

Pool Duration Influences Age and Body Mass at Metamorphosis in the Western Spadefoot Toad: Implications for Vernal Pool Conservation

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ABSTRACT. The vernal pools of California's Central Valley support an assemblage of four species of native amphibians, Western Spadefoot Toad (*Spea* [*Scaphiopus*] *hammondi*), Pacific Chorus Frog [treefrog] (*Psuedacris* [*Hyla*] *regilla*), Western Toad (*Bufo boreas*), and California Tiger Salamander (*Ambystoma californiense*). Age, body size, and stored fat at metamorphosis are thought to be important correlates of fitness in amphibians. In this paper I report the results of field studies on the link between these features of life history, breeding pool duration, and the risk of mortality due to drying in several populations of larval *S. hammondi*. The larval period ranged from 30-79 days (n=8 pools). Body size at metamorphosis ranged from 1.5-10.4 grams (9 pools) and stored body fat at metamorphosis ranged from 13-29% (5 pools). Each of these variables was positively correlated with pool duration. Successful metamorphosis was observed in pools that were filled for 36-133 days (9 pools) and three of 11 pools monitored (27%) dried on or before the day larvae completed development. The association between pool duration and several correlates of fitness suggests that pool duration should be given consideration when planning vernal pool preserves and wetland restoration projects.

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INTRODUCTION

The distribution and abundance of amphibians in California has been in a state of change for over 100 years (Jennings and Hayes, 1985). Native and introduced amphibians now occupy artificial wetlands (e.g., stock tanks) where none previously existed, and declines of native frogs have been reported with increasing frequency since Moyle's (1973) description of declines among native frogs in the San Joaquin Valley twenty five years ago. Studies on changing distribution and declines among amphibians in central California continue to be an important conservation biology theme (Drost and Fellers, 1996; Fisher and Shaffer, 1996). Many causal mechanisms are currently being explored and several environmental factors may be contributing to these declines (Fisher and Shaffer, 1996; Reaser, 1996). The best explanation for observed changes in distribution and abundance of low elevation central California amphibians, including obligate ephemeral pool natives such as the California Tiger Salamander (*Ambystoma californiense*) and the Western Spadefoot Toad (*Spea* [*Scaphiopus*] *hammondi*) is habitat loss caused by urbanization and irrigated agriculture. However, changes in distribution and abundance are occurring even in areas where human-caused changes have been less extensive. Fisher and Shaffer (1996) attribute losses of native amphibians in part to human

alteration of wetlands that have allowed, and probably promoted, the invasion of exotic predators.

Because they have a biphasic life history, any conservation approach for the amphibians that inhabit ephemeral pool ecosystems such as California's vernal pools will need to address both the aquatic larval stage and the terrestrial stage. In general, the terrestrial life history stage of amphibians has not been well studied (Werner, 1986). From a conservation perspective, this is unfortunate because besides being the reproducing life history stage it is also the stage where most growth occurs as well as the stage capable of overland dispersal. The aquatic larval stage has received more attention from amphibian ecologists and is commonly viewed as the stage in which the advantages of rapid aquatic stage growth and large size at metamorphosis are pitted against the risks of mortality, primarily drying, in the larval habitat (Pomeroy, 1981; Newman, 1989; 1992; Pfennig, 1992). This view assumes that if successful metamorphosis occurs, subsequent fitness is accurately predicted by body size at metamorphosis (Wilbur and Collins, 1973). In this paper I summarize my observations on the ponding duration of the larval habitat, age at metamorphosis, risk of mortality due to drying, and body size and condition at metamorphosis in the Western Spadefoot Toad (*S. hammondi*). The results allow me to

evaluate the relationship between the aquatic environment of the larval life history stage and the fitness prospects of the terrestrial life history stage.

MATERIALS AND METHODS

I studied 11 widely distributed pools used as breeding sites by *S. hammondi* in coastal central and southern California (Riverside and San Luis Obispo Counties) during the spring of 1991. Breeding was restricted to March, a period of heavy rains that year. The ponding duration of the aquatic habitat was evaluated in two ways: 1) the number of days a pool persisted after the first bout of breeding; and 2) the time between the day the fastest developing larvae from the first bout of breeding completed their aquatic development, and the day the pool dried. To accomplish this, pools in which eggs were deposited were visited once a week. Until the fastest developing larvae from the first bout of breeding transformed, a subsample of larvae were staged and weighed during each visit. After metamorphosis, each pool was visited sufficiently often to determine the day of drying. During each visit, a sample ($n = 10$) of the oldest cohort of larvae were staged (Gosner, 1960) and weighed, either in the field with a hand-held balance (to the nearest 0.1 g), or in the laboratory on an electronic balance (to the nearest 0.001 g). I used this information to construct curves of growth and development. At the time of metamorphosis, a small number of transforming individuals (Gosner stage 42) were collected from each pool and preserved for determination of stored body fat. Each preserved individual was dissected and all food was removed from the intestine. The empty intestine was placed with the carcass and both were dried at 55° C until weight became constant. Each carcass (including cleaned intestine) was then immersed in successive baths of diethyl ether until a constant mass after drying was obtained. The difference between the total dry weight and the dry weight after the ether extraction of fat is a measure of stored body fat (Reznick and Braun, 1987).

RESULTS

Larval Growth, Development, and Stored Body Fat

Growth and development in the field (Figure 1) followed the general anuran pattern of rapid growth during the mid-larval stages (prometamorphosis) followed by loss of mass during the metamorphic climax. The external morphological changes associated with metamorphosis are complete when the tail is completely resorbed (Gosner stage 46). It is approximately at this stage when spadefoot toadlets initiate terrestrial feeding (Morey and Janes, 1994). At the initiation of successful terrestrial feeding the body mass of *S. hammondi* is about half of the maximum larval mass, which is usually attained by Gosner stage 38 (Figure 1). In eight pools for which a reliable estimate was available, the average period of larval development (hatching to metamorphosis) was 58 days (range 30-79 days, 1 SE \pm 5 days)

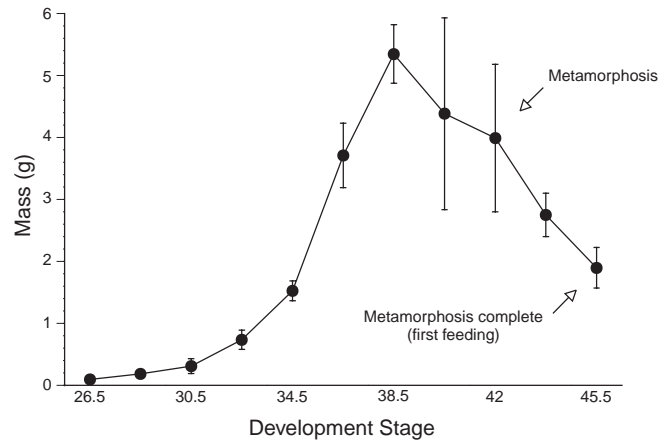


FIGURE 1. Larval growth curve based on live body mass and Gosner's developmental stage. Each symbol is the mean of the sample means for 8 naturally occurring pools from which larvae were sampled. Metamorphosis (emergence of the first forelimb) is at stage 42. Metamorphosis is virtually complete when terrestrial feeding begins. At this point only a tiny remnant of the larval tail remains.

and the average mass at metamorphosis in the nine pools in which successful metamorphosis occurred was 3.7 g (range 1.5-10.4 g, 1 SE \pm 0.9 g). Comparisons among pools revealed that longer larval period tended to be associated with larger size at metamorphosis (Figure 2), but the relationship was not strong ($r = .42$, $P = .306$, $d.f. = 7$). Because of the positive correlation between stored fat and body mass (Figure 3), pools that produced large larvae also produced transforming individuals with high amounts of stored body fat. In five pools for which a sample was obtained the average per cent body fat at metamorphosis was 21.6 % (range 13.1-28.9%, 1 SE \pm 2.36%). The stored body fat in a pooled sample of 21 individuals collected from five pools revealed a nonlinear relationship between stored fat and body mass, with larger individuals containing proportionally more stored fat at metamorphosis than smaller individuals (Figure 3).

Pool Duration and Its Consequences for Age, Size at Metamorphosis, and the Risk of Mortality Due to Drying

After a several day period of rain which ended in mid-March, no substantial additional rainfall occurred in the study area. Larger pools and deeper pools remained filled longer than the smaller and shallower pools. In pools that remained filled long enough to produce transforming juveniles, the average number of days the pool persisted after the first bout of breeding took place was 83 days (range 36-133). Larval period was positively correlated with pool duration ($r = .85$, $P = .007$, $d.f. = 7$; Figure 4a). Larvae from longer lasting pools also tended to be larger at metamorphosis than larvae from shorter duration pools, but the relationship was not particularly strong ($r = .68$, $P = .062$, $d.f. = 7$; Figure 4b). Of the 11 pools monitored, two pools dried be-

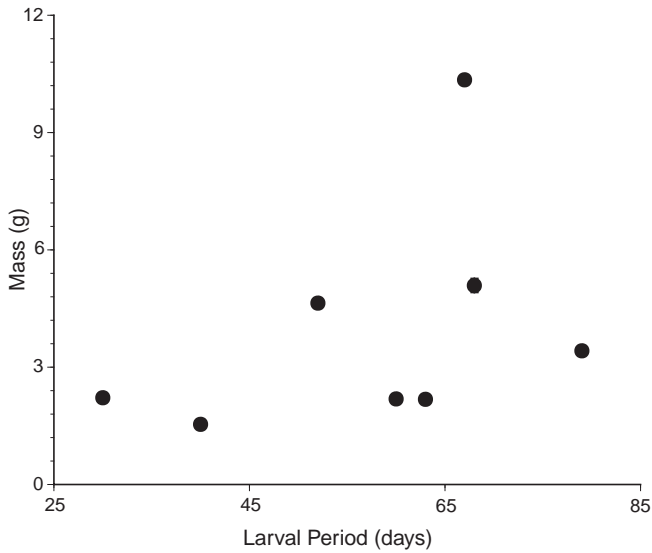


FIGURE 2. Relationship between larval period and mass at metamorphosis. Each symbol represents the sample mean for larvae from a single naturally occurring pool. Pool duration is the number of days from the deposition of the first eggs until no standing water remained in the pool. Larval period is the number of days from hatching to metamorphosis of the fastest developing larvae from the oldest cohort.

fore the larvae completed aquatic development, resulting in mortality of all individuals in these pools. A third pool dried on the same day the fastest developing individuals from the oldest cohort of larvae transformed. A small number of transforming individuals did survive to complete metamorphosis but a large number of slower developing larvae from the same cohort, and all larvae from later bouts of breeding, desiccated prior to completing metamorphosis. The eight longer-duration pools remained filled between 7 and 62 days longer than required for the larvae within to complete aquatic development, indicating substantial variation in risk of mortality due drying of the larval environment.

DISCUSSION

The fastest observed time for completion of larval development was 30 days. This occurred in a very small pool in Riverside County, in southern California. Jennings and Hayes (1994) suggest that larvae can complete development in as little as three weeks. This is certainly possible because in the laboratory larvae have developed from hatching to metamorphosis (Gosner stage 42) in as little as 14 days (Morey, 1994). However, Western Spadefoot Toads in the wild rarely, if ever, complete larval development in pools drying sooner than 30 days after embryos hatch.

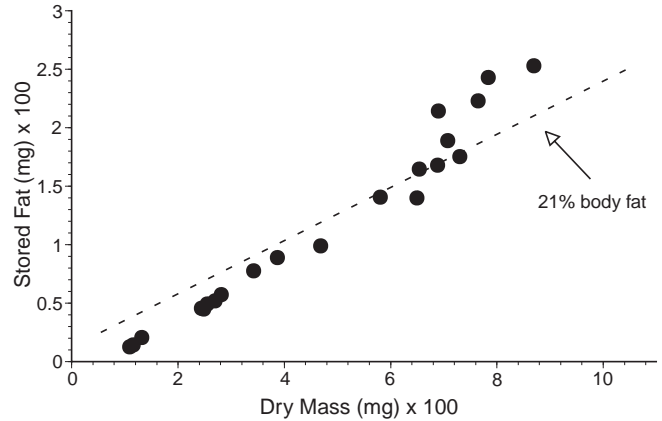


FIGURE 3. Relationship of mass and stored body fat at metamorphosis. Symbols indicate individuals and the graph are based on the pooled sample of transforming larvae from 5 naturally occurring pools. The dashed line represents a constant percent body fat. It is based on the mean percent body fat for the entire sample and is included simply to illustrate the non-linear nature of fat storage.

The causes of the observed variation in the period of larval development were not investigated in this study. However, variation in development time is not unexpected because amphibians, including spadefoot toads, are notable for expressing substantial phenotypic plasticity in both age and size at metamorphosis. A large number of studies on amphibians have described the plastic response of larval development to variation in environmental factors including temperature, food supply and quality, density, competition, and risk of predation (e.g., Wilbur, 1977; Smith-Gill and Berven, 1979; Semlitsch and Caldwell, 1982; Travis, 1984; Alford and Harris, 1988; Newman, 1989; Pfennig, 1990; Skelly and Werner, 1990; Simovich et al., 1991; Blouin, 1992). In the wild it takes about 4-6 days for embryos to hatch once they have been deposited and a minimum of 30 days for larvae to complete development. Therefore, in general, pools must hold water at least 5 weeks after *S. hammondi* breed to support successful metamorphosis. This period is usually sufficient for larval development of each of the other amphibians that breed in central California vernal pools, with the exception of *A. californiense*, which can take several weeks longer (Jennings and Hayes, 1994).

Although the causes of the observed variation in length of the larval period and body mass at metamorphosis were not investigated, both of these important life history traits were positively correlated with pool duration. Larvae from longer-lived pools developed more slowly, which delayed metamorphosis. Slower developing larvae transformed at a larger size than they would if they had the same developmental rate as larvae from shorter-duration pools. The important result is that larvae born in long-duration pools tend to be large at metamorphosis, a life history trait related to higher terrestrial fitness in temperate

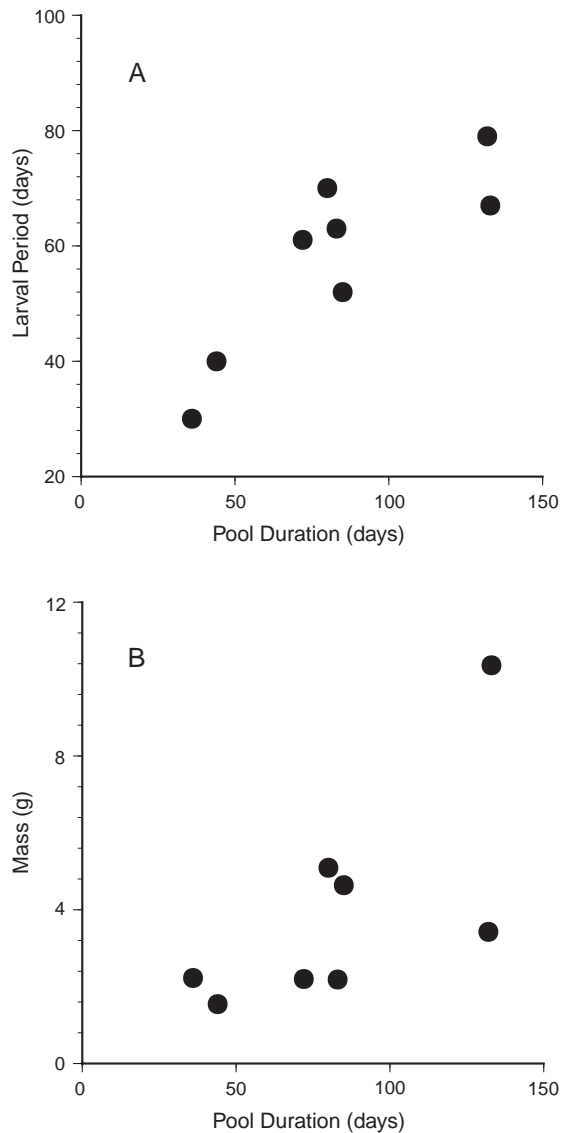


FIGURE 4. Relationship of pool duration with (A) larval period, and (B) mass at metamorphosis. Each symbol represents the sample mean from a naturally occurring pool. Pool duration is the number of days from the deposition of the first eggs until no standing water remained in the pool. Larval period is the number of days from hatching to metamorphosis of the fastest developing larvae from the oldest cohort.

amphibians (Berven and Gill, 1983; Smith, 1987; Semlitsch et al., 1988; Berven, 1990; Scott, 1994). I also observed considerable variation in the proportion of stored body fat at metamorphosis, however almost all of the observed variation in this trait is accounted for by differences in body size. The allometry of fat storage in juvenile *S. hammondi* is described by Figure 3 which shows that among newly transformed juveniles, larger individuals will be proportionally fatter than smaller individuals. Amount of stored body fat has been positively linked to

terrestrial fitness in newly transformed salamanders (Scott, 1994) and spadefoot toads (Pfennig, 1992). These studies demonstrated that fatter juveniles were more resistant to starvation and had better survivorship than their leaner siblings.

I draw two main conclusions from the uncontrolled field observations reported in this paper. First, size and somatic condition, two closely associated life history traits which have been linked to fitness in other temperate amphibians, are positively correlated with pool duration in *S. hammondi*. Second, in pools that dry sooner than about 35 days after breeding, the risk of mortality due to drying increases sharply. Because pool duration can have important fitness consequences for amphibians, it should be considered when preserves or wetland restoration programs are planned. The extent to which the distribution and abundance of amphibians in vernal pool landscapes is influenced by the distribution of pool durations is not well known but some conclusions are easily drawn. First, pools need to persist at least 5 weeks after breeding takes place, which typically occurs in February and March, to support successful metamorphosis of *P. regilla*, *B. boreas*, and *S. hammondi* larvae. Second, vernal pool landscapes must have some pools that are very long-lived if they are to support *A. californiense* (Jennings and Hayes, 1994). Finally, human-caused changes in the distribution of pool durations, such as those described by Fisher and Shaffer (1996) will probably effect each of the native amphibians differently, resulting in changes in the composition, distribution, and abundance of the local amphibian assemblages. For example, the creation of large, deep, long-duration pools will favor *A. californiense* where they are present, and exotic species such as the Bullfrog (*Rana catesbeiana*).

California's vernal pool ecosystems have been fragmented and reduced in size by anthropogenic habitat alterations including urban and suburban development, water projects, and irrigated agriculture (U.S. Fish and Wildlife Service, 1994). Fisher and Shaffer (1996) observed that even where vernal pool habitat still exists it has often been altered by the construction of stock tanks and farm ponds. Irrigation ditches and artificial wetland creation projects further contribute to a changing distribution in the duration of ponding within natural vernal pool habitats. In addition, permanent artificial wetlands often invade otherwise unaltered vernal pool terrain inadvertently when upstream urban development results in increased runoff. Fisher and Shaffer (1996) found that native vernal pool amphibians such as *B. boreas*, *S. hammondi*, and *A. californiense* were able to survive and breed even in pools created or altered by humans. Native amphibians were often absent in pools inhabited by introduced fishes and frogs. They concluded that habitat modifications have allowed exotic species to invade, thus contributing to the declines they observed in native amphibians.

Among the amphibians inhabiting California's vernal pool ecosystems the terrestrial stage is the much longer-lived life-his-

tory stage; it is the stage that reproduces; it is the stage where most growth occurs; and, it is the stage capable of overland dispersal. In spite of this, the terrestrial lives of California's vernal pool amphibians remain virtually unknown. The effects of habitat fragmentation on dispersal, the distance and nature of migrations to and from summer refuge sites, and the relationship of native amphibians and native burrowing mammals all remain unstudied, but each has important consequences for conservation. For example, a recent field study by Loredo et al. (1996) found that most adult *A. californiense* retreated to California Ground Squirrel (*Spermophilus beecheyi*) burrows when they left pools after breeding. Because tiger salamanders are poor burrowers, the use of ground squirrel and other rodent burrows may provide an essential summer habitat for *A. californiense*. If this is true, ground squirrel (Marsh, 1987) and Pocket Gopher (*Thomomys bottae*) control in California may be having a negative effect on *A. californiense* by reducing the availability of moist summer refuges in an otherwise hostile summer landscape.

Conservation strategies aimed at recovering declining species will need to take into account and treat the underlying causes of observed declines if they are to prevent extinctions (Caughley, 1994). Successful amphibian conservation strategies will need to embrace the attributes and requirements of both the aquatic and terrestrial life history stages. While additional life history studies, especially on terrestrial stage natural history and habitat requirements are badly needed, the conclusions and recommendations of Jennings and Hayes (1994), Fisher and Shaffer (1996), and Loredo et al. (1996) already provide important guidance for those involved in planning vernal pool conservation and wetland restoration programs. Any good recipe for reversing declines of native vernal pool amphibians will need to address, at a minimum, the consequences of planned and inadvertent changes in pool duration, control of exotic predators, effects of habitat fragmentation and population isolation on dispersal, and the habitat requirements of the terrestrial life history stages.

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LITERATURE CITED

Alford, R.A. and R.N. Harris. 1988. Effects of larval growth history on anuran metamorphosis. *American Naturalist* 131:91-106.

- Berven, K.A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology* 71:1599-1608.
- Berven, K.A. and D.E. Gill. 1983. Interpreting geographic variation in life-history traits. *American Zoologist* 23:85-97.
- Blouin, M.S. 1992. Comparing bivariate reaction norms among species: time and size at metamorphosis in three species of *Hyla* (Anura: Hylidae). *Oecologia* 90:288-293.
- Caughley, G. 1994. Directions in Conservation Biology. *Journal of Animal Ecology* 63:215-244.
- Drost, C.A. and G.M. Fellers. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. *Conservation Biology* 10:414-425.
- Fisher, R.N. and H.B. Shaffer. 1996. The decline of amphibians in California's Great Central Valley. *Conservation Biology* 10:1387-1397.
- Gosner, K.L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183-190.
- Jennings, M.R. and M.P. Hayes. 1985. Pre-1900 overharvest of California red-legged frog (*Rana aurora draytonii*) the inducement for bullfrog (*Rana catesbeiana*) introduction. *Herpetologica* 41:94-103.
- Jennings, M.R. and M.P. Hayes. 1994. Amphibian and Reptile Species of Special Concern in California. California Department of Fish and Game.
- Loredo, I., D. Van Vuren and M.L. Morrison. 1996. Habitat use and migration behavior of the California tiger salamander. *Journal of Herpetology* 30:282-285.
- Marsh, R.E. 1987. Ground squirrel control strategies in Californian agriculture. Pages 261-276 in: C.G.J. Richards and T.Y. Ku (Editors). *Control of Mammal Pests*. Taylor and Francis, London, Great Britain.
- Morey, S.R. 1994. Age and size at metamorphosis in spadefoot toads: A comparative study of adaptation to uncertain environments. Doctoral Dissertation, University of California, Riverside. 235 pp.
- Morey, S.R. and D.N. Janes. 1994. Variation in larval habitat duration influences metamorphosis in *Scaphiopus couchii*. Pages 159-165 in: P.R. Brown and J.W. Wright (Editors). *Herpetology of the North American Deserts: Proceedings of a symposium*, Special Publication Number 5.
- Moyle, P.B. 1973. Effects of introduced bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. *Copeia* 1973:18-22.
- Newman, R.A. 1989. Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. *Ecology* 70:1775-1787.
- Newman, R.A. 1992. Plasticity in amphibian metamorphosis. *Bioscience* 42:671-678.
- Pfennig, D.W. 1990. The adaptive significance of an environmentally-cued developmental switch in an anuran tadpole. *Oecologia* 85:101-107.
- Pfennig, D.W. 1992. Polyphenism in spadefoot toad tadpoles as a locally adjusted evolutionarily stable strategy. *Evolution* 46:1408-1420.

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- Pomeroy, L.V. 1981. Developmental polymorphism in the tadpoles of the spadefoot toad *Scaphiopus multiplicatus*. Ph. D. dissertation, University of California, Riverside.
- Reaser, J.K. 1996. The elucidation of amphibian declines. *Amphibian & Reptile Conservation* 1:4-9.
- Reznick, D.N. and B. Braun. 1987. Fat cycling in the mosquitofish (*Gambusia affinis*): fat storage as a reproductive adaptation. *Oecologia* 73:401-413.
- Scott, D.E. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. *Ecology* 75:1383-1396.
- Semlitsch, R.D. and J.P. Caldwell. 1982. Effects of density on growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrooki*. *Ecology* 69:184-192.
- Semlitsch, R.D., D.E. Scott, and J.H.K. Pechman. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. *Ecology* 69:184-192.
- Simovich, M.A., C.A. Sassaman, and A. Chovnick. 1991. Postmating selection of hybrid toads (*Scaphiopus multiplicatus* and *Scaphiopus bombifrons*). *Proceedings of the San Diego Society of Natural History* 5:1-6.
- Skelly, D.K. and E.E. Werner. 1990. Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology* 71:2313-2322.
- Smith, D.C. 1987. Adult recruitment in chorus frogs: effects of size and date at metamorphosis. *Ecology* 68:344-350.
- Smith-Gill, S.J. and K.A. Berven. 1979. Predicting amphibian metamorphosis. *American Naturalist* 112:563-585.
- Travis, J. 1984. Anuran size at metamorphosis: experimental test of a model based on interspecific competition. *Ecology* 65:1155-1160.
- U.S. Fish and Wildlife Service. 1994. Endangered and threatened wildlife and plants; determination of endangered status for the Conservancy fairy shrimp, longhorn fairy shrimp, and vernal pool tadpole shrimp; and threatened status for the vernal pool fairy shrimp. *Federal Register* 59:48136-48153.
- Werner, E.E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *American Naturalist* 128:319-341.
- Wilbur, H.M. 1977. Propagule size, number and dispersion pattern in *Ambystoma* and *Asclepias*. *American Naturalist* 111:43-68.
- Wilbur, H.M. and J.P. Collins. 1973. Ecological aspects of amphibian metamorphosis. *Science* 182:1305-1314.