



310
2007

HARVARD UNIVERSITY



Ernst Mayr Library
of the Museum of
Comparative Zoology

MCZ
LIBRARY

DEC 4 2006

HARVARD
UNIVERSITY

Post-Mating Selection of Hybrid Toads (*Scaphiopus multiplicatus* and *Scaphiopus bombifrons*)

Marie A. Simovich

Biology Department, University of San Diego, San Diego, California 92110 and San Diego Natural History Museum,
San Diego, California 92112

Clay A. Sassaman

Biology Department, University of California, Riverside, California 92521

Amy Chovnick

Pharmacia LKB Biotechnology, Inc., 1025 Atlantic Ave., Suite 101, Alameda, California 94501

ABSTRACT.—High frequencies of F_1 hybrids and the offspring of backcrosses occur in a hybrid zone between the spadefoot toads *Scaphiopus multiplicatus* and *S. bombifrons* in southeastern Arizona. To assess potential post-mating isolating mechanisms between these species, reproductive characteristics, tadpole growth rates, and survivorship in the laboratory of the parental species and hybrids were measured and compared.

Hybrid males are sterile; hybrid females, although fertile, produce only about half as many eggs as either parental species and are thus at a selective disadvantage. On a heterogeneous diet including naturally occurring foods, tadpoles of all types develop faster and are larger than those fed a trout-food diet. Hybrid tadpoles have higher survival rate on both diets and develop faster on a mixed diet than does either parental species. At metamorphosis hybrids are intermediate in size between the parental species. These developmental advantages may afford hybrids some compensation for adverse fertility and fecundity selection.

INTRODUCTION

Investigations of hybridization and hybrid zones have been important in the development of our understanding of the processes of evolution (Barton and Hewitt, 1981; Templeton, 1981; Hewitt, 1988). The hybrid systems that are most informative are those for which we can evaluate not only the conditions under which interbreeding occurs but also the factors affecting the hybrid offspring produced and the way in which they respond to their environment.

An area of hybridization between the spadefoot toads *Scaphiopus multiplicatus* and *Scaphiopus bombifrons* (subgenus *Spea*) in the San Simon Valley of southeastern Arizona was investigated over a four-year period (Simovich, 1985, in press). In this area hybridization and introgression allow the frequencies of hybrid tadpoles to vary spatially and temporally from 0 to 40%, forming a dynamic mosaic. A portion of this variability can be accounted for by the observation that mating in large ponds is species-specific, but in small (crowded) ponds more heterotypic matings occur and hybrid tadpoles are more frequent (Simovich, 1985).

Significant pre-mating isolating mechanisms in at least the large ponds might indicate that interbreeding lowers fitness, and that hybrid offspring are at a disadvantage relative to non-hybrid offspring. However, frequencies of adult hybrids are as high as 31% in some breeding choruses, and substantial numbers of introgressed

genotypes are often present. This suggests that other forces are at work. For example, heterotic effects in the development or survivorship of hybrid offspring, such as have been reported in other systems (Wasserman, 1957, 1963; Thornton, 1955; Volpe, 1960; Pasdar et al., 1984; Samollow and Soulé, 1983), might buffer other fitness reductions.

This paper reports on laboratory measurement of several aspects of post-mating selection in *Scaphiopus*, including adult fertility and fecundity, egg viability, and tadpole survivorship and developmental rate.

MATERIALS AND METHODS

Pairs in amplexus and unmated females were collected from ponds and cattle tanks in the San Simon Valley of southeastern Arizona. The identity of individuals was determined by protein electrophoresis methods described by Simovich and Sassaman (1986). The toads were identified to one of six classes: *S. multiplicatus* (M), *S. bombifrons* (B), F_1 hybrids (H), backcross-M (BKM), the offspring of a mating between a female hybrid and a male *S. multiplicatus*, backcross-B (BKB), the offspring of a mating between a female hybrid and a male *S. bombifrons*, or double-backcross (DBK), the offspring of matings involving these backcrosses. This procedure uses four independent loci and can cor-

rectly identify pure species, F_1 hybrids, and 87% of individuals resulting from backcrosses (Simovich and Sassaman, 1986).

Fertility and Fecundity.—Amplexed pairs were allowed to breed in buckets in the laboratory. The number of eggs laid was counted, and random samples (averaging 160) were transferred to plastic trays of aerated water. Embryos were raised to the point where they could swim freely (about four days old), at which time fertility and the percent successful hatch was determined. Comparisons of fertility and successful hatch were made for the three most frequent crosses (the two intraspecific crosses and the backcross of F_1 hybrid females to *S. multiplicatus* males).

To estimate fecundity in unmated females, egg counts of a weighed subsample of ovary were extrapolated to the total ovarian weight. Comparisons were limited to the three most common classes of females (*S. multiplicatus*, *S. bombifrons*, and F_1 hybrid). The ovaries from some of the females that had bred were also examined, and since none of these had significant numbers of mature eggs remaining, the numbers of eggs laid by mated females in the fertility experiments were also used to estimate fecundity.

Survival and Developmental Rate.—Tadpoles from selected crosses were combined in an experiment designed to determine if the developmental patterns of the classes differed and if diet or density had significant effects on these patterns. For this, mixtures of tadpoles were kept under two density (high and low) and two food (trout food and mixed diet) regimes. Unfortunately, raccoons destroyed the low-density treatment, so only early, qualitative comparisons are available.

In the high-density treatment, groups of swimming tadpoles (which had hatched on the same day during the fertility experiments) were placed in four 10-liter buckets. Each group consisted of 60 *S. multiplicatus* (M) (sampled from three clutches), 60 *S. bombifrons* (B) (also sampled from three clutches), and 59 F_1 hybrids (H) (from the one clutch that was available).

The buckets were kept outdoors in a screened enclosure that received late morning and afternoon sunlight. Water temperatures were taken daily, and buckets were rotated so that similar temperatures could be maintained. Two replicates of each food treatment were used. The first was a trout-food treatment, in which tadpoles were fed *ad libitum* with commercial high-protein trout chow. The second was a mixed-diet treatment, in which the *ad libitum* trout diet was supplemented daily with live fairy shrimp (an important component of the natural diet) in excess of demand.

Toadlets that had completed metamorphosis were collected and frozen at two-day intervals. Those that died in the process were frozen as found. The experiment was terminated while some tadpoles still remained, and these were also frozen. All individuals were identified by electrophoresis, and three aspects of performance were determined: survivorship (the proportion of the initial sample surviving at the end of the experiment), successful metamorphosis (proportion of survivors completing metamorphosis by the end of the experiment), and developmental rate (average number of days to metamorphosis). Size at metamorphosis was also recorded for each individual.

RESULTS

Fertility, Fecundity, and Hatching Success.—Female *S. multiplicatus* and *S. bombifrons* did not differ from each other in fecundity, but hybrid females produced about 45% of the number of eggs that pure females produced (Table 1). Analysis of a subset of females for which somatic weights were available showed the same fecundity differences despite the intermediate weight of hybrid females ($\bar{x} = 11.66$ g, $n = 5$) and a significant difference in the weights of pure females, with *S. bombifrons* ($\bar{x} = 13.68$ g, $n = 11$) heavier than *S. multiplicatus* ($\bar{x} = 10.34$ g, $n = 7$) (ANOVA, $F = 5.06$, $df = 2/20$, and multiple range tests, $p < 0.05$). There was no correlation between somatic weight and number of eggs produced within each species for this subset of data. Although Woodward (1987) found that in New Mexico *S. bombifrons* produced more eggs than did *S. multiplicatus*, we found no significant difference. If there is any bias, it is not in favor of the heavier *S. bombifrons*.

Hybrid males from the San Simon Valley are apparently sterile (Table 2). Of eight amplexed pairs involving hybrid males, seven

TABLE 1. Fecundity of female *Scaphiopus* toads.

	<i>S. multiplicatus</i>	<i>S. bombifrons</i>	F_1 hybrids
No. of clutches	24	15	9
Mean clutch size	1139 ^a	1042 ^a	447
Standard error	69	108	83
$F_{(2,45)} = 12.925^b$	$p < 0.05$		

^aNot significantly different

^b F of ANOVA

TABLE 2. Fertility and hatch success of natural matings of *Scaphiopus* toads.

Cross (Male × Female) ^a	Number of Pairs	Number of Pairs with Eggs	Percentage of Clutches Fertilized	Percentage of Eggs Hatching ^b
M × M	43	36	97	91 (11) ^c
B × B	25	25	100	85 (11) ^c
M × H	8	8	100	82 (3) ^c
H × H	7	7	0	—
M × B	5	1	100	88 (1)
B × M	2	0	—	—
H × M	1	0	—	—
B × H	1	1	100	8 (1)
M × BKM	1	1	100	98 (1)
B × DBK	1	1	100	99 (1)
DBK × B	1	1	100	96 (1)

^aM, *S. multiplicatus*; B, *S. bombifrons*; H, F_1 hybrid; BKM, backcross-M; DBK, double backcross

^bNumber of crosses on which percent hatch is based in parentheses

^cNo significant heterogeneity in the percent hatch for the three most common crosses (arcsin transformed; one-way ANOVA and multiple range tests; $F = 1.197_{(2,22)}$, $p > 0.05$).

were hybrids crossed *inter se*. Although eggs were laid after all of these matings, none cleaved. This failure of hybrid-hybrid crosses was not caused by female sterility because hybrid females were fertile in backcrosses. (The remaining mating involving a male hybrid was with a female *S. multiplicatus* that did not lay eggs.) The only male other than a hybrid that failed to fertilize eggs was one of 46 *S. multiplicatus*. Even some eggs from a mating of *S. couchi* (a member of the other subgenus, *Scaphiopus*) with *S. multiplicatus* were fertilized and developed partially beyond gastrulation.

The three most common types of crosses (two pure species and the hybrid *S. multiplicatus*) did not differ in the percentage of eggs that hatched (Table 2). The percent hatch of eggs was also high for most of the other crosses, with the exception of the one cross of a male *S. bombifrons* to a female hybrid. Of the seven *S. bombifrons*-*S. multiplicatus* pairs collected, six did not produce eggs; however, the one that did showed 88% hatching success (Table 2).

Survival and Developmental Rate.—In this experiment, both differences between genotypic classes and the effect of diet on development were compared. (Within-treatment replicates generally did not differ [contingency χ^2] and were pooled.) Diet had a significant effect on the development but not on the survival of each class when compared to itself. Within each class more survivors metamorphosed by the end of the experiment (contingency χ^2 , $p < 0.05$) and the average number of days to metamorphosis was lower (t test, $p < 0.05$) on a mixed diet than on a trout-food diet. (One replicate within *S. multiplicatus* indicated a possible effect of food on survival but the other did not.)

When the various classes on the two diet regimes were compared against each other, significant differences were also seen (Table 3). On both food regimes hybrids showed the highest survival, *S. bombifrons* was intermediate, and *S. multiplicatus* showed the lowest survival. The classes also differed in the average number of days to metamorphosis. On a mixed diet, hybrids metamorphosed sooner than did either parental class, and on a trout-food diet they metamorphosed sooner than did *S. bombifrons*.

On a mixed diet, hybrids began and completed metamorphosis about four days earlier than did either parental class, as illustrated by the cumulative proportion of survivors metamorphosing over time (Fig. 1). In contrast, on a trout-food diet, although hybrids may have had a slight advantage, differences between classes were not as clear. Furthermore, none of the three classes had completed

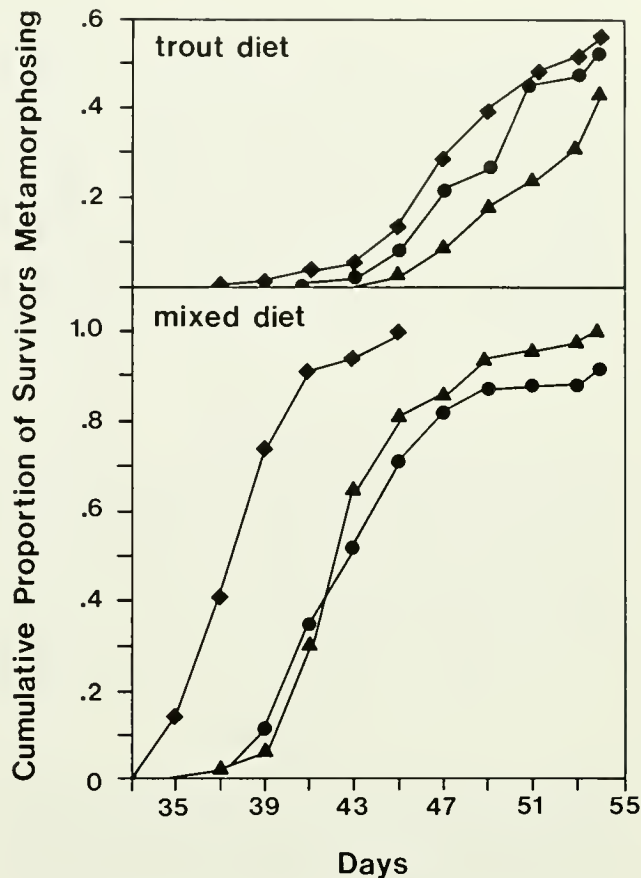


Figure 1. Cumulative proportion of survivors successfully completing metamorphosis under two food treatments. Replicates have been pooled. Triangles, *Scaphiopus bombifrons*; circles, *S. multiplicatus*; diamonds, hybrids.

TABLE 3. Survival and development of *Scaphiopus* tadpoles.^a

	<i>S. multi- plicatus</i>	F ₁ hybrids	<i>S.</i> <i>bombifrons</i>	Comparison Procedure ^b
Initial number of individuals	120	118	120	
Mixed Diet				
Proportion surviving to the end of experiment	0.14*	0.67 [†]	0.44 [‡]	A
Proportion of survivors metamorphosing	0.94 [†]	1.00 [‡]	1.00 ^{†,‡}	A
Mean day to metamorphosis	43.94*	38.67 [†]	43.81*	B
Trout Diet				
Proportion surviving to the end of experiment	0.36*	0.70 [†]	0.54 [‡]	A
Proportion of survivors metamorphosing	0.54*	0.56*	0.45*	A
Mean day to metamorphosis (underestimates)	48.91*	47.91*	50.79 [†]	B

^aCommon superscripts indicate values that do not differ significantly ($p > 0.05$).

^bA, Ryan's procedure for chi square; B, one-way ANOVA with multiple-range test.

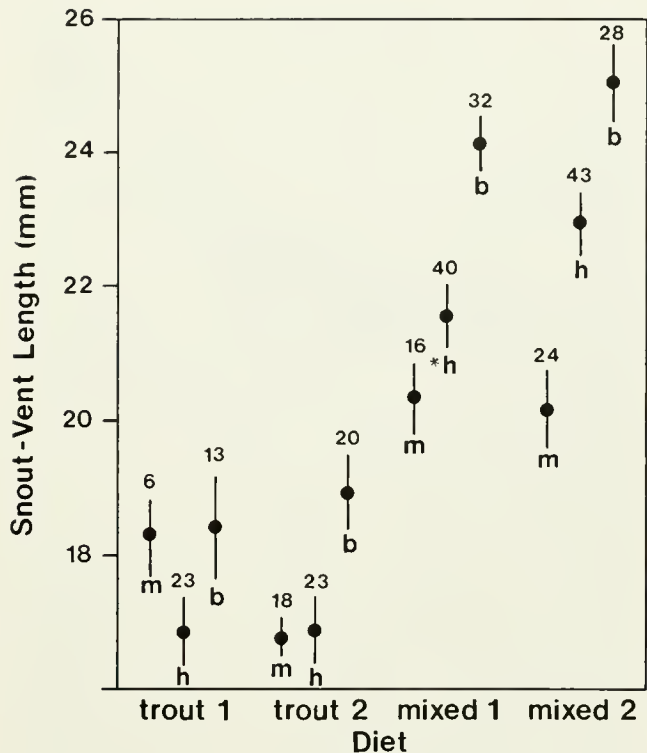


Figure 2. Average size at metamorphosis of toads under two food treatments. Vertical bars indicate the 95% confidence interval. Replicate experiments are plotted separately. Multiple-range tests from ANOVA indicate significant differences between all categories within replicates except M and B of trout-food replicate 1 and M and H of trout-food replicate 2. B, *Scaphiopus bombifrons*; M, *S. multiplicatus*; H, hybrids.

metamorphosis by the end of the experiment on the trout-food diet, yielding an underestimate of the average time to metamorphosis.

In addition, before their loss to raccoons, animals in the concurrent low-density replicates were larger and developing faster than those at high density. This could have been expected from similar findings in other studies on density effects (see, for example, Travis [1984]). Furthermore, of the low-density groups, the mixed-food treatment groups were larger than those on trout food and were developing more rapidly.

Size at metamorphosis was a function of both genotypic class and food regime (ANOVA) (Fig. 2). Diet affected the size of all classes, and the differences among classes were accentuated on a mixed diet (ANOVA with multiple range tests). On a trout food diet, *S. bombifrons* toadlets were always significantly larger than hybrids, but the ranking of *S. multiplicatus* differed in the two replicates. All classes were larger on a mixed diet (95% confidence interval) than on trout food (Fig. 2), and on a mixed diet, all classes differed significantly in size with *S. bombifrons* being largest, hybrids intermediate, and *S. multiplicatus* smallest in both replicates.

DISCUSSION

In the San Simon Valley zone of sympatry, *Scaphiopus* hybrids exhibit low reproductive potential relative to the parental species. Females are fertile but exhibit considerably reduced fecundity, and males are sterile. This pattern of the reproductive potential of male hybrids being lower than that of females is not uncommon in toads (e.g., Volpe, 1960; Wasserman, 1963). However, the observation of male sterility in this area is interesting, since fertile hybrid males

are reported elsewhere.

One source of this heterogeneity in males may be geographical differentiation within *S. bombifrons*. Two call types of *S. bombifrons* are known, a "slow call" type in the eastern portion of the species' range and a "fast call" type in the southwest (Pierce, 1976). Although the two call types differ little in electrophoretic characters (Sattler, 1980), it may be (as noted by Pierce in Wasserman [1970]) that crosses involving the "fast call" type of *S. bombifrons* (as found in the San Simon Valley) inherently produce sterile males, while at least some hybrid males from areas where the "slow call" form is found are fertile (Forester, 1969, 1975). A second possibility is that the fertility of the offspring of reciprocal crosses differs, as has commonly been shown in other anurans including *Rana*, *Bufo*, and *Scaphiopus* (e.g., Frost, 1982; Thornton, 1955; Volpe, 1952; Wasserman, 1957, 1963). Because in the San Simon Valley most of the direct interspecific crosses appear to be of *S. multiplicatus* males with *S. bombifrons* females (Simovich, 1985), we could not address this possibility with our data from field-captured pairs.

The interfertility levels of crosses between the two parental species were comparable to or higher than those previously reported by Brown (1967), Forester (1969, 1975), Littlejohn (1959), Sattler (1978), or Wasserman (1964). Any variation in hatching success could be due to differences in rearing or breeding conditions. Discrepancies could also result from inherent differences in the genetic compatibility of the two call types of *S. bombifrons* (Pierce, 1976) with *S. multiplicatus*. This geographic variability underscores the importance of quantifying such components of selection as interfertility for specific areas in any effort to quantify the dynamics of a hybrid interaction.

Hybrid females, when backcrossed to *S. multiplicatus* males, do not suffer any additional loss of fitness due to reduced fertility or offspring survival under controlled, noncompetitive conditions. The alternative hybrid \times *S. bombifrons* cross is rare and more data are needed. The results suggest that direct interspecific F_1 (M \times B) crosses, although highly fertile, may produce eggs less frequently than pure crosses, but we have no indication as to how frequently this occurs in nature or if it is simply that *S. multiplicatus* females do not always lay eggs.

It is of considerable interest that despite low reproductive fitness due to reduced fecundity and fertility, hybrids may have higher fitness for later components of selection such as tadpole survival and developmental rate. The data indicate that on a diet including live food (as in most natural ponds) and at fairly high densities, several important differences between genotypic classes appear. First, emerging *S. bombifrons* toadlets are largest, hybrids are intermediate, and *S. multiplicatus* are smallest. This ranking is the same as found in toadlets emerging from natural ponds (Simovich, 1985). Second, hybrids show significantly higher survival and develop significantly faster than either parental species. In the field, however, *S. bombifrons* metamorphoses sooner than does *S. multiplicatus* (Simovich, 1985). Possibly the dietary needs of *S. bombifrons* are more exacting than those of *S. multiplicatus* or hybrids, and laboratory conditions did not permit optimum development. Our laboratory, for example, was at a higher elevation and thus at lower temperatures than the desert where these toads (especially *S. bombifrons*) are found.

The differences we found among genotypic classes in their responsiveness to diet and density are consistent with some but not all previous investigations of anuran development. Our results do seem to agree with Travis et al. (1985) and Alford (1986) that variable ecological conditions can alter the relative fitness of intraspecific sibships and that competition can affect growth and survival even if food is not limited. However, the details of these responses are not in accordance with those found in other amphib-

ians. Wilbur and Collins (1973), Collins (1975, 1979), and Travis (1980, 1983, 1984) have discussed an intraspecific model in which some species exhibit a size/rate tradeoff, with slower developers being larger at metamorphosis above a minimum threshold size (see also Newman, 1988a, and Crump, 1989). In *Hyla*, furthermore, Crump (1989) has shown faster development and smaller size in rapidly drying environments. In contrast, in *Bufo* Woodward (1987) has shown environment to affect growth rate but not size at metamorphosis. Our study indicates a different relationship. Slow developers were actually smaller at metamorphosis both within and between species. Most studies in which decreased growth rate was related to smaller size at metamorphosis involved increased densities of intra- and/or interspecific competitors (Travis, 1980, 1983, 1984; Travis et al., 1985; Wilbur, 1977; Wilbur and Collins, 1973; Collins, 1979). We do not have the density comparisons with which to confront this issue. It does appear that size, survival, and developmental characters differ between the parental species and hybrids and that the full expression of these differences is dependent on the developmental environment, including diet.

Interestingly, the genotypic classes that were largest and fastest in development in this experiment, hybrids and *S. bombifrons*, also expressed the carnivore morphology (characteristic of some species of spadefoot toads) most often in the field (Simovich, 1985, in press). The expression of extreme carnivore morphology has been tied to a diet of live food, and since carnivores tend to develop faster and be larger than conspecific omnivores (Pomeroy, 1981), there may be a correspondence between the tendency to develop carnivore morphs and the other developmental differences between genotypic classes. Because we cannot develop extreme carnivore morphs in the laboratory, we do not know the genetic basis of the morphologies or if other dietary requirements are involved in the full expression of the morph.

All things considered, the ephemeral ponds in which these species breed and develop can present extremely harsh selective conditions. Life cycles must be precisely timed to the availability of a temporary and frequently unpredictable resource. The toads must emerge and breed on the first night of summer rains (Bragg, 1965; Ruibal et al., 1969; Dimmitt and Ruibal, 1980) so that the tadpoles can develop and metamorphose in the short time that the ponds remain. If rainfall is sparse, these small ponds dry very quickly, creating crowded conditions for all inhabitants. Owing to aquatic predators and desiccation, tadpole mortality can be quite high (Mayhew, 1965; Licht, 1974; Creuser and Whitford, 1976; Wilbur, 1977; Caldwell et al., 1980; Travis, 1980, 1983; Alford, 1986; Woodward, 1987).

There is thus a premium on fast growth, rapid development, and early metamorphosis (Wilbur and Collins, 1973; Licht, 1974; Wilbur, 1977; Caldwell et al., 1980; Travis, 1980, 1983; Smith, 1983). Reduction of the time animals are exposed to aquatic predators should be advantageous (Travis et al., 1985). Fast-developing tadpoles should be favored in years when ponds dry quickly. Furthermore, early emergence may allow a longer period of terrestrial feeding to build up fat reserves for overwintering. Larger size at metamorphosis may also decrease the risk of post-metamorphic desiccation (Martof, 1956) and afford later advantages should those individuals continue to grow faster and reach breeding size sooner (Collins, 1975; Wilbur et al., 1978). In tradeoff models, these pre- and post-metamorphic attributes are alternatives, either fast development/small size or slow development/large size, and plasticity is retained by fluctuating selection (i.e., variation in pond longevity) (Wilbur, 1977; Travis, 1983, 1984; Newman, 1988b).

In the *Scaphiopus* hybrids, rapid development occurs without a concomitant reduction in size at metamorphosis. Unfortunately, the genetic basis of the success of hybrids is still unclear. Several possibilities exist, including heterosis, maternal influence, and

simple dominance. Laboratory evidence points to intermediate expression of size characters but heterosis in developmental rate. Heterosis has been seen in other hybrid spadefoot toads (Wasserman, 1957, 1963) and other anurans (Thornton, 1955; Volpe, 1960). However, maternal influence in development (Volpe, 1952) and temperature tolerance have also been documented (Brown, 1967). Also, in fish reciprocal hybrids have been shown to differ in growth rate (Pasdar et al., 1984). Since most hybrids in the San Simon Valley appear to result from crosses in one direction, these possibilities remain to be addressed. Further tests evaluating the development of hybrids generated from both reciprocal F_1 crosses are needed in order to determine which model is most applicable.

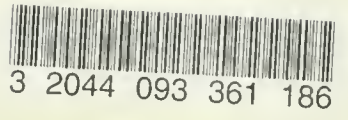
ACKNOWLEDGMENTS

We thank R. Tinsley and his wonderful co-workers, G. Bell, and the numerous researchers at the Southwestern Research Station for their invaluable help catching toads in the pouring rain and counting thousands of eggs. We also thank L. Nunney, V. Shoemaker, S. Morey, R. Dingman, and J. Graves for reviewing this manuscript. This work was funded in part by grants from the National Science Foundation, the Theodore Roosevelt Memorial Fund, Sigma Xi, and the Chancellor's Patent Fund (University of California at Riverside).

LITERATURE CITED

- Alford, R. A. 1986. Habitat use and positional behavior of anuran larvae in a northern Florida temporary pond. *Copeia*, pp. 408-423.
- Barton, N. H., and G. M. Hewitt. 1981. Hybrid zones and speciation. Pp. 109-145 in W. R. Archley and D. S. Woodruff (eds.), *Essays on Evolution and Speciation in Honor of M. J. D. White*. Cambridge University Press, Cambridge, England.
- Bragg, A. N. 1965. *Gnomes of the Night*. University of Pennsylvania Press, Philadelphia.
- Brown, H. A. 1967. Embryonic temperature tolerance and genetic compatibility in two allopatric populations of the spadefoot toad, *Scaphiopus hammondi*. *Evolution* 21:742-761.
- Cadwell, J. P., J. H. Thorp, and T. O. Jervey. 1980. Predator-prey relationships among larval dragonflies, salamanders, and frogs. *Oecologia* 46:285-289.
- Collins, J. P. 1975. A comparative study of the life history strategies in a community of frogs. Ph.D. thesis, University of Michigan, Ann Arbor.
- Collins, J. P. 1979. Intrapopulation variation in the body size at metamorphosis and timing of metamorphosis in the bullfrog, *Rana catesbeiana*. *Ecology* 60:738-749.
- Creuser, F. M., and W. G. Whitford. 1976. Ecological relationships in a desert anuran community. *Herpetologica* 32:7-18.
- Crump, M. L. 1989. Effect of habitat drying on development time and size at metamorphosis in *Hyla pseudopuma*. *Copeia*, pp. 794-797.
- Dimmitt, M., and R. Ruibal. 1980. Environmental correlates of emergence in spadefoot toads (*Scaphiopus*). *Journal of Herpetology* 14:21-29.
- Forester, D. C. 1969. Reproductive isolation and hybridization between the spadefoot toads *Scaphiopus bombifrons* and *Scaphiopus hammondi* in west Texas. M. S. thesis, Texas Tech University, Lubbock.
- Forester, D. C. 1975. Laboratory evidence for potential gene flow between two species of spadefoot toads, *Scaphiopus bombifrons* and *Scaphiopus hammondi*. *Herpetologica* 31:286-288.
- Frost, J. S. 1982. Functional genetic similarity between geographically separated populations of Mexican leopard frogs (*Rana pipiens* complex). *Systematic Zoology* 31:57-67.
- Hewitt, G. M. 1988. Hybrid zones—natural laboratories for evolutionary studies. *Trends in Ecology and Evolution* 3:158-167.

- Licht, L. E. 1974. Survival of embryos, tadpoles, and adults of the frogs *Rana aurora* and *Rana pretiosa pretiosa* sympatric in southwestern British Columbia. *Canadian Journal of Zoology* 52:613-627.
- Littlejohn, M. J. 1959. Artificial hybridization within the Pelobatidae and Microhylidae. *Texas Journal of Science* 11:57-59.
- Martof, B. 1956. Growth and development of the green frog, *Rana clamitans*, under natural conditions. *American Midland Naturalist* 55:101-117.
- Mayhew, W. W. 1965. Adaptations of the amphibian *Scaphiopus couchii* to desert conditions. *American Midland Naturalist* 74:95-109.
- Moore, W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. *Quarterly Review of Biology* 52:263-277.
- Newman, R. A. 1988a. Genetic variation for larval anuran (*Scaphiopus couchii*) development time in an uncertain environment. *Evolution* 42:763-773.
- Newman, R. A. 1988b. Adaptive plasticity in development of *Scaphiopus couchii* tadpoles in desert ponds. *Evolution* 42:774-783.
- Pasdar, M., D. P. Philipp, and G. S. White. 1984. Enzyme activities and growth rates in two sunfish species and their hybrids. *Journal of Heredity* 75:453-456.
- Pierce, J. R. 1976. Distribution of two mating call types of the plains spadefoot *Scaphiopus bombifrons*. *Southwestern Naturalist* 20:578-582.
- Pomeroy, L. V. 1981. Developmental polymorphism in the tadpoles of the spadefoot toad *Scaphiopus multiplicatus*. Ph.D. dissertation, University of California, Riverside.
- Ruibal, R., L. Tevis, Jr., and V. Roig. 1969. The terrestrial ecology of the spadefoot toad *Scaphiopus hammondi*. *Copeia*, pp. 571-584.
- Samollow, P. B., and M. E. Soulé. 1983. A case of stress-related heterozygote superiority in nature. *Evolution* 37:646-649.
- Sattler, P. W. 1978. Biochemical genetic investigations of introgressive hybridization and systematic relationships in the spadefoot toads, genus *Scaphiopus*. Ph.D. dissertation, Texas Tech University, Lubbock.
- Sattler, P. W. 1980. Genetic relationships among selected species of N. American *Scaphiopus*. *Copeia*, pp. 605-610.
- Simovich, M. A. 1985. Analysis of a hybrid zone between the spadefoot toads *Scaphiopus multiplicatus* and *Scaphiopus bombifrons*. Ph.D. dissertation, University of California, Riverside.
- Simovich, M. A., and C. A. Sassaman, 1986. Four independent electrophoretic markers in spadefoot toads. *Journal of Heredity* 77:410-414.
- Simovich, M. A. in press. The dynamics of a spadefoot toad hybrid system. *Proceedings of Southwestern Herpetologists' Society Conference on the Herpetology of the North American Deserts*. Southwestern Herpetologists' Society Special Publication 5.
- Smith, D. C. 1983. Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royal, Michigan. *Ecology* 64:501-510.
- Templeton, A. R. 1981. Mechanisms of speciation—a population genetic approach. *Annual Review of Ecology and Systematics*, 12:23-48.
- Thornton, W. A. 1955. Interspecific hybridization in *Bufo woodhousei* and *Bufo valliceps*. *Evolution* 9:455-468.
- Travis, J. 1980. Phenotypic variation and the outcome of interspecific competition in hyloid tadpoles. *Evolution* 34:40-50.
- Travis, J. 1983. Variation in development patterns of larval anurans in temporary ponds. I. Persistent variation within a *Hyla gratiosa* population. *Evolution* 37:496-512.
- Travis, J. 1984. Anuran size at metamorphosis: Experimental test of a model based on intraspecific competition. *Ecology* 65:1155-1160.
- Travis, J., W. Keen, and J. Juillanna. 1985. The effects of multiple factors on viability selection in *Hyla gratiosa* tadpoles. *Evolution* 39:1087-1099.
- Volpe, E. P. 1952. Physiological evidence for natural hybridization of *Bufo americanus* and *Bufo fowleri*. *Evolution* 6:393-406.
- Volpe, E. P. 1960. Evolutionary consequences of hybrid sterility and vigor in toads. *Evolution* 14:181-193.
- Wasserman, A. D. 1957. Factors affecting interbreeding in sympatric species of spadefoot toads. *Evolution* 11:320-338.
- Wasserman, A. D. 1963. Further studies of hybridization in spadefoot toads (genus *Scaphiopus*). *Copeia*, pp. 115-118.
- Wasserman, A. D. 1964. Recent and summarized interspecific hybridization within the Pelobatidae. *Texas Journal of Science* 16:334-341.
- Wasserman, A. D. 1970. Chromosomal studies of the Pelobatidae (Salientia) and some instances of ploidy. *Southwestern Naturalist* 15:239-248.
- Wilbur, H. M. 1977. Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. *Ecology* 58:196-200.
- Wilbur, H. M., and J. P. Collins. 1973. Ecological aspects of amphibian metamorphosis. *Science* 182:1305-1314.
- Wilbur, H. M., D. I. Rubenstein, and L. Fairchild. 1978. Sexual selection in anurans: The roles of female choice and body size. *Evolution* 32:264-270.
- Woodward, B. D. 1987. Interactions between Woodhouse's toad tadpoles. *Copeia*, pp. 380-386.



3 2044 093 361 186

