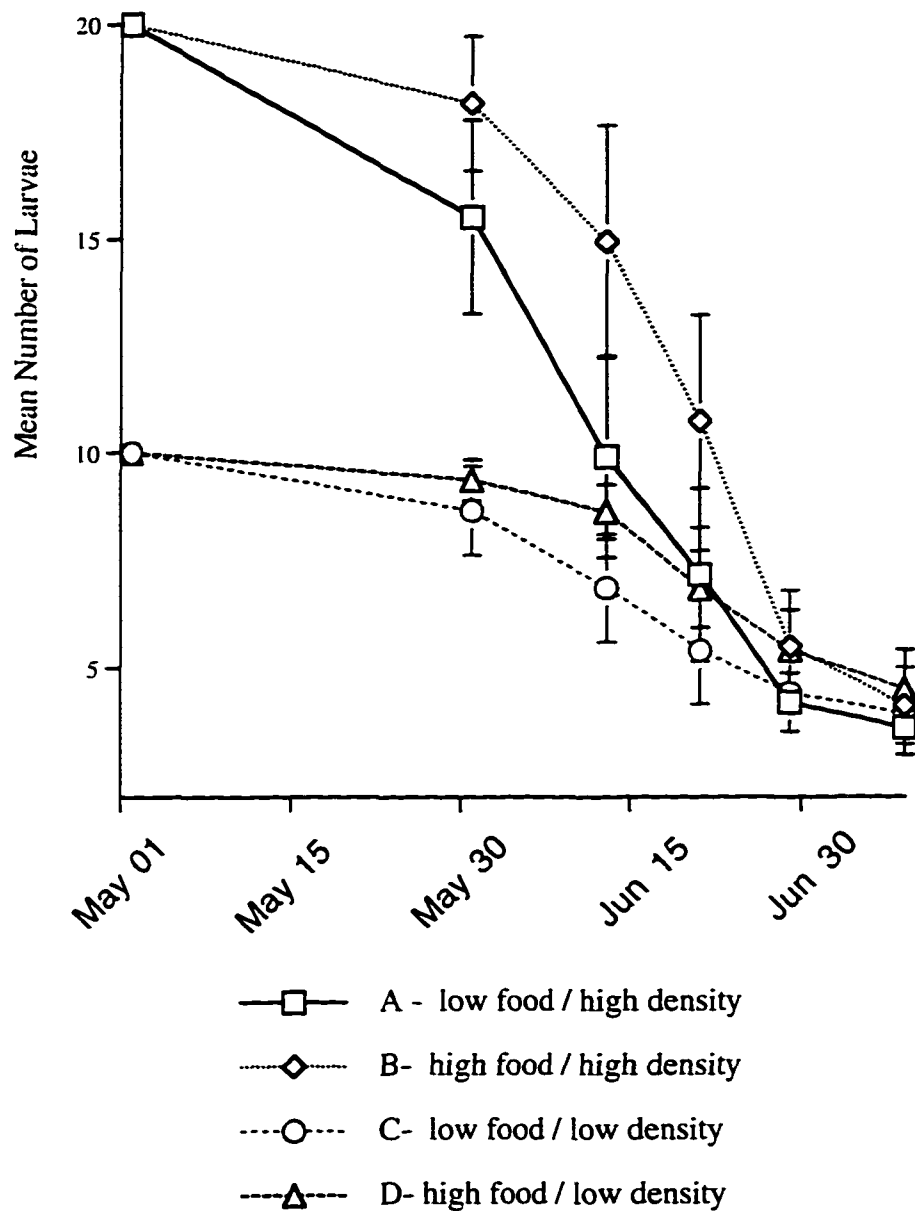


Figure 15. Mean number of surviving *Bufo americanus* larvae in each of the treatments of the 1996 laboratory experiment, during the first 70 days.

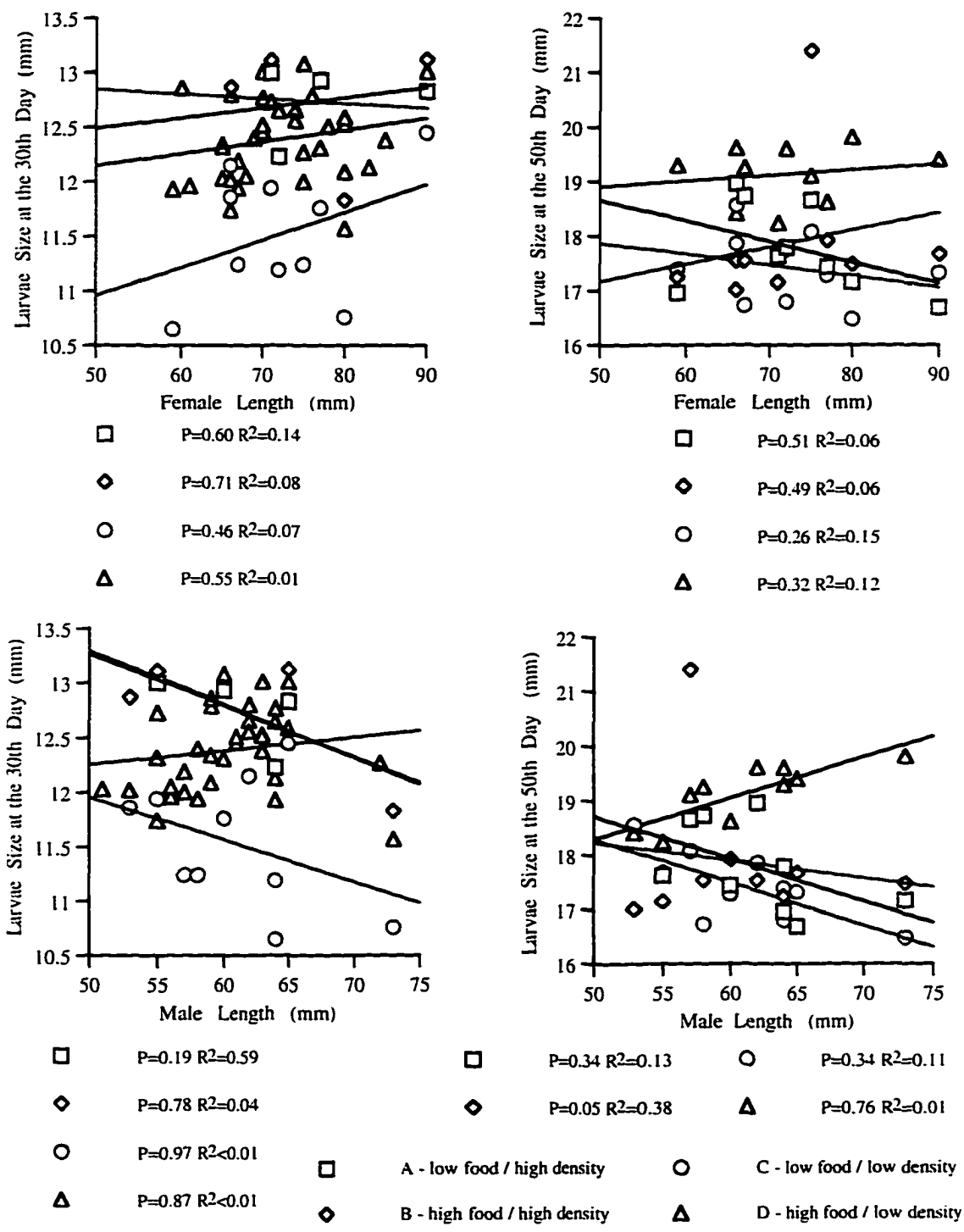


Figure 16. Relationship between the length of *Bufo americanus* larvae at the day 30 and day 50 of the larval period, and snout-vent length of both parents in each of the treatments of the 1995 laboratory experiment.

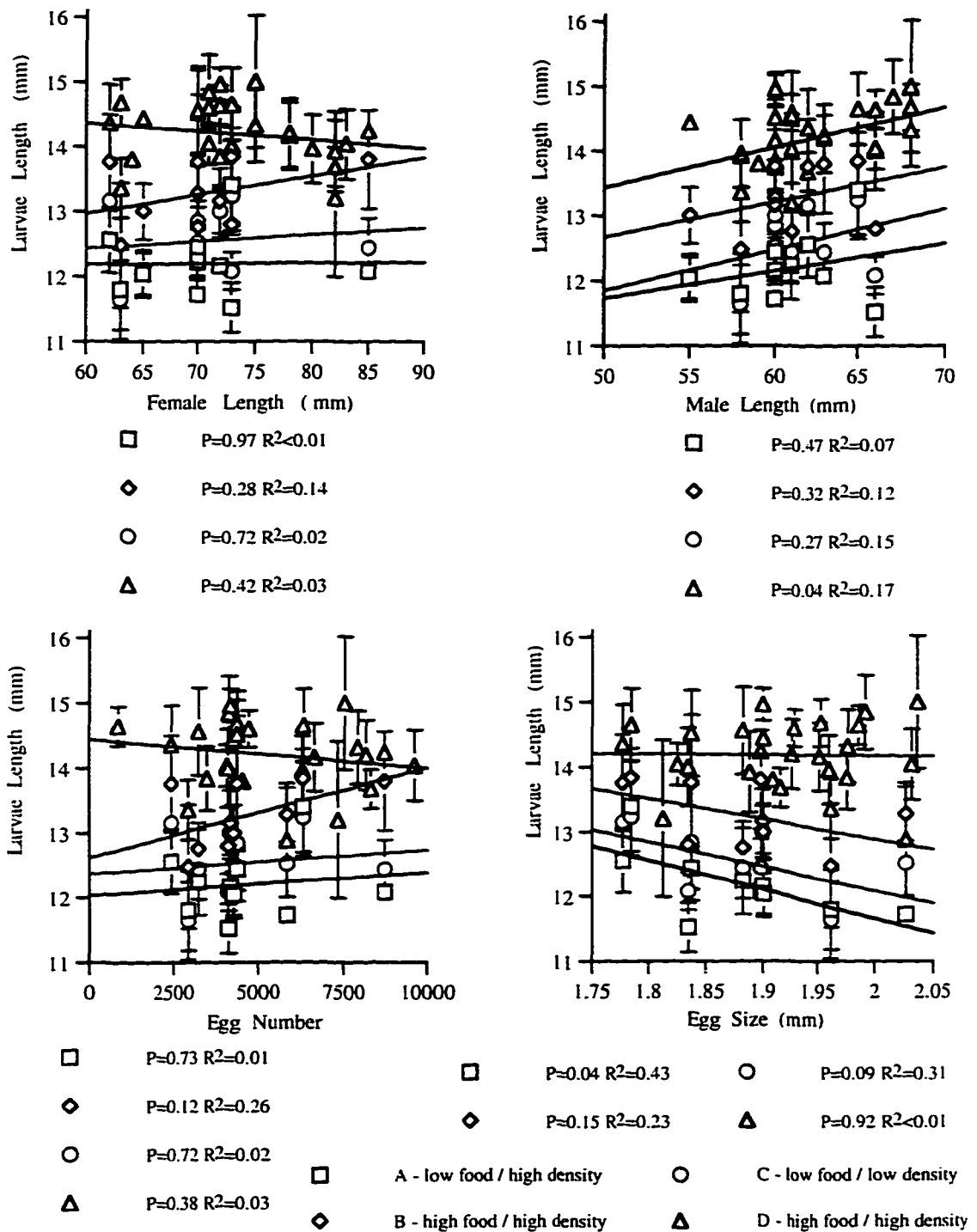


Figure 17. Relationships between the length of the *Bufo americanus* larvae at the day 40 of the larval period, and length of both parents, and number and size of the eggs, in each of the treatments of the 1996 laboratory experiment.

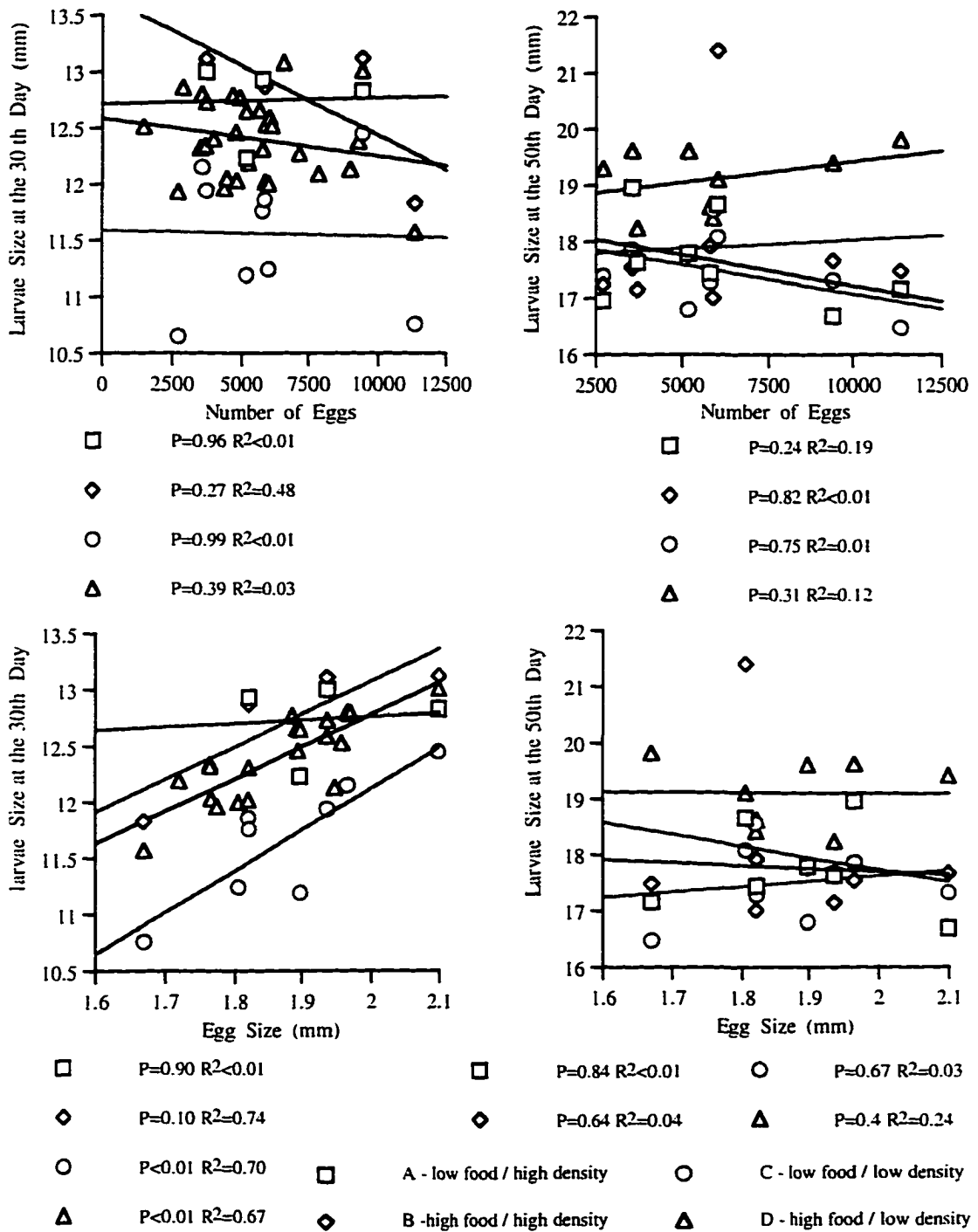


Figure 18. Relationships between the length of *Bufo americanus* larvae at the day 30 and day 50 of the larval period and number and size of the eggs in each of the treatments of the 1995 laboratory experiment.

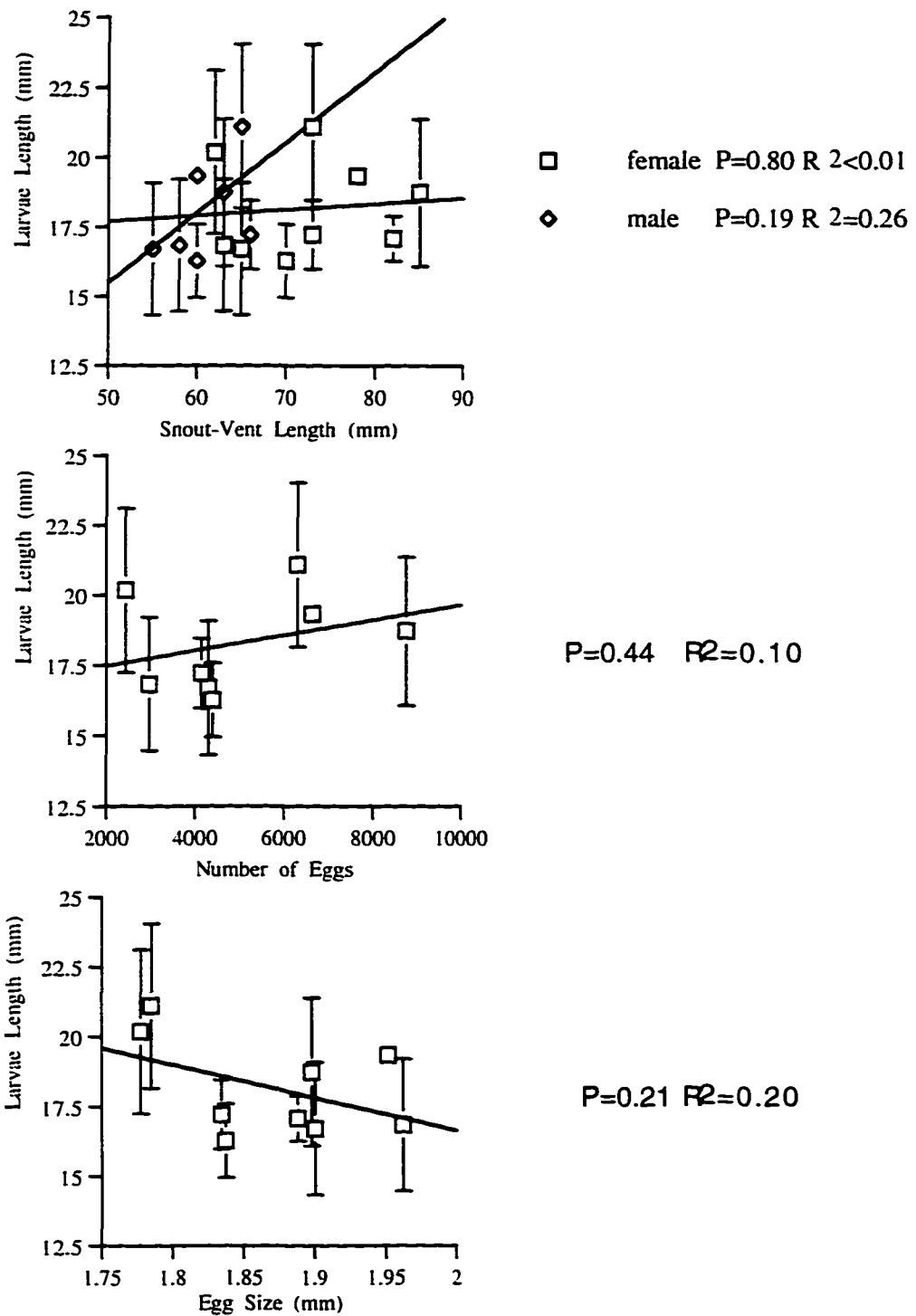
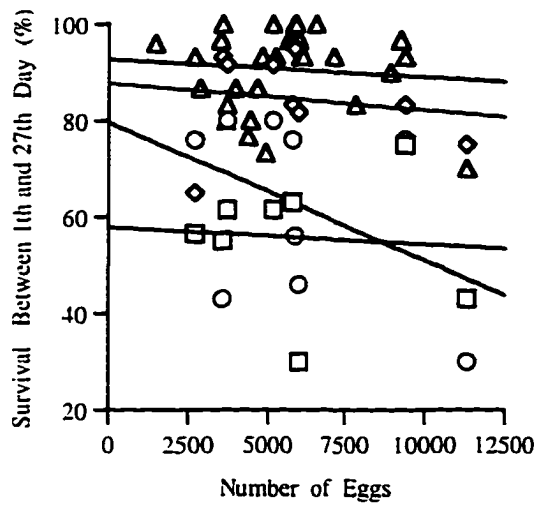
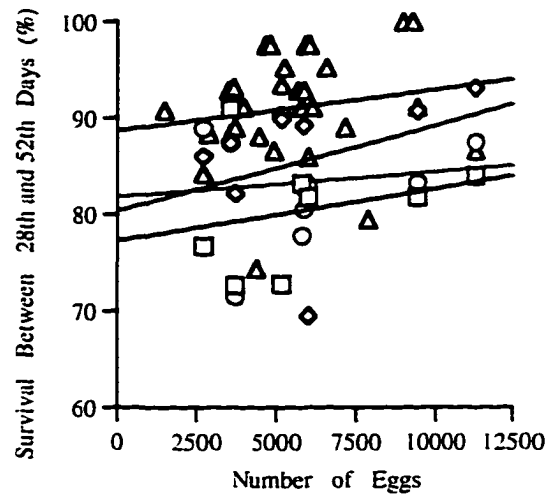


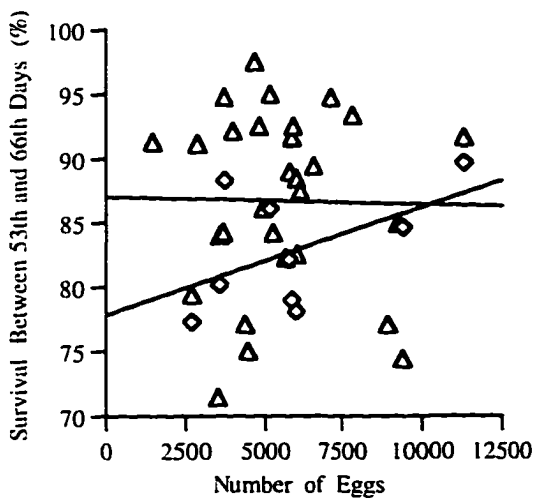
Figure 19. Relationships between mean length of the *Bufo americanus* larvae at the day 50 of larval life, and snout-vent length of both parents, and number and size of the eggs in the field experiment.



- P=0.70 R²=0.02
- ◇ P=0.62 R²=0.03
- P=0.20 R²=0.20
- △ P=0.59 R²=0.01



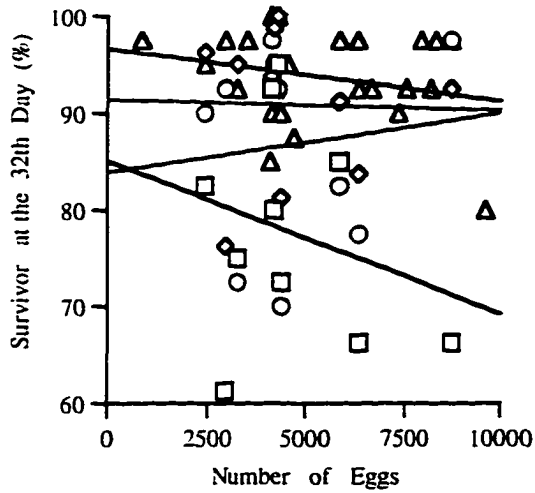
- P=0.53 R²=0.07
- ◇ P=0.19 R²=0.27
- P=0.75 R²=0.01
- △ P=0.40 R²=0.03



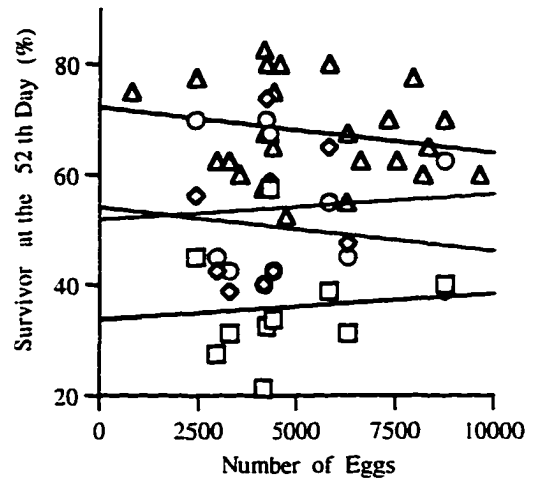
- ◇ P=0.15 R²=0.27
- △ P=0.92 R²<0.01

- A - low food / high density
- ◇ B - high food / high density
- C - low food / low density
- △ D - high food / low density

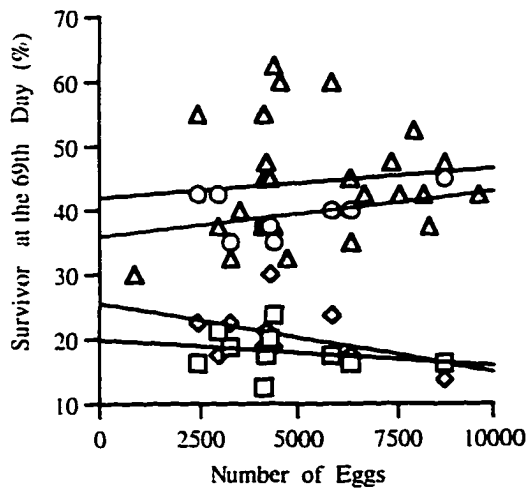
Figure 20. Relationships between percent of survival and number of eggs in larvae *Bufo americanus* in each of the treatments of the 1995 laboratory experiment.



- P = 0.47 R² = 0.07
- ◇ P = 0.94 R² = 0.001
- P = 0.76 R² = 0.01
- △ P = 0.23 R² = 0.06



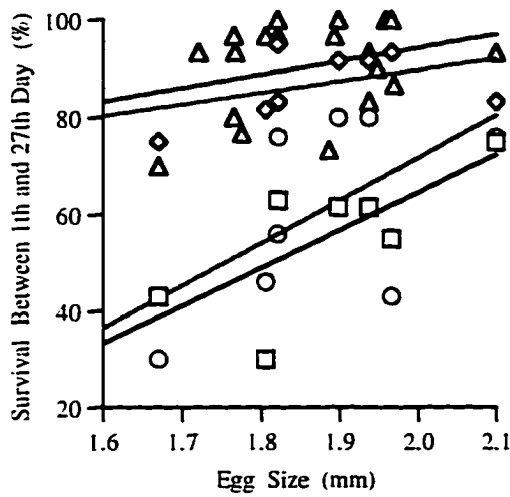
- P = 0.81 R² = 0.007
- ◇ P = 0.74 R² = 0.01
- P = 0.85 R² = 0.005
- △ P = 0.30 R² = 0.04



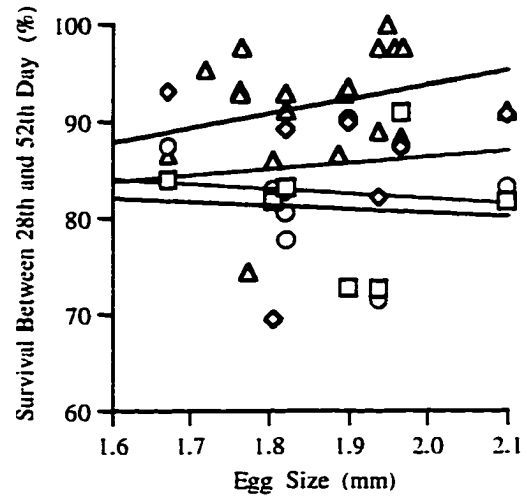
- A - low food / high density
- ◇ C - low food / low density
- B - high food / high density
- △ D - high food / low density

- P = 0.51 R² = 0.056
- ◇ P = 0.19 R² = 0.20
- P = 0.25 R² = 0.15
- △ P = 0.59 R² = 0.01

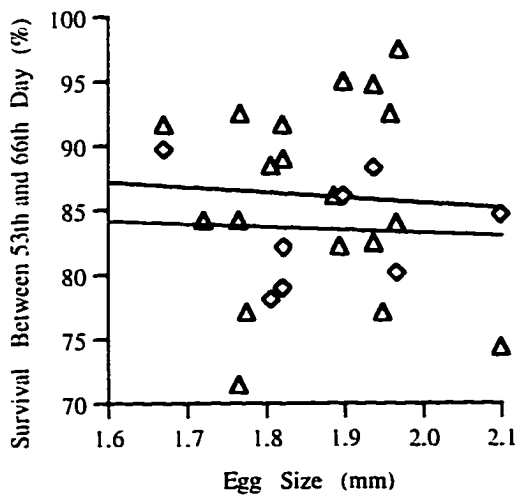
Figure 21. Relationships between percent of survival and number of eggs in *Bufo americanus* larvae in each of the treatments of the 1996 laboratory experiment.



□ P=0.05 R²=0.53
 ◇ P=0.27 R²=0.19
 ○ P=0.13 R²=0.33
 △ P=0.19 R²=0.10



□ P=0.87 R²<0.01
 ◇ P=0.77 R²=0.01
 ○ P=0.81 R²=0.01
 △ P=0.25 R²=0.08



◇ P=0.89 R²<0.01
 △ P=0.85 R²<0.01

□ A - low food / high density ○ C - low food / low density
 ◇ B - high food / high density △ D - high food / low density

Figure 22. Relationships between percent of survival and size of the eggs in *Bufo americanus* larvae in each of the treatments of the 1995 laboratory experiment.

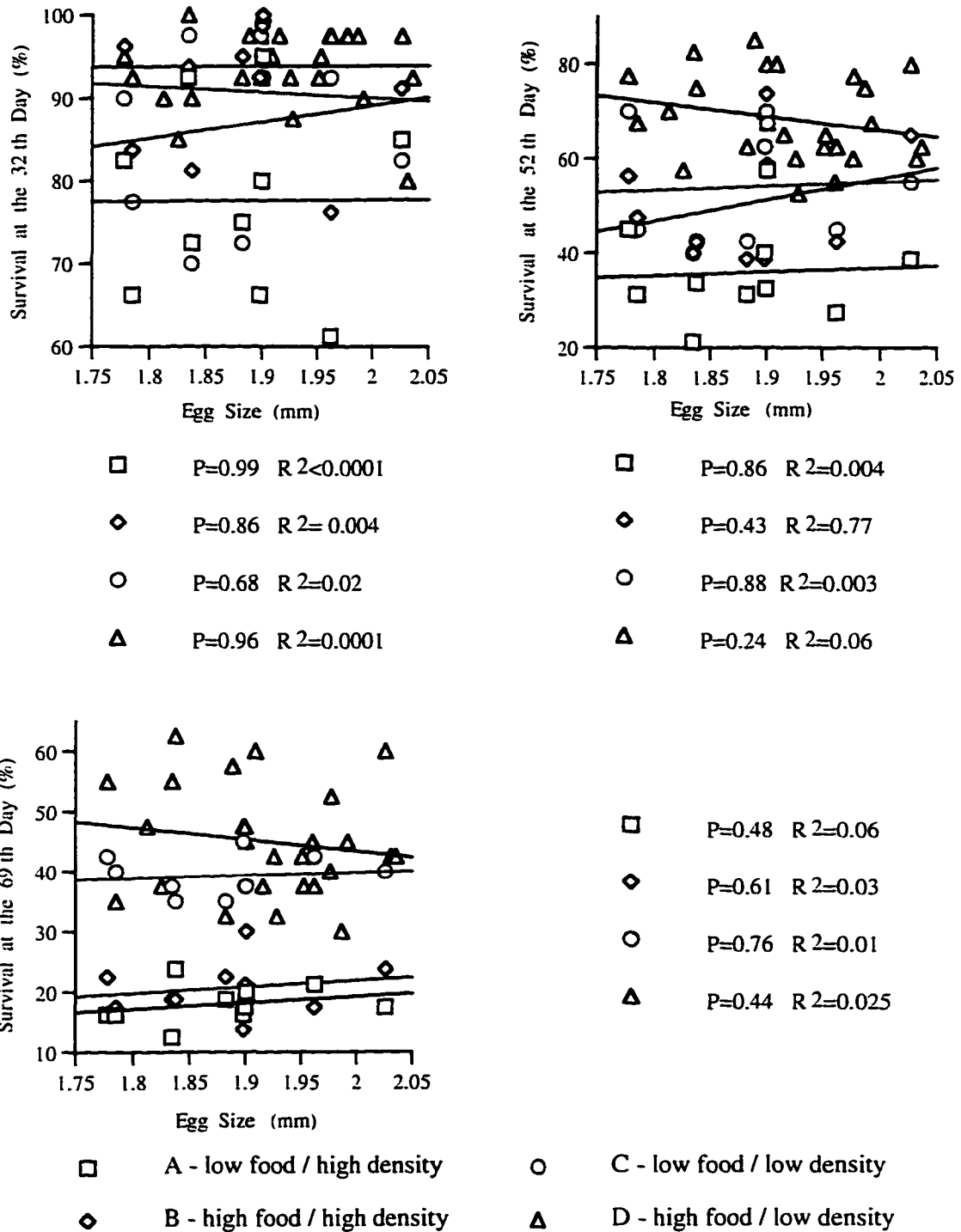


Figure 23. Relationships between percent of survival and egg size in *Bufo americanus* larvae in each of the treatments of the 1996 laboratory experiment.

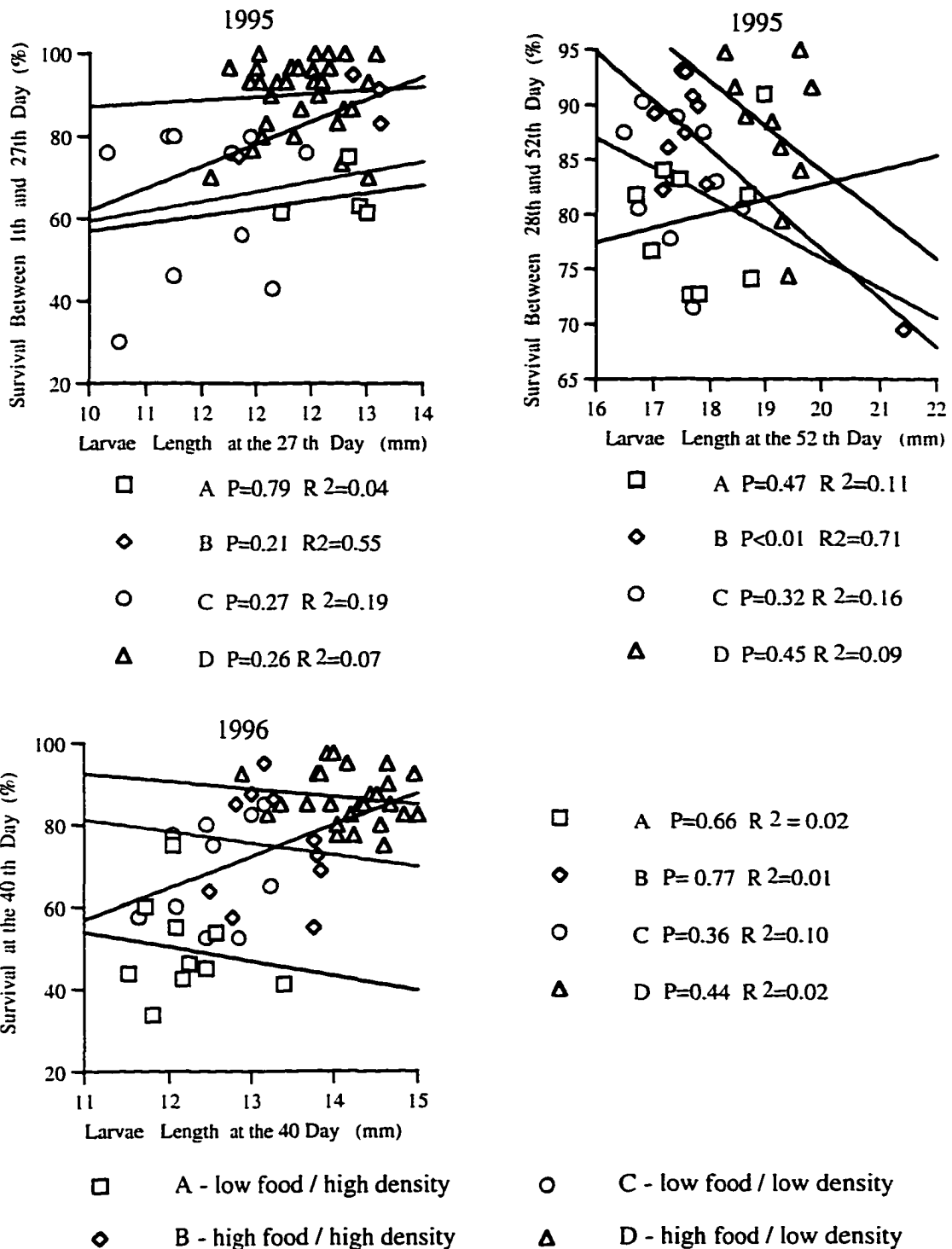


Figure 24. Relationships between percent of survival and *Bufo americanus* larvae length in each of the treatments of the 1995 and 1996 laboratory experiments.

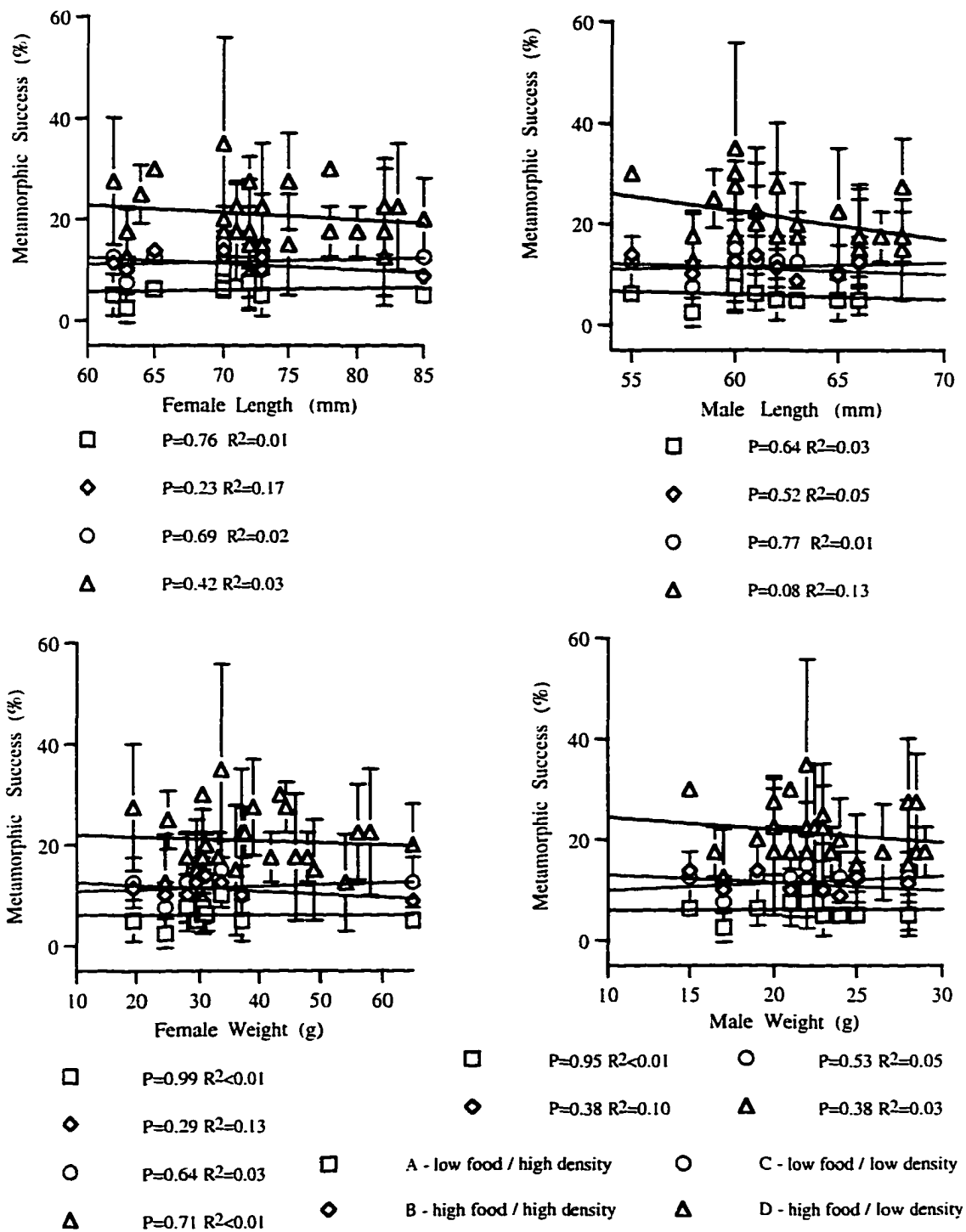


Figure 25. Relationships between the percentage of *Bufo americanus* larvae that successfully complete metamorphosis and snout-vent length and weight of both parents, in each of the treatments of the 1996 laboratory experiment.

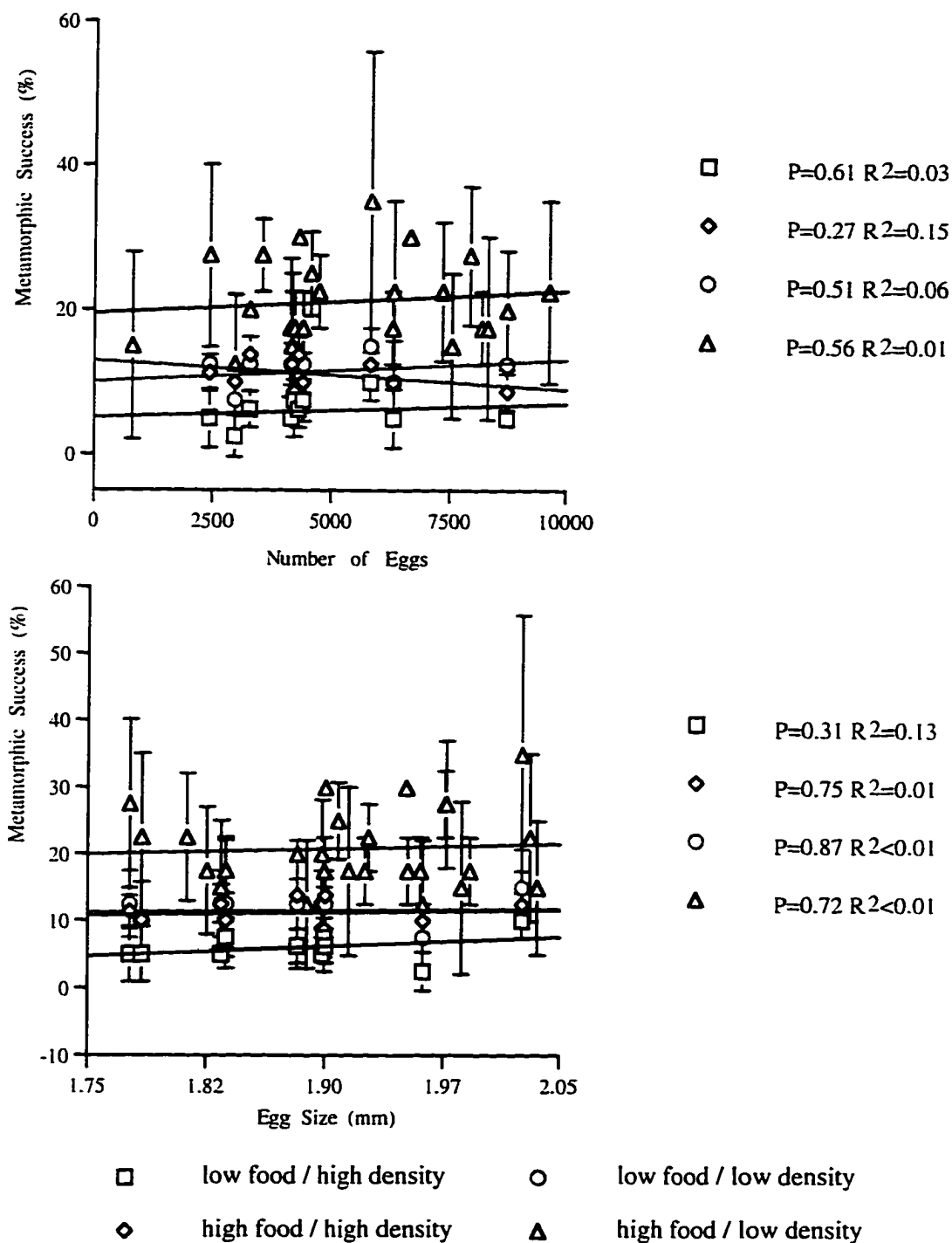


Figure 26. Relationships between percentage of *Bufo americanus* larvae that successfully complete metamorphosis, and clutch and egg size, in each of the treatments of the 1996 laboratory experiment.

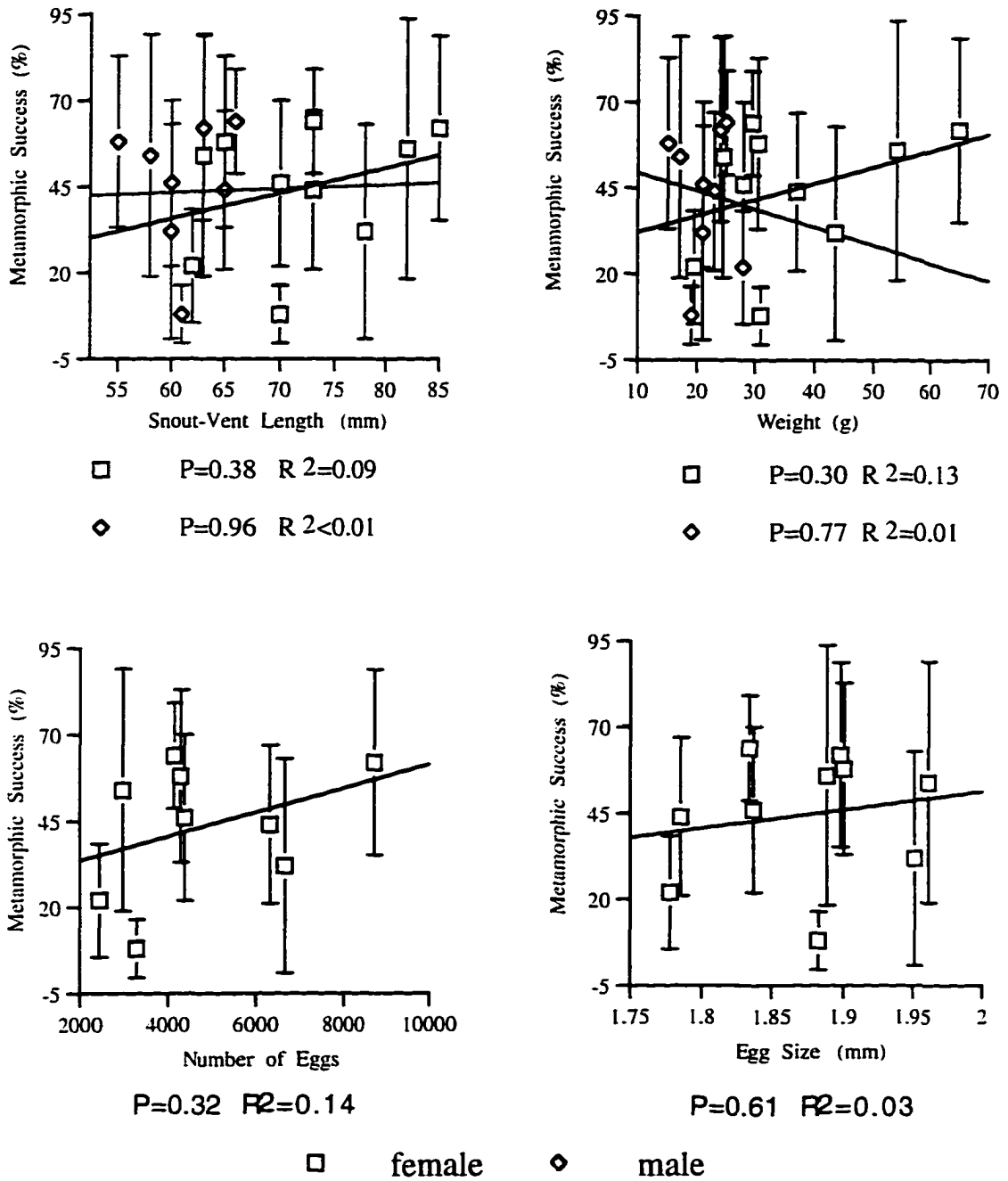


Figure 27. Relationships between the percent of *Bufo americanus* larvae that successfully completed metamorphosis, and snout-vent length of both parents, and number and size of the eggs, in the 1996 field experiment.

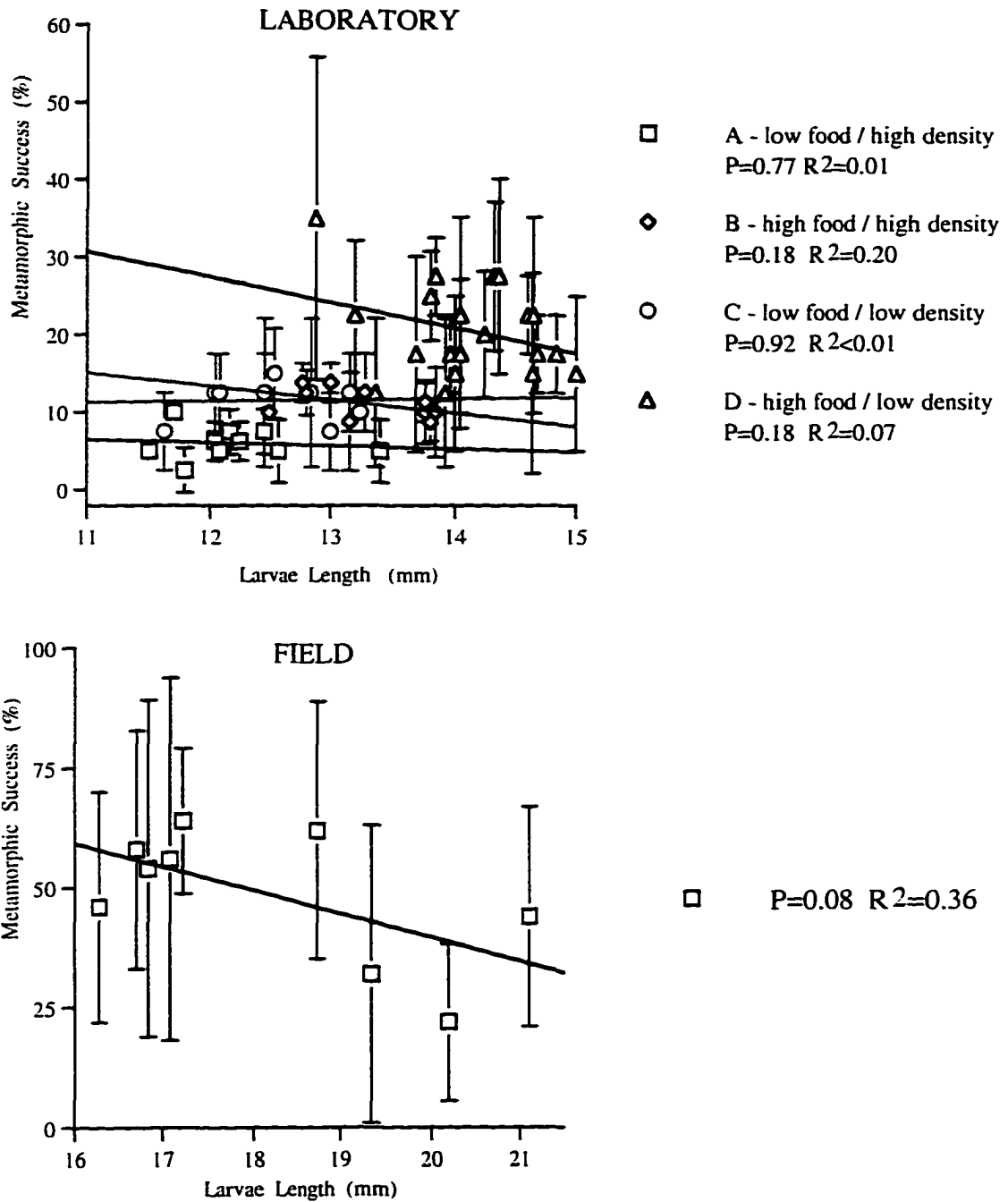


Figure 28. Relationships between the percent of larvae that successfully completed metamorphosis, and length of the *Bufo americanus* larvae at day 40 (laboratory experiment) or day 50 (field experiment) of the larval period, in each of the treatments of the laboratory experiment, and in the field experiment.

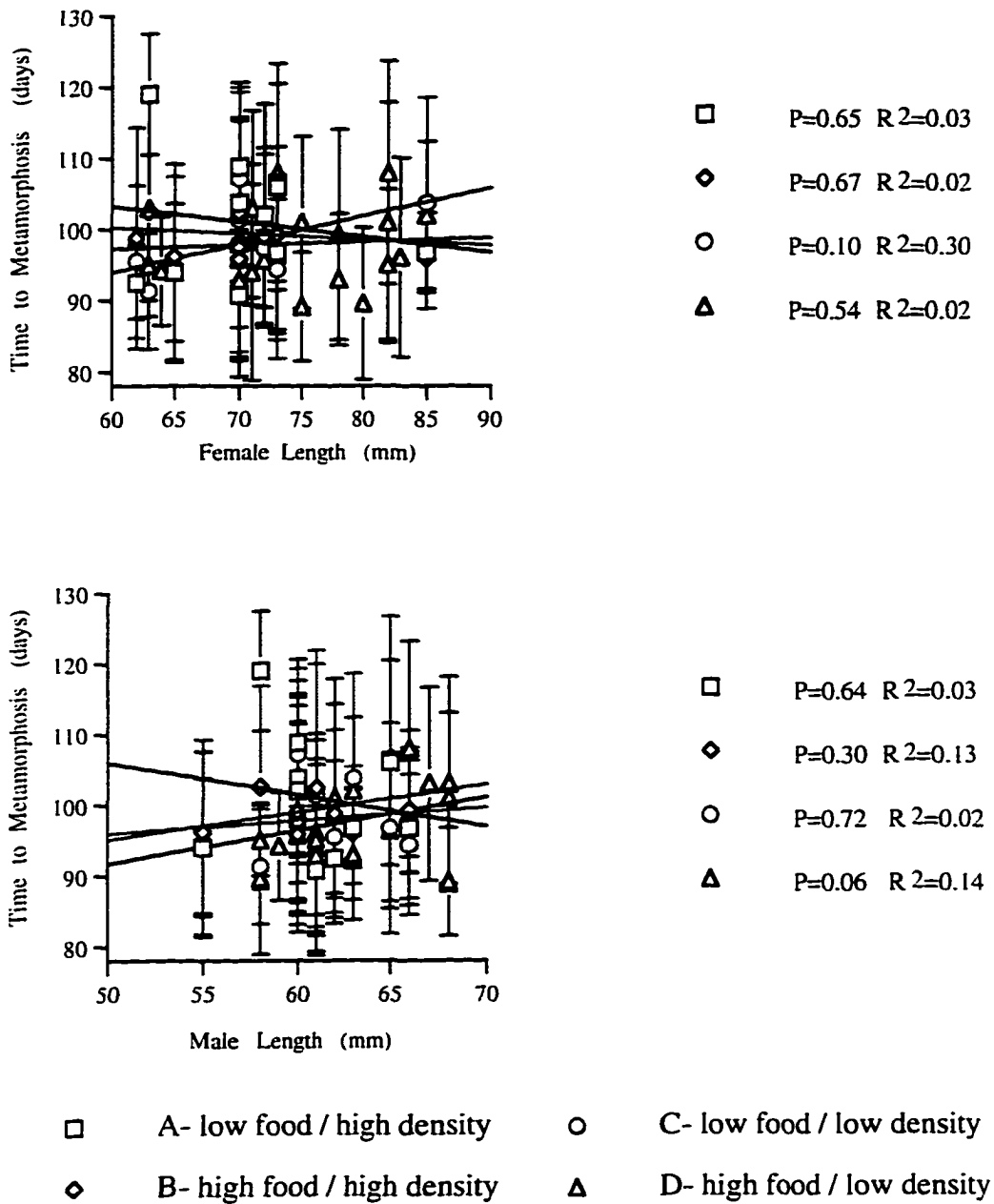


Figure 29. Relationships between duration of *Bufo americanus* larval period and body length of both parents in each of the treatments of the 1996 laboratory experiment.

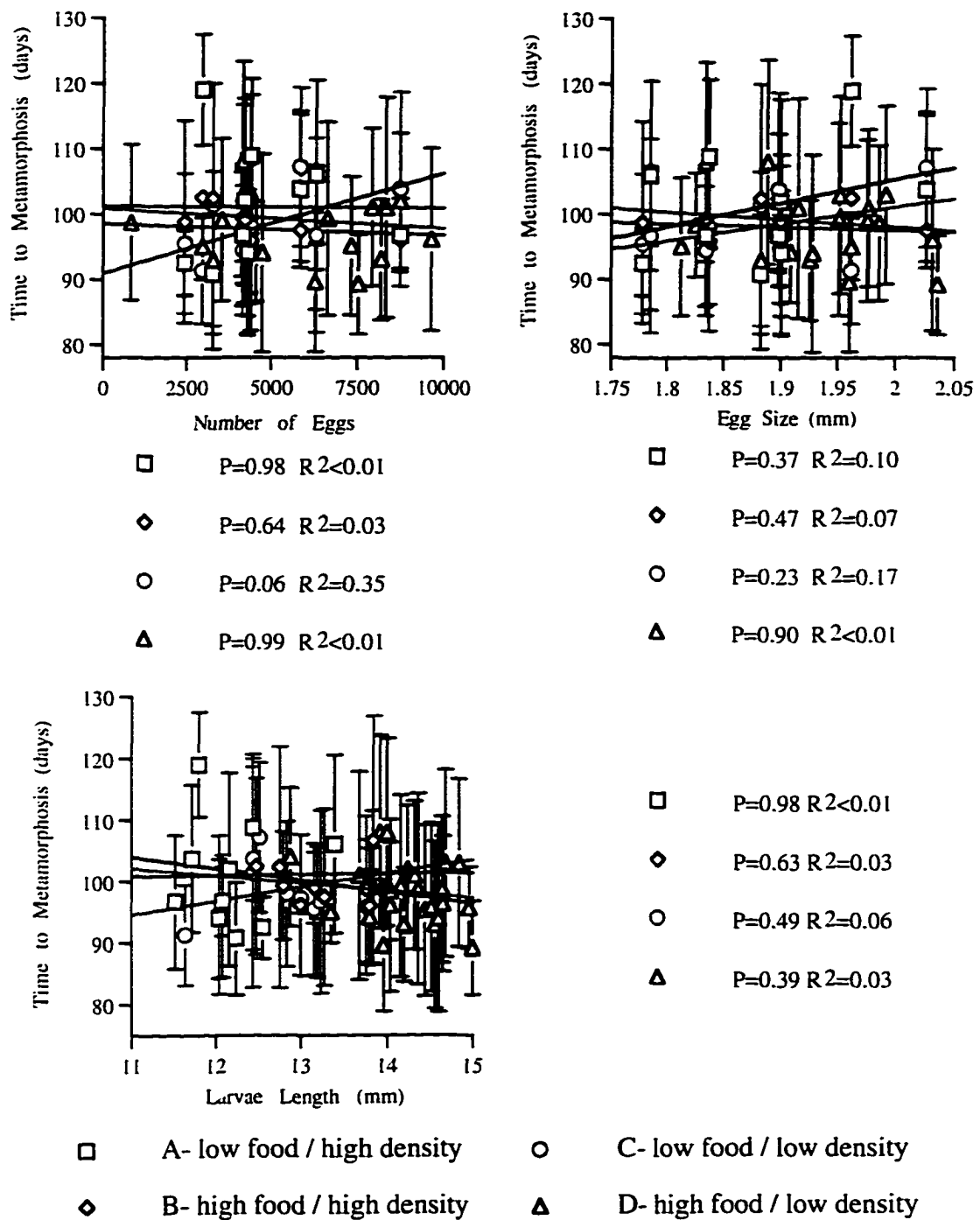


Figure 30. Relationships between duration of the *Bufo americanus* larval period and clutch and egg size, and tadpole length at the day 40 of the larval period, in each of the treatments of the 1996 laboratory experiment.

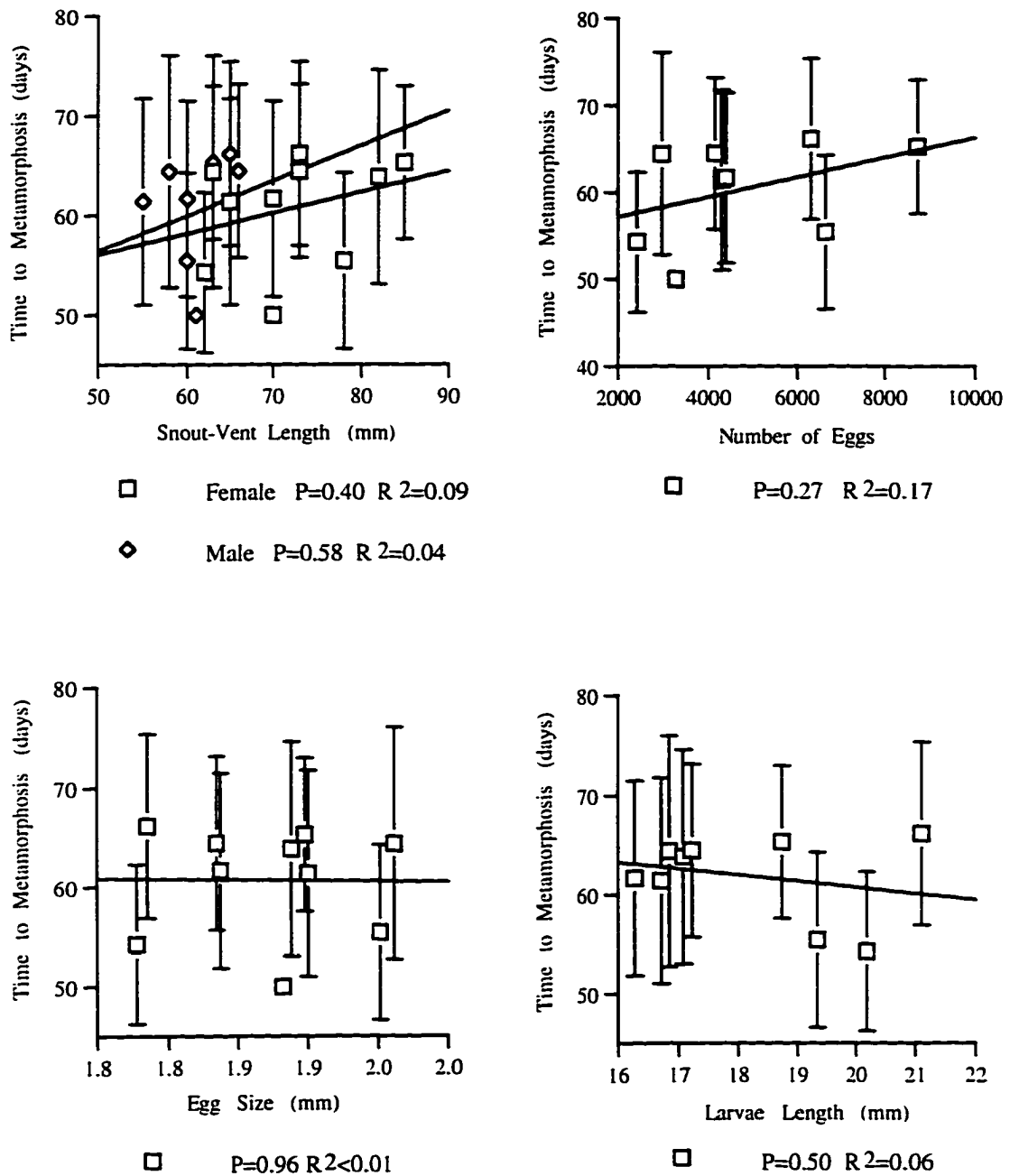


Figure 31. Relationships between duration of the *Bufo americanus* larval period, and body length of both parents, clutch and egg size, and larvae length at the day 50 in the 1996 field experiment.

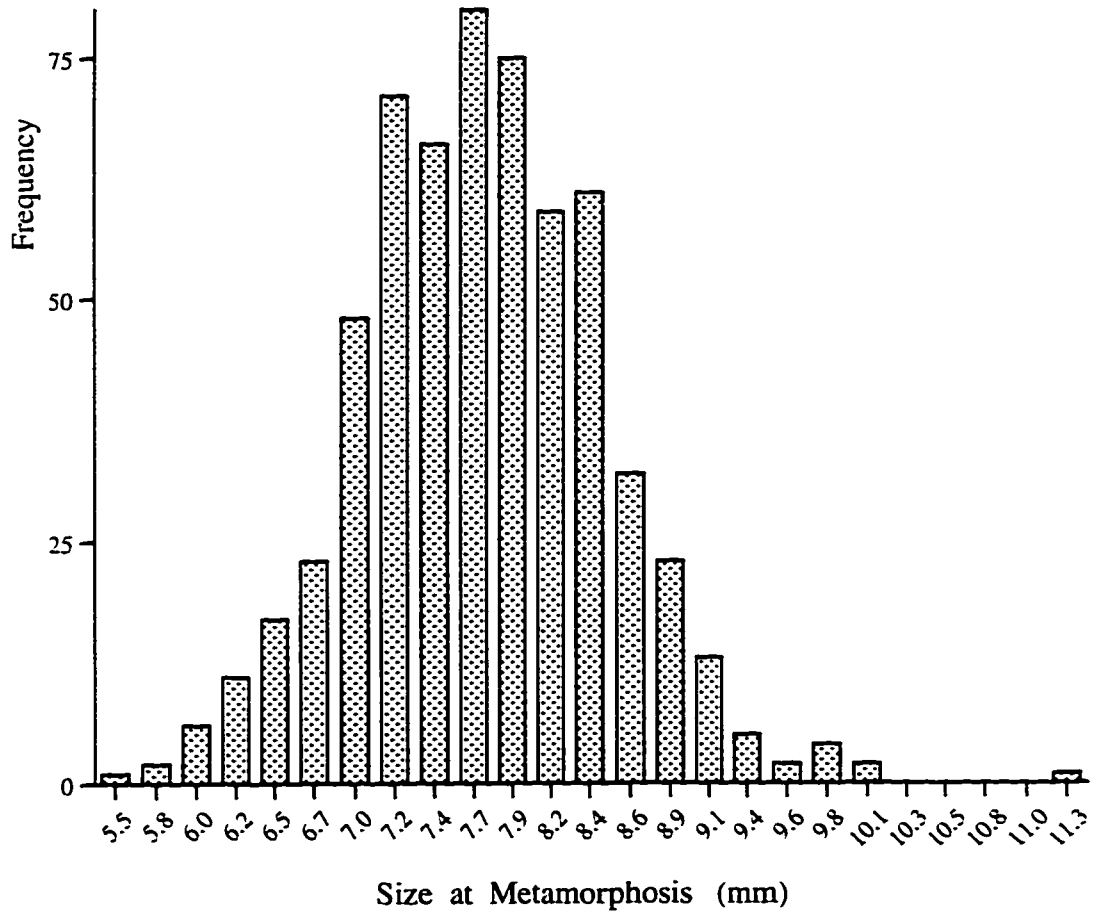


Figure 32. Frequency distribution of size at metamorphosis in *Bufo americanus* .

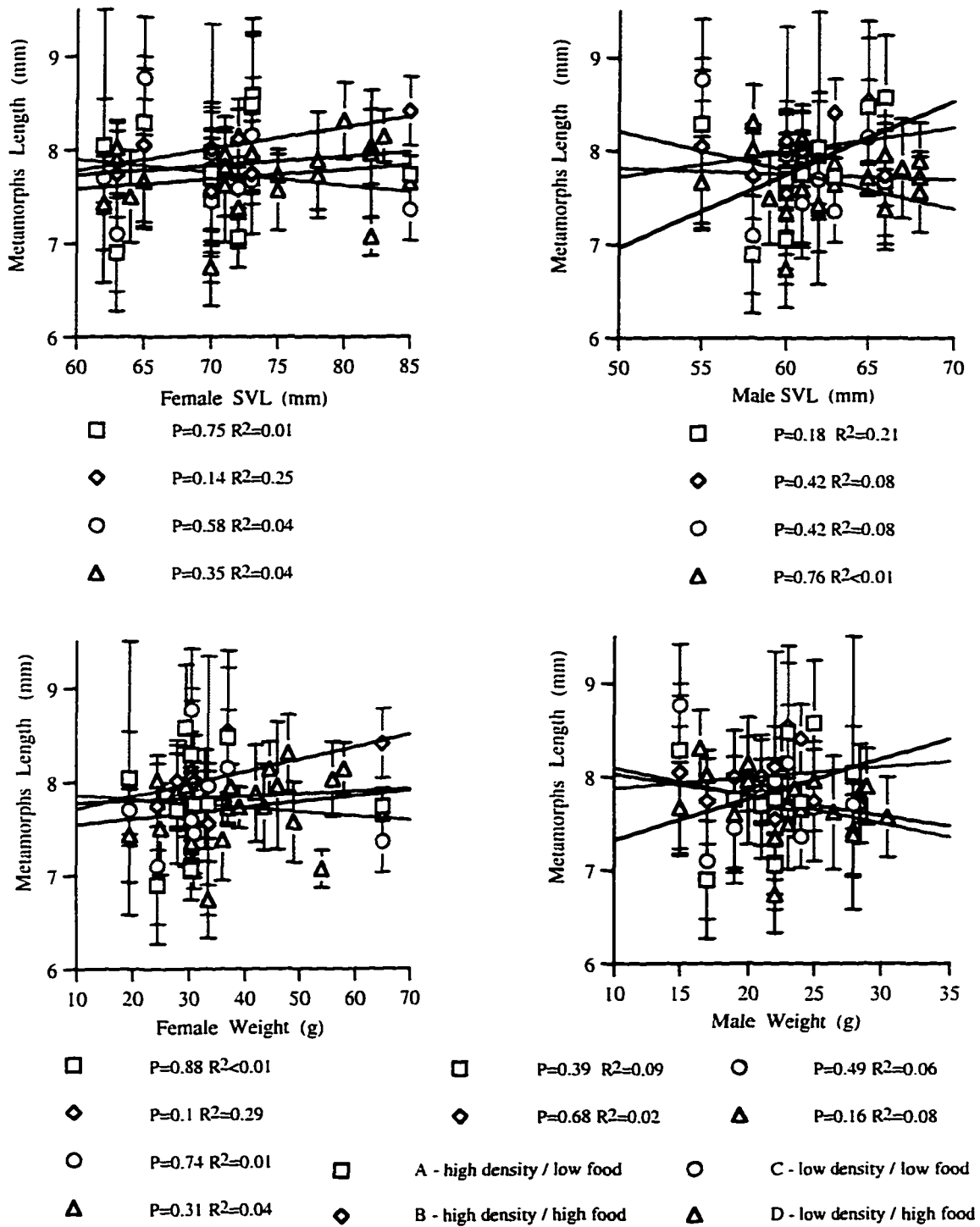


Figure 33. Relationships between length of the *Bufo americanus* metamorphs and snout-vent length (SVL) and weight of both parents, in each of the treatments of the 1996 laboratory experiment.

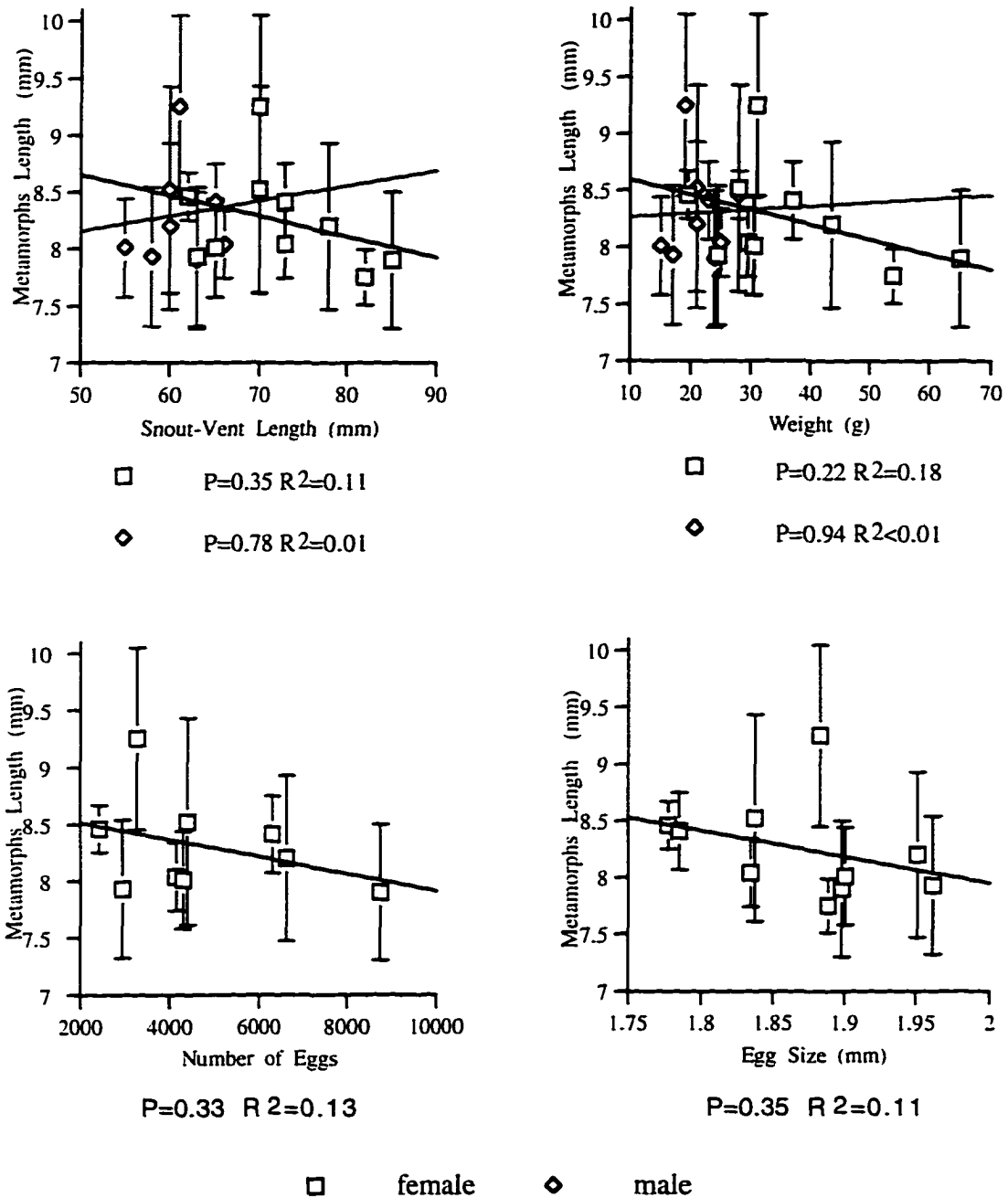
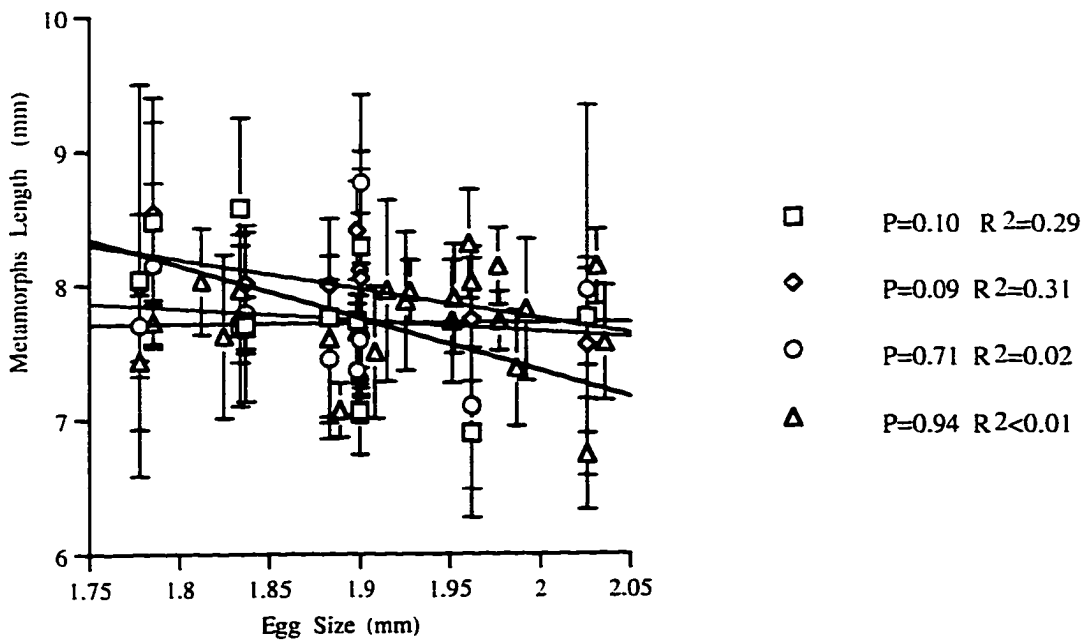
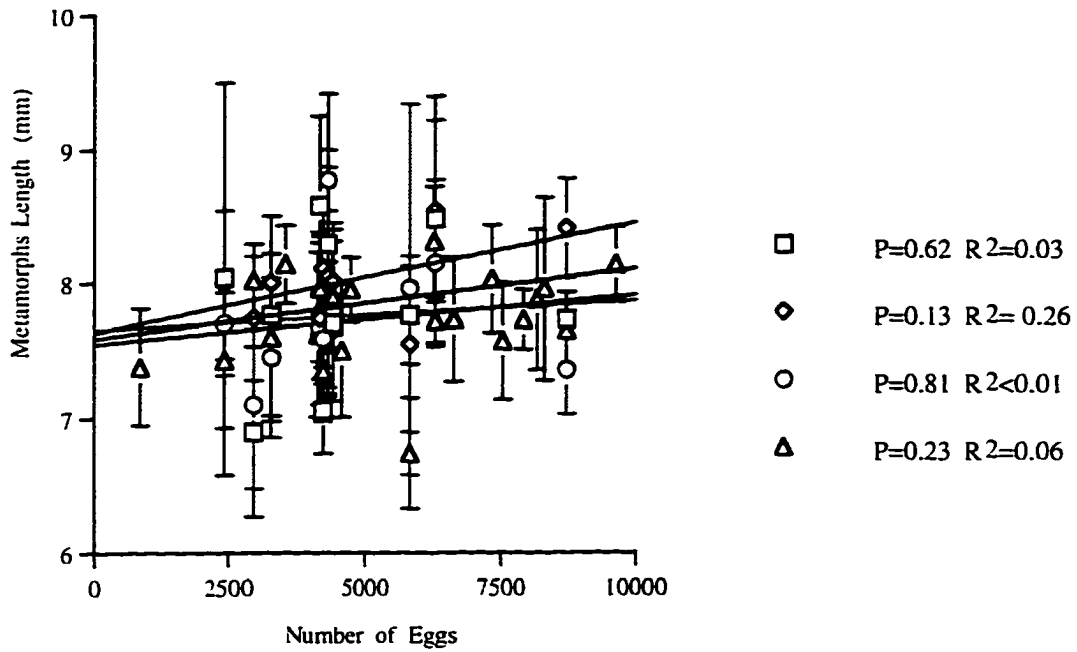


Figure 34. Relationships between length of the *Bufo americanus* metamorphs and snout-vent length (SVL) and weight of both parents, and number and size of the eggs in the 1996 field experiment.



- A-low food / high density
- ◇ B-high food / high density
- C- low food / low density
- △ D- high food / low density

Figure 35. Relationships between length of the *Bufo americanus* metamorphs and number and size of the eggs, in each of the treatments of the 1996 laboratory experiment.

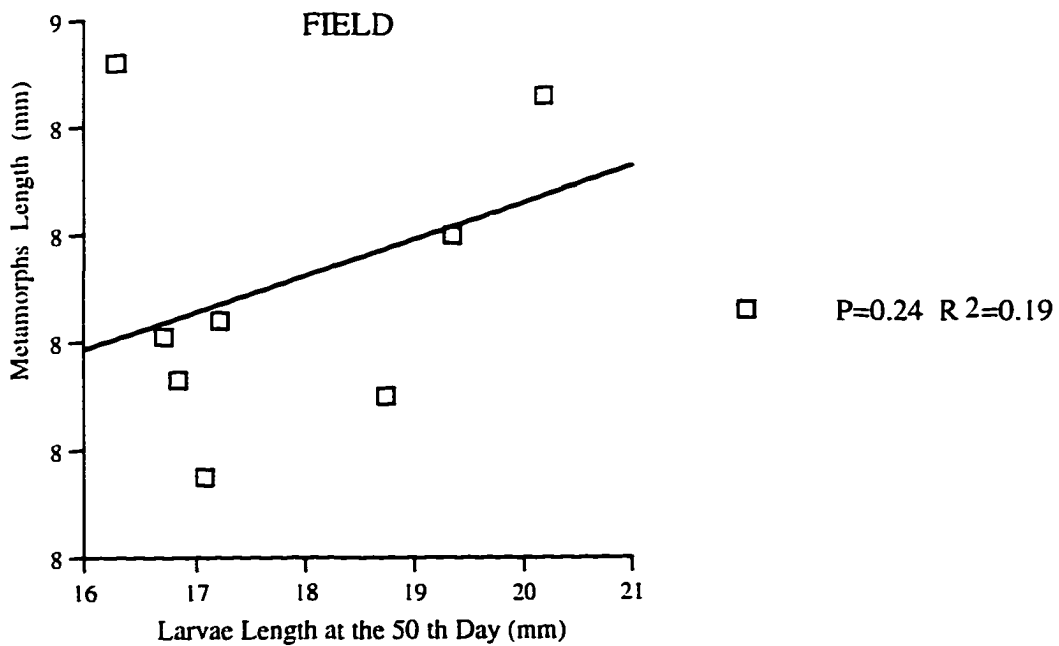
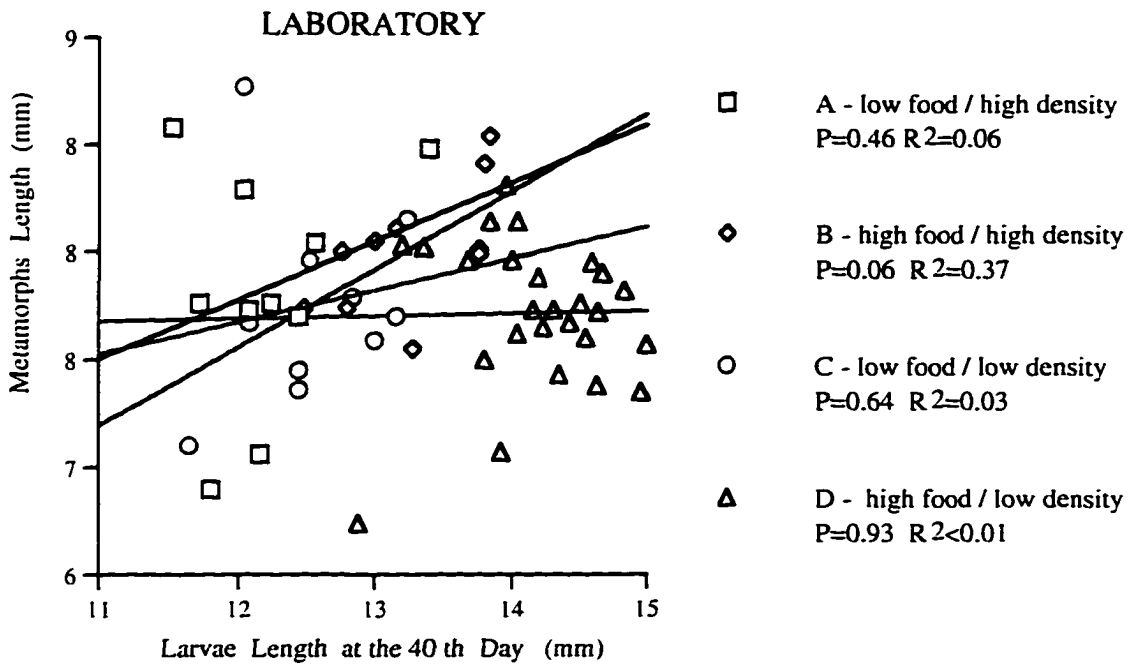


Figure 36. Relationships between *Bufo americanus* metamorphs length and larva length in each of the treatments of the 1996 laboratory experiment, and in the 1996 field experiment.

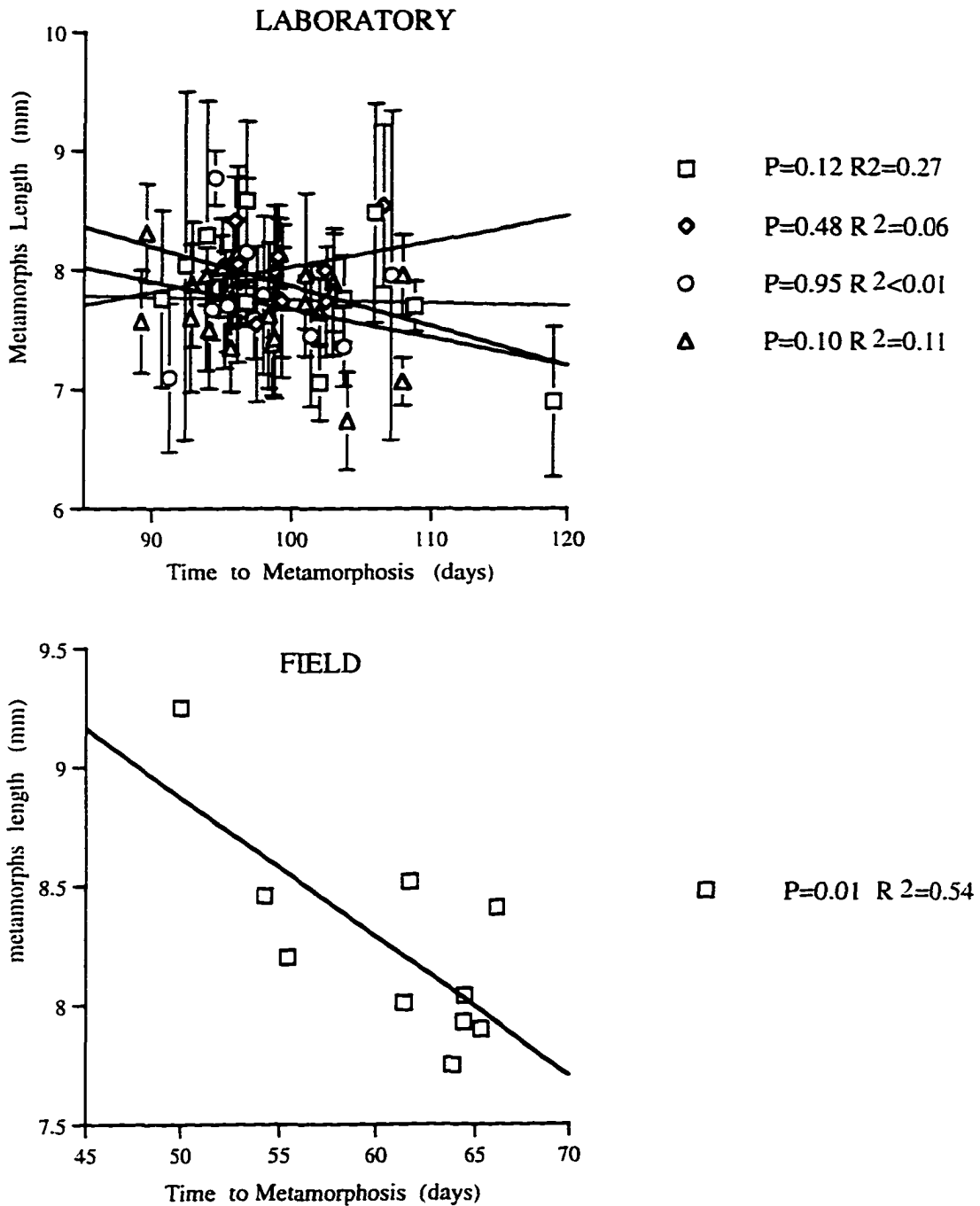


Figure 37. Relationships between length of *Bufo americanus* metamorphs and duration of the larval period in each of the treatments of the 1996 laboratory experiment, and in the 1996 field experiment.

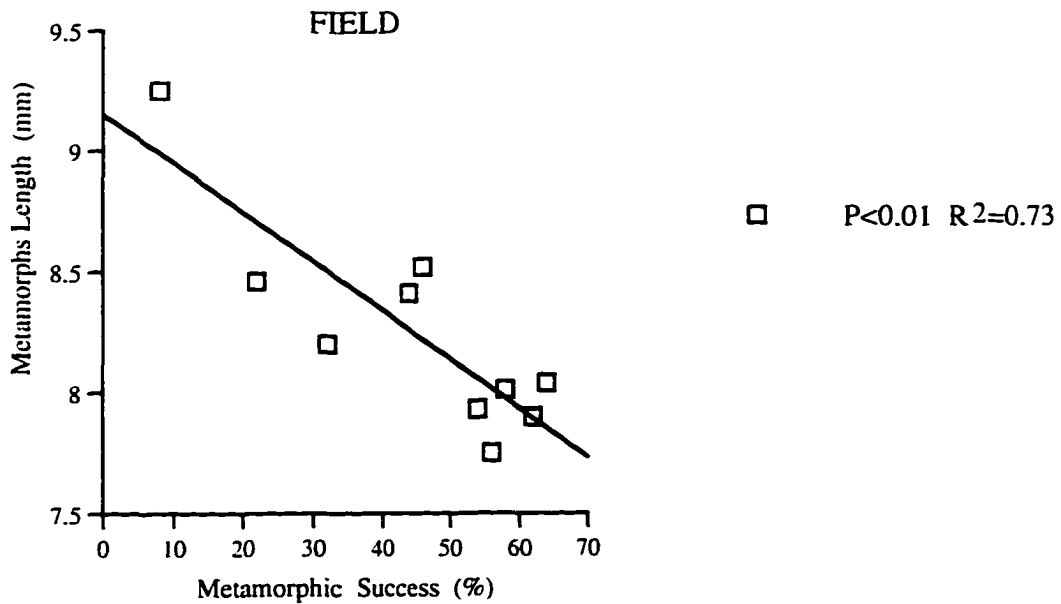
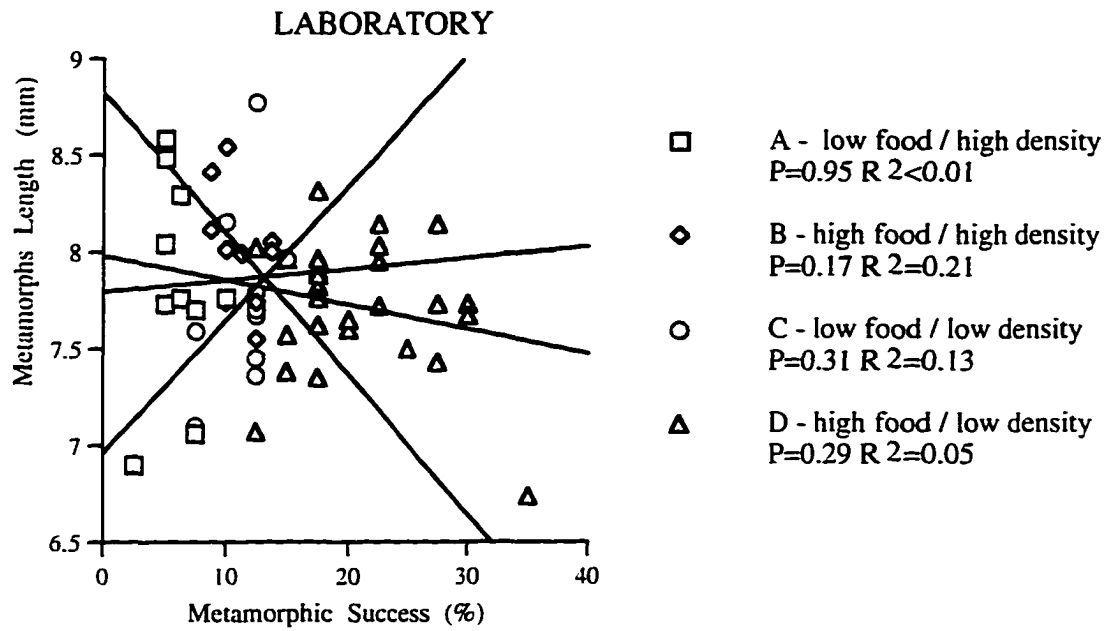


Figure 38. Relationships between size at metamorphosis and percent of *Bufo americanus* larvae that successfully completed metamorphosis in each of the treatments of the 1996 laboratory experiment, and in the field experiment.

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