The Dynamics of a Spadefoot Toad
(Spea multiplicata and S. bombifrons)
Hybridization System

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INTRODUCTION

The phenomenon of hybridization has long fascinated evolutionary biologists. Over the years numerous questions concerning the geographical location, structure, and longevity of hybrid zones (D. Woodruff, 1973) as well as the causes and consequences of hybridization have been addressed (ex. Endler, 1977, 1982; Barton, 1979; Barton and Hewitt, 1981, 1985; Hewitt, 1988; Moore, 1977). This work has revealed considerable variation in hybrid systems. Not only do systems differ from one another, but the interactions of a given species pair can vary spatially and/or temporally (Templeton, 1981), seemingly as a result of differences in the responses of pure and mixed genotypes to the variable selectivity of spatially or temporally patchy environments. The result is a complex or long-lived hybrid zone (e.g. Frost, 1982; Frost and Bagnara, 1977; Gartside, 1980; Gerhardt et al. 1980; Gollmann, 1991; Harrison and Arnold, 1983; Hillis, 1981; McDonnell et al. 1978; Mechem, 1960; Patton et al. 1979; Platz, 1981; Rand and Harrison, 1989). These complex systems are particularly informative because the genetic make-up of each component species remains comparatively uniform. This consistency makes it easier to evaluate the role of external forces (e.g., crowding, habitat variation) acting both before and after mating, and their effect on the outcome of hybridization.

Among anurans, numerous studies have investigated factors responsible for the breakdown of normally efficient pre-mating isolating mechanisms (Forester, 1969, 1973; Frost and Platz, 1983; Gartside, 1980; Martof, 1961). These studies have examined how variation in factors such as habitat disturbance or breeding site condition can result in variation in the proportion of mixed-species matings. Extensive literature also addresses the role of post-mating selection, through differences in fertility, fecundity, and development on the survival of hybrid offspring (e.g. Brown, 1967; Forester, 1969, 1975; Frost, 1982; Sattler, 1978; Thornton, 1955). The interplay of pre- and post-mating selection, however, has seldom been evaluated directly in nature. In most cases, the dynamics of hybrid systems have been inferred from frequencies of genotypic classes sampled at a single stage (usually the adult) or from breedings in the laboratory. Such inferences may give an incomplete or even misleading picture, for, while revealing something about the result of the hybridization, single-stage samples tell us little or nothing about its cause. For this reason, information on the contribution of a number of aspects of selection operating throughout the life cycle is important to the evaluation of hybridization systems. This paper is one part of a study of a complex hybrid zone between two species of spadefoot toads in Arizona. In it, pre- and post-mating aspects of selection, including assortative mating, differences in fertility and fecundity, and differences in survival and developmental rate, are investigated.

The System:

The ranges of the spadefoot toads *Spea multiplicata* and *S. bombifrons* overlap widely (Brown, 1976; Stebbins, 1985). Although considered to be the most distantly related species within the genus (see for discussion Wiens and Titus, 1991), the species are known to hybridize in a number of areas to varying extents (Brown, 1976; Forester, 1973; Hughes, 1965; Sattler, 1978, 1985), resulting in a complex hybrid system. One of these areas, the San Simon Valley of southeastern Arizona, is part of a suture zone (sensu Remmington, 1968), an area where biomes intergrade and congeners meet and frequently hybridize. The valley itself has a large number of ponds and cattle tanks where the toads breed.

Breeding in ephemeral desert ponds constrains the spadefoot’s life cycle into precise synchrony with a very temporary aquatic environment. The toads breed “explosively” (Wells, 1977), emerging from their burrows and going to temporary ponds and playas that fill on the first night of heavy summer rains (Bragg, 1965; Dimmitt and Ruibal, 1980; Forester, 1969; Ruibal et al. 1969). The breeding congresses that form are often dense and contain both species (some contain other genera of toads as well) (Bragg, 1965; Brown, 1976; Creuser and Whitford, 1976), taking part in what has been termed “scramble competition” for mates (Wells, 1977). The females respond positively to the calls of conspecific males, and the males of the two species call from different positions in the pond (Forester, 1969, 1975). Males are quite indiscriminate and will mate with either species or hybrids (Blair, 1958; Bragg, 1965; and personal observation). Under these conditions, the effectiveness of call and calling position as mechanisms of assortative mating may be much reduced (Wasserman, 1957; Wells, 1977), and females may be grabbed by an incorrect male en route to a conspecific.

The eggs are laid during the breeding congress and hatch the next day. The tadpoles develop and metamorphose in just three to four weeks. The tadpoles of these two species are dimorphic, occurring in an omnivore or a carnivore morph (see Pomeroy, 1981). Omnivores are scavenger/grazers of normal morphology, while carnivores are pred-}

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The role of pre-mating isolation was also addressed. Breeding adults were sampled in several breeding congresses. Assortative mating was efficient in large or uncrowded ponds; there were few mismatches, and few hybrid tadpoles resulted. Crowded breeding conditions (due to low rainfall or the use of small ponds) decreased the efficiency of assortative mating, increased mismatching, and increased the generation of hybrids and backcrossed offspring. Most of the backcrosses resulted from a male *S. multiplicata* (the more common of the parental species) mating with a female hybrid. Although the frequency of the mixed-genotype classes in tadpoles was correlated with the frequency of mismatches by breeding adults, the proportion of hybrid tadpole types could not be predicted precisely solely from the degree of adult mispairing. The discrepancy suggested that there was selection after as well as before mating (Simovich, 1985).

Analysis of intraspecific and interspecific crosses from this area (Simovich et al., 1991) showed that hybrid males are sterile and that hybrid females, although fertile in backcrosses, produce only 45% as many eggs as the pure species produce. This difference in reproductive potential could affect the frequency of tadpole classes by limiting the production of *F*$_2$ hybrids. Mixed genotypes, however, are common in the zone of hybridization. Frequencies of hybrid adults range from 0 to 31% and of hybrid tadpoles from 0 to 40%.

Laboratory experiments further showed that on a diet including live food (fairy shrimp), as in natural ponds, hybrid tadpoles survive in higher numbers, develop faster, and enjoy better net success to metamorphosis than do tadpoles of either pure species. In the lab, hybrid toadlets were intermediate in size between toadlets of the parental species of the same age (Simovich et al., 1991). Such differences should give rise to differences in the success of the various genotypic classes and could allow substantial numbers of hybrids to persist.

In the present study the possibility that both pre- and post-mating aspects of selection were operating was investigated in the field by following cohorts of larvae to metamorphosis, and assessing the relative performance or success of each genotypic class at numerous points in the cycle.

**METHODS**

Over three years, toads in three ponds were sampled periodically to metamorphosis. Six more cohorts at two other ponds were sampled for at least some consecutive post-breeding stages. Ponds are coded and locations are given in Simovich (1985). Figure 1, a schematic outline of the anuran life cycle, indicates the stages sampled and used in predicting values, as well as the relevant stage comparisons made to determine differential performance of genotypic classes for the several points in the life cycle.

These classes are defined and abbreviated as pure *S. multiplicata* (M), pure *S. bombifrons* (B), hybrid (H referring to *F*$_1$ hybrids only) backcross to *S. multiplicatus* (BKM), backcross to *S. bombifrons* (BKB), and double backcrosses (DBK), the offspring of two or more backcrosses. "Mixed" denotes hybrids plus all backcross classes. All animals were identified to genotype by electrophoresis of tissue samples, which were scored for four allozyme systems representing four unlinked diagnostic gene loci (Simovich and Sassaman, 1986).

**Sampling:**

Ponds were monitored nightly until they first filled with water. After filling, toads were allowed to enter undisturbed. Late in the evening, amplexed pairs were sampled by hand net. It is estimated that the samples included 75-80% of the pairs in most cases. Tissue samples were taken (toe clippings), and the pairs were released to continue breeding. The genetic class of each partner was determined by allozyme analysis, and the frequencies of all combinations were calculated. Ponds were checked for several succeeding nights and after subsequent storms to determine if there were further breeding congresses. Although a small number of males may call for a few nights after a rain, observations at these and numerous other ponds in the area revealed only one instance of significant mating after the first congress (>0.5%). Furthermore, subsequent rains did not bring breeding congresses back to a pond once a full congress had convened at that pond.
Figure 1. Summary of the *Spea* life cycle, indicating the stages sampled and comparisons made.

1) A comparison of sampled and predicted early tadpole class distributions
   a) Sampled versus unmodified predictions, generated from adult pair combinations, incorporating assortative mating only.
   b) Sampled versus modified predictions, incorporating both assortative mating and laboratory measurements of differences in reproductive potential.
2) Difference in goodness-of-fit between la and lb.
3) A comparison of early versus late tadpole class distributions.
4) A comparison of earliest metamorphosing toadlets and slow developers.
5) Time sequence of emergence of classes as toadlets.
6) A comparison of early tadpoles versus earliest metamorphosing toadlets.

Following breeding, early tadpoles (7 to 10 days old) were sampled from ponds by hand net and typed electrophoretically. Late tadpoles (with hind legs well developed on at least some individuals and usually 12 to 20 days old) were later sampled and typed in the same manner. The exact day of sampling was determined by the rate of development of tadpoles in the various ponds.

Ponds were then checked daily to determine when tadpoles began to metamorphose. Toadlets metamorphosing early (emerging on the first 1 days of metamorphosis) were collected from under rocks and debris at the periphery of the pond. These were then typed as well. Consecutive samples of metamorphosing individuals were taken at five-day intervals from some ponds. Not all ponds could be sampled sequentially through tadpole metamorphosis because of population size. In some ponds only the group emerging first was sampled. The criterion used to determine if toadlets had metamorphosed recently (24 to 48 hrs. from emergence) was the possession of a tail stub still long enough to wiggle. Toadlets were measured for size (snout-vent length) at the completion of metamorphosis, and the mean size of genetic classes was compared. For this, only toadlets that had lost their tadpole beak and much of the tail (and were therefore of toadlet size and form) were used (toadlets' snout-vent length decreases while they lose their beaks and tails). Developing tadpoles remaining in the pond after the first group had metamorphosed were then sampled and typed in the same manner earlier tadpoles. For lack of a better term these are called slow developers.
Analysis:

From the matrix of mated pairs, the expected arrays of offspring classes were generated for each cross (given the Mendelian assortment of the unlinked loci). Each mating was then assigned two offspring, which were allocated proportionately into the classes expected from that cross. This assignment of two replacements maintains the same sample size as in adults. The predicted distribution was based initially on the assumption of equal fertility, fecundity, and viability of classes and all crosses. It does, however, account for the accuracy of identification of backcrosses arising from the use of only four markers (87%) (Simovich and Sassaman, 1986) and the degree of assortative mating observed.

For each matrix, the combined effects of differential fertility, fecundity, and early aquatic viability were then evaluated as an early composite component of selection by comparing (Contingency Chi Square) the observed distributions of early tadpole types with the predicted values generated as described above (Fig. 1, comparison 1a).

Next, to account for differences in the fertility and fecundity of adult hybrids as determined under laboratory conditions (Simovich, et al. 1991), a modified predicted distribution of classes was generated and compared (Contingency Chi Square) with the sampled distribution (Fig. 1, comparison 1b). For this modification, two correction factors were employed. First, to account for the sterility of hybrid males, predicted distributions eliminated the offspring contribution of that proportion of pairs involving F₁ hybrid males. Second, to account for the reduced fecundity of hybrid females, the predictions were modified by multiplying the offspring contribution of pairs with hybrid females by 0.45 (value from Simovich et al., 1991). These two modifications had little effect on the predicted proportions of hybrids (since most were produced by direct F₁ crosses of the pure species) but they drastically reduced or eliminated expected proportions of some multiply mixed classes. The modifications increased the expected proportions of the pure species. To determine if the modifications produced a significant decrease in the difference between predicted and sampled distributions, the F ratio (ratio of variances) of the Chi Square values of the two prediction comparisons was determined (Fig. 1, comparison 2).

The differences in post-embryonic survival through the tadpole stage were then evaluated by comparing the frequencies of the classes in the samples of early and late tadpoles (Fig. 1, comparison 3). The extent of differences between classes in developmental synchrony was next assessed by comparing the arrays for the early metamorphosing tadpoles to those for the slow developers (Fig. 1, comparison 4). This is not a direct measure of fitness, since concurrent rather than sequential samples were compared. Where available, samples of tadpoles metamorphosing at consecutive five-day intervals were also compared to determine the time sequence of the metamorphosis of each class (Fig. 1, comparison 5). For a further indication of differences in developmental rate, early metamorphosing toadlets and early tadpoles were compared (Fig. 1, comparison 6). A final measure of difference in the representation of the genotypic classes was assessed by comparing the distribution of classes among early metamorphosing tadpoles to that of the breeding adults (Fig. 1, comparison 7). No comparison of adults versus all metamorphosing toadlets was made because of the prolonged time members of some classes took to develop and the damage this would have on the populations. Some samples of tadpoles from these and other ponds were also scored for carnivore/omnivore morphology.

For each comparison, heterogeneity among the full arrays of classes at various stages of development was tested by Contingency Chi Square analysis (Chi Square values were considered significant at p<.05). Also, for each comparison, a relative performance value (or difference value in the case of developmental rate) was calculated for each class relative to the population:

\[ W = \frac{\text{sampled frequency}}{\text{predicted frequency}} \]

or,

\[ W = \frac{\text{frequency in a stage}}{\text{frequency in preceding stage}} \]

The value W is a measure of the change in relative frequency of a class compared to that in a preceding stage.
stage or of a difference relative to a predicted value. Performance values greater than 1.0 indicate a higher than predicted frequency of a class or increased relative representation of a class through the cycle.

Comparisons were then standardized by comparing the performance of each class relative to that of the predominant species, S. multiplicata. Significant heterogeneity in performance relative to S. multiplicata in individual ponds was determined by Contingency Chi Square analysis. To then evaluate the net performance relative to S. multiplicata over all tests, a Z statistic was calculated as $Z = \text{Chi square}/N'$ (Everitt, 1977). For this statistic, Chi values for each separate stage-stage comparison relative to S. multiplicata were summed over all N cohorts. Values greater than 1.96 indicate net performance better than that of S. multiplicata over all cohorts for that comparison. Values of -1.96 or less indicate poorer net performance. A summary of the results of individual tests for heterogeneity in the performance relative to S. multiplicata of each class at each development stage are given in Appendix 1.

**RESULTS**

Comparison of sampled versus predicted arrays shows significant differences among classes which includes fertility, fecundity and hatchability. The raw proportions of the classes of breeding adults alone are not good indicators of those of the early tadpoles. Predicted proportions of tadpole classes based on mated pair combinations alone differ significantly from observed proportions (Contingency Chi Square) (Table 1). Modifications incorporating laboratory measurements of reproductive differences between adult classes improve the fit (Table 1). The improvement is due primarily to a reduction in the total number of genetic classes expected. This reduction results from the elimination of crosses involving hybrid males and a reduc-

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Table 1. Summary of comparisons of predicted and sampled tadpole class distributions. Contingency Chi square test for heterogeneity between: 1) sampled versus predicted distributions which incorporate assortative mating, 2) sampled versus modified predicted distributions which incorporate assortative mating and differential reproduction, 3) F-ratio between first and second test to determine significance of decrease in heterogeneity, an asterisk indicates significance at 0.05 level.
tion in the expected frequency of offspring from crosses involving hybrid females. These classes of offspring (e.g., double backcrosses) are, in fact, rare or absent in the samples. Incorporation of fertility and fecundity data thus brings the predicted number of classes closer to the observed number in most cases. In one congress, no hybrid males were found in pairs; therefore, the modification does not change the prediction substantially. Genetic types resulting from backcrosses to S. multiplicata are not generally eliminated but are reduced. These backcrossed classes are the major classes affected by the low fecundity of hybrid females in crosses to S. multiplicata males. The expected frequencies of hybrids and S. bombifrons are not changed as radically by modifications, since these tadpoles are produced by the rarer pure species and F₁ crosses that, in the laboratory, do not differ in reproductive potential.

Among the early larvae S. multiplicata is over-represented relative to expectations (Fig. 2). Over all comparisons (Z values, summed Chi Square), S. bombifrons, hybrids, and backcrosses to S. multiplicatus are significantly scarcer (Fig. 3-1b) than expected. The deficiencies of tadpoles of S. bombifrons cannot be explained adequately on the basis of laboratory measurements of fecundity because the two pure species do not differ in fecundity (under laboratory conditions). Thus, some other factor seems to be affecting S. bombifrons offspring adversely in a way not detectable in the laboratory. In four of five cases they performed significantly more poorly than did S. multiplicata (Appendix 1-1b). Laboratory data are also inadequate to account for all adverse selection affecting hybrids. But, hybrids' reduced reproductive potential can explain some of the difference between the values for the backcrossed classes.

There is a slight difference in survival between classes when early and later tadpoles are compared. Z values (summed Chi Square) show that overall S. bombifrons performs significantly better than S. multiplicata. In no case did S. multiplicata tadpoles show significantly better survival (increased representation) than did S. bombifrons tadpoles. In the laboratory post-embryonic viability of the offspring of backcrosses to S.
multiplicata is also somewhat lower under some conditions (Simovich, 1985). For hybrids there is a fair degree of heterogeneity among cohorts in survival, but the Chi Square values are insignificant relative to S. multiplicata (Appendix 1-3) and show no net difference. Backcross survival is somewhat worse (Fig 3-3).

When the earliest toadlets are compared to slow developers, S. bombifrons, hybrid, and backcross-M classes are overrepresented relative to S. multiplicata over all comparisons (summed Chi Square, Fig. 3-4). The relative frequency of S. bombifrons and hybrids in samples of the earliest toadlets is usually higher than in samples of the slow developers. In only one case was S. multiplicata significantly better (Appendix 1-4). In one pond, S82, the tadpoles metamorphosed quickly and synchronously in less than two weeks. Slow developers were too sparse to sample; however, the frequencies of hybrid and S. bombifrons toadlets in the first sample were higher than that of S. multiplicata and showed an increase relative to the early tadpole samples.

In those ponds from which consecutive samples are available (Fig. 4), hybrids and S. bombifrons are in higher than initial frequency in the samples metamorphosing earliest, and the later samples are composed mostly of S. multiplicata, indicating that hybrids and S. bombifrons complete metamorphosis sooner and that their survivors leave the aquatic environment sooner.

In the comparisons of the proportions of classes from early tadpoles to early metamorphosis, hybrids were more successful than S. multiplicata in six of ten cases (five significant), than S. bombifrons in six of seven cases (all significant), and than backcrossed to S. multiplicata in two of eight cases (both significant) (Appendix 1-6). In only one case was the poorer representation of S. bombifrons relative to S. multiplicata significant.

Figure 3. Summary of performance differences relative to S. multiplicata. Plotted are Z statistic values which summarize performance comparisons over all N cohorts. Where Z is greater than 1.96, there is overall better performance of a class relative to S. multiplicata; where Z is less than -1.96 there is overall poorer performance. B = S. bombifrons, H = hybrid, BKM = backcross to S. multiplicata.
S. multiplicatus was frequently under-represented, and hybrids and S. bombifrons were over-represented among the early metamorphosing toadlets in comparison to their initial frequency among the early tadpoles (Fig. 4). Summed Chi square values (Z) indicate that over all ponds sampled, S. bombifrons and hybrids performed better than S. multiplicata, while backcrosses to S. multiplicata did not differ (Fig. 3-6). The results indicate that S. bombifrons and hybrids generally develop faster than does S. multiplicata.

Comparison between the breeding adults and early metamorphosing toadlets show no clear differences in the representation of classes.

Size At Emergence:
S. bombifrons toadlets were larger than S. multiplicata toadlets in all ponds containing both species. Sizes of hybrid toadlets were generally intermediate between those of the pure species of the same age but overlapped with that of S. bombifrons in some ponds (Fig. 5). This is the same rank order found in laboratory experiments (Simovich, 1985). In only one pond did hybrids overlap with S. multiplicata. The number of hybrids in that sample (Shot 82-2) was quite low, and hybrids were larger than S. multiplicata in the first sample of the sequence. Backcrosses to S. multiplicata, when present, may also be larger than S. multiplicata. The size of toadlets within a species varies from pond to pond. But, when sequential samples are available within a pond, the late emerging S. multiplicata (the species for which we have the most data) are not larger than the early emergers of the same species, and thus are not benefiting from a prolonged aquatic period by metamorphosing at a larger size.
Figure 5. Variation in toadlet size between classes and between ponds. Average snout-vent length (mm.) and 95% C.I. for emerging toadlets. Asterisk indicates cases where multiple range tests of ANOVA indicate a significant difference despite overlap of the 95% C.I. Dotted lines connect like genotypes appearing in sequential samples from individual ponds of the same cohort. Abbreviations below are individual pond codes. Not all classes were present in all ponds.
Carnivore Morphology:

In all mixed species ponds analyzed, the proportion of \textit{S. bombifrons} and hybrid tadpoles with the carnivore morphology was higher than that in \textit{S. multiplicata}. \textit{Spea multiplicata} never develops carnivores in proportions as high as \textit{S. bombifrons} does, even in those ponds where it is the only \textit{Spea} present (Fig. 6). However, carnivores are somewhat more frequent in \textit{S. multiplicata} itself when that species far outnumbers \textit{S. bombifrons} (e.g., Alb 81) or when no \textit{S. bombifrons} is present (ponds of pure \textit{S. multiplicata}). Carnivore tadpoles from backcrosses of hybrids to \textit{S. multiplicata} are more frequent than in \textit{S. multiplicata} (more as in \textit{S. bombifrons}).

**DISCUSSION**

It has been shown that much of the variation in the level of hybridization and in the frequencies of the various classes of tadpoles in this area can be accounted for by variation in assortative mating (Simovich, 1985). Mating is more random and more tadpoles of mixed genotype are produced when ponds are small and crowded at the time of breeding. This pre-mating aspect of selection was addressed in this study by sampling the actual mated pairs from a particular pond and then using this information to predict the frequency of genotypic classes among the resulting tadpoles. Because the observed frequencies of classes differ significantly from these predictions, post-mating selection must be involved.

A significant portion of the discrepancy between observation and prediction can be accounted for by post-mating selection in the form of reduced reproductive potential of hybrids as measured in the laboratory (Simovich et al., 1991). Modifying the predictions to reflect the difference in hybrids’ reproductive potential qualitatively accounts for the low frequencies of some backcrosses and suggests that the fertility differences measured in the laboratory are real and likely to be important in nature. There is, however, a further portion of the discrepancy that this investigation has not explained, the low initial representation of \textit{S. bombifrons} tadpoles. It is possible that the early success of \textit{S. bombifrons} in nature is more closely tied to environmental conditions than is that of the other classes.

Despite adverse selection in early compo-

![Figure 6](image)
nents of fitness, *S. bombifrons* and hybrids often constitute the majority of the first tadpoles to metamorphose. Laboratory experiments had predicted fast development of *S. bombifrons* but had demonstrated that hybrids develop faster than either parental species when live food (fairy shrimp from natural ponds) is available (Simovich, 1991). The variability in the expression of developmental differences in the field again raises the possibility that the expression of these differences may vary in response to environmental conditions.

Several studies have shown that anuran developmental rates can be affected by variations in environmental conditions; these include temperature, drying, food availability, and crowding (e.g., see Collins, 1979; Crump, 1989; Harkey and Semlitsch, 1988; Newman, 1988a, 1988b; Semlitsch and Wilbur, 1988; Travis, 1983, 1984; Wilbur, 1977; and Wilbur and Collins, 1973). In the field portion of this study variation in environmental conditions from pond to pond could not be controlled. The ponds all retained water throughout the larval period of the toads, though all experienced a reduction in volume. Trends in developmental rates observed in different ponds and in the laboratory were largely consistent. This strongly suggests that there is an important genetic (phylogenetic) component to developmental rate difference. The fitness advantage conferred by fast development to avoid desiccation and predation (Caldwell et al., 1980; Collins, 1975, 1979; Licht, 1974; Mayhew, 1965; Travis, 1980, 1983) cannot be ignored. In drought years, this advantage could well be enjoyed by *S. bombifrons* and hybrids over *S. multiplicata*.

Faster development of *S. bombifrons* relative to *S. multiplicata* is accompanied by larger size. Hybrids, in the field as in the laboratory, are intermediate in size. Being larger at metamorphosis may increase first-year survival and the probability of early maturation (Collins, 1975, 1979; Martof, 1956; Mayhew, 1965; Wilbur et al. 1978). In many anurans, slower developers attain a larger size (Crump, 1989; Collins, 1979; Newman, 1988; and Travis 1980, 1983, 1984). In *S. multiplicata* and *S. bombifrons* however, this tradeoff is not apparent between or within the species. The species with the longer period of metamorphosis, *S. multiplicata*, does not seem to gain a size advantage by prolonging the larval period.

Interestingly, the classes that are largest and develop fastest, hybrids and *S. bombifrons*, also express the carnivore morph most frequently in the field. The expression of carnivore morphology is quite plastic and has been tied to a diet of live food, and since carnivores tend to develop faster and be larger than omnivores (Pomeroy, 1981), there may well be a direct relationship between the development of carnivore morphs and the other developmental differences between classes. As carnivore morphs do not develop well in the laboratory, we do not currently understand the relative contributions of genetics, diet, or other variables to this polymorphism.

Substantial numbers of hybrids can be produced and survive under some conditions. Although selected against early in the life cycle and in subsequent reproductive potential, hybrids and *S. bombifrons* may be favored during the larval phase because of their rapid rates of growth and development. Because of this their net fitness may be higher than that of the more prevalent species, particularly if ponds dry early. Furthermore, this allows substantial introgression of alleles between species at least in some areas. Hybrid females can be frequent enough to produce significant numbers of backcross offspring (especially with the more common *S. multiplicata* males) despite their low fecundity. Introgression may then constitute a ready source of new variation and may have evolutionary importance within the system.

The intensity and direction of selection in this system can vary at different parts of the life cycle and under different conditions. The distributions and net fitness of each genotypic class varies in response to the environment. The condition--small pond size--increasing the production of hybrids, by decreasing the efficiency of isolation (crowding), could also favor their survival.

The vegetation and runoff patterns in the San Simon Valley have changed significantly in the past 100 years. The valley was once primarily grassland, but now mesquite has invaded from hillsides far into the valley. Rainfall in the summer months of the monsoon season can be very spotty, Southwestern Herpetologists Society
and the runoff is now diverted into a number of cattle tanks installed by ranchers. A large cienega at the northern end of the valley has been reduced. The result is that the toads now breed in many small, scattered ponds. It has been speculated that the effect of habitat modifications on hybridization between species can be exacerbated by drought (Cousineau and Rogers, 1991). These changes have altered the breeding sites, which were partitioned by the two species prior to the establishment of the cattle industry, and may have increased the probability of pool crowding and thus mismatching. The same conditions could increase the probability of early drying, selecting against the slower developing species at times. Whatever the cause of the hybridization, environmental variation now, at times, facilitates the production and survival of substantial numbers of hybrids and their offspring.

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LITERATURE CITED


Appendix 1. Analysis of the six classes relative to *S. multiplicata* (M). For each component the stages or predicted values compared are indicated. For each comparison, the changes in frequency of a class between stages or differences between expected and observed frequencies (performance value) are evaluated relative to those of *S. multiplicata* by Contingency Chi Square Analysis. Shown are the number of comparisons where a class increased ↑, or decreased ↓, relative to M (denominator) and the number of those differences which were significant (numerator) and the number which did not differ (=).

<table>
<thead>
<tr>
<th>Component and Comparison</th>
<th>Direction Relative to M</th>
<th>Classes</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>H</td>
</tr>
<tr>
<td>1a Early vs J, 2/5 3/7 6/7 5/7 5/6</td>
<td>↑</td>
<td>0/2</td>
</tr>
<tr>
<td>Mod. Pred. =</td>
<td>↓</td>
<td>2/5</td>
</tr>
<tr>
<td>1b Early vs J, 2/4 vs 4/7 1/2 0 1 0</td>
<td>↑</td>
<td>0/3</td>
</tr>
<tr>
<td>Mod. Pred. =</td>
<td>↓</td>
<td>2/4</td>
</tr>
<tr>
<td>3 Late vs Early =</td>
<td>↑</td>
<td>1/6</td>
</tr>
<tr>
<td>4 Meta vs Slow =</td>
<td>↑</td>
<td>4/4</td>
</tr>
<tr>
<td>6 Meta vs Early =</td>
<td>↑</td>
<td>5/6</td>
</tr>
<tr>
<td>7 Meta vs Adults =</td>
<td>↑</td>
<td>2/2</td>
</tr>
</tbody>
</table>


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Southwestern Herpetologists Society


