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Life History and Demographic Variation in the California Tiger Salamander (*Ambystoma californiense*)

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In December 1991, we initiated a long-term study of the California Tiger Salamander (*Ambystoma californiense*) at a breeding pond in Monterey County, California. Because of habitat loss, this species is a candidate for federal endangered species status, but many basic features of its life history and demography have not been studied in detail. During the first seven years of this study, we captured, measured, individually marked, and released 657 breeding adults and 1895 newly metamorphosed juveniles at the drift fence encircling this pond. We also used skeletochronology to investigate age structure in cohorts of breeding adults. Numbers of breeding adults varied by more than a factor of four among years, and annual juvenile production ranged from 121–775 metamorphs. Contrary to the results of related studies, total juvenile production was positively related to the total biomass of breeding females. Both skeletochronology and mark-recapture data indicate that most individuals do not reach sexual maturity until 4–5 years of age, and, although individual longevity can exceed 10 years, less than 50% of individuals returned to breed a second time. These results suggest that this breeding population was a reproductive sink during the period of this study and that isolated breeding ponds may be insufficient for the long-term maintenance of viable populations of *A. californiense*.

LARVAL amphibians have long been a model system for the study of ecological processes (Wilbur, 1980); however, our knowledge of the demography, ecology, and even basic life history of postmetamorphic amphibians lags far behind. It has been repeatedly suggested that regulation of amphibian populations occurs primarily during the larval stage, but knowledge of the demography of postmetamorphic individuals is also crucial for determining the relative importance of events during the larval phase (Semlitsch et al., 1988; Berven, 1990; Scott, 1994). Recent population models also indicate the importance of terrestrial survival for population viability (Taylor and Scott, 1997). Finally, studies of networks of breeding ponds over multiple years indicate that many consistently used ponds are reproductive sinks in most years, emphasizing the importance of postmetamorphic survival and immigration (Gill, 1978; Sinsch, 1992). Although secretive terrestrial behavior and lifespans ranging from years to decades pose serious difficulties for studying postmetamorphic amphibians, drift fence sampling at breeding ponds has proven a reliable method for censusing breeders and recently transformed juveniles (Storm and Pimentel, 1954; Gibbons and Semlitsch, 1982).

Metamorphic ambystomatid salamanders generally spend their entire juvenile lives and the vast majority of their adult lives in terrestrial habitats, where they are difficult to study. Numerous drift fence studies at breeding ponds have extensively documented population dynamics, demography, and the life history of ambystomatid salamanders in the eastern United States (e.g., Husting, 1965; Shoop, 1974; Semlitsch et al., 1996). In contrast, just two short-term drift fence studies of western ambystomatids exist (*Ambystoma macrodactylum*, Beneski et al., 1986; *Ambystoma californiense*, Loredo and VanVuren, 1996). Our considerable knowledge of the life histories of ambystomatid salamanders, including climatic cues for breeding migration, variable adult sex ratios and size distributions, determinants of metamorph size and production, and survivorship of all life stages, comes largely from these studies (Petranka, 1998). Although general conclusions are relatively few, it seems clear that rainfall is a key trigger for many life-history activities and that species, and even regional populations of the same species, have unique attributes that limit extrapolation among taxa.

Although drift fence studies often require many years of effort to collect data on longevity and population age structure, similar data can be acquired more rapidly using skeletochronology to estimate individual ages (Castanet and Smirina, 1990). With skeletochronology, age is estimated by counting lines of arrested growth (LAG) in thin cross-sections of elongate bones. Because toe bones provide sufficient skeletochronological material for many species, nondestructive aging is often possible, and toe clippings produced as a byproduct of marking can be used. Thus, skeletochronology has become an increasingly common technique in recent studies of amphibian demography (Tinsley and Tocque, 1995; Wake and Castanet, 1995; Castanet et al., 1996). However, few investigators have validated the assumption that LAG are formed annually and represent good estimates of age (Kazmer, 1986).

The California Tiger Salamander (*A. californiense*) is an endemic member of the California grassland community. Unlike any other North American ambystomatid, this species occupies a region with Mediterranean climatic features (Storer, 1925; Loredo et al., 1996). Although this species still inhabits its full historic range, throughout the central valley and surrounding foothills and valleys, from Sonoma County south to Santa Barbara County, it has become increasingly rare over large portions of its range (Barry and Shaffer, 1994; Sorenson, 1994; Fisher and Shaffer, 1996). In 1991, we began a long-term study of *A. californiense* at a breeding pond in Monterey County. In addition to surrounding the pond with a permanent drift fence and pitfall traps, we have individually marked all captured breeding adults and newly metamorphosed juveniles and used skeletochronology to further investigate the age structure of cohorts of breeding adults. Our goal in this paper is to describe the life history and demography of *A. californiense* at this locality and investigate the relationships among these attributes and abiotic factors. We report data from the first seven years of the study, focusing on annual variation in the timing and magnitude of breeding migrations, size and age structure of breeding adults, production of metamorphic juveniles, and rates of mortality from metamorphosis through adulthood. We discuss the implications of these results for population stability and management.

MATERIALS AND METHODS

Study site.—Our long-term study site is situated on Oak Ridge Ranch, immediately adjacent to the Hastings Natural History Reservation in the upper reaches of Carmel Valley, Monterey County, California (36°20′N; 121°33′W; elevation 490 m). Blomquist Pond (BP) is a 0.07-ha pond constructed in the early 1970s by damming an intermittent creek. BP was initially created as a water source for cattle, but since 1991 cattle have been excluded by a fence. The edges of the pond are sparsely vegetated, and the pond bottom is mostly open mud and sand. The pond is approximately 2 m at its deepest point and dries completely each summer. North of BP are 12 additional ponds, also supporting breeding populations of *A. californiense* (Trenham, 1998). Distances from BP to these ponds range from 550–3000 m. The surrounding terrain is hilly, and the landscape is dominated by open grassland with scattered valley (*Quercus lobata*) and blue (*Q. douglasii*) oaks and stands of mixed deciduous woodland. Weather data were logged hourly at a point 500 m south of BP and at the same elevation.

Census methods.—In December 1991, we completely encircled BP with a 156 m drift fence of 25 cm tall aluminum flashing with 35 pairs of 2-liter pitfall cans irregularly spaced on each side of the fence. We checked pitfall cans each morning and recorded all captures. All *A. californiense* captured at the fence were marked for individual identification. In the first year, we marked adults by toe clipping, but in all subsequent years, we used passive integrated transponder (PIT) tags. Between October 1995 and April 1997, we also clipped single toes from adults for use as skeletochronological material. In 1993, of the newly metamorphosed juveniles that we marked and released alive, 100 were PIT tagged and 196 were toe clipped; in all other years, we marked new juveniles by toe clipping.

We recorded trap number, ID, reproductive status (adult or juvenile), and sex (adults only) for all captured *A. californiense* and transported individuals to the Hastings laboratory in coolers for measurement and marking. We measured snout–vent length (SVL) from the tip of the snout to the anterior end of the vent, total length (TL), and mass for all individuals. In October 1996, we began sedating all salamanders in a 0.03% solution of Benzocaine prior to measurement and marking (Vanable, 1985). We released adults on the opposite side of the fence, at the point at which they were captured. We released juveniles at the entrances to ground squirrel burrows on the outside of the fence (Loredo et al., 1996). All animals were released within 24 h of capture.

Skeletochronology.—We prepared skeletochronological samples following the methods of Leclair and Castanet (1987) with the following modifications. We stored clipped toes at −80 C or in 70% ethanol and subsequently fixed them in 10% buffered formalin for at least 48 h. We removed formalin by several washes with deionized water and manually stripped bones of soft tissue; phalanges furthest from the toe tip, generally the third and/or second, were used. Phalanges were decalcified in 3% nitric acid for 2 h, washed with distilled water, and dehydrated in a standard alcohol series. We embedded samples in paraffin, and made 18 μm cross-sections through the diaphysis that were then mounted on individual glass slides. We cleaned samples of paraffin, rehydrated, and stained them for 20 min with Harris' hematoxylin. Finally, we destained samples to optimal intensity and counted LAG at 250× magnification.

LAG were clearly visible in most of our samples. We first inspected samples from five known-age individuals that we had marked as emerging metamorphs and recaptured as breeding adults, to determine the characteristics of annual and false LAG. False LAG (Caetano et al., 1985) occurred commonly but were much lighter and less continuous, and no endosteal resorption was observed (J. Castanet, pers. comm.). PCT made counts of LAG for each sample on two separate occasions, always blind to sample identity. Finally, we reinspected any samples for which counts differed on the two occasions, and a ''consensus'' count was reached or the sample was discarded.

To estimate error in this technique, we made LAG counts using the same methodology on a sample of 23 known-age samples mixed with 23 randomly chosen individuals that had only been captured as breeding adults and had already been aged. We compared LAG counts with actual ages for known-age samples and with previous LAG counts for the other samples.

Data treatment.—We report data for seven years, defined as 1 September to 31 August. Years are referred to throughout by the later year because this is when most adults were captured and all juveniles metamorphosed (i.e., 1991/1992 = 1992). We used parametric statistics where the required assumptions were met and used a significance level of $\alpha = 0.05$ for statistical tests. We report means ± SD unless otherwise noted.

All drift fence studies report that migrating individuals sometimes enter or exit ponds without being captured at the fence (Semlitsch, 1983, 1985; Gill, 1985). These events are referred to as trespasses. At BP, trespass was likely facilitated during periods of flood, when sections of the drift fence were displaced by high inlet and outlet flows, and throughout the year by ground squirrel burrows that extend beneath the fence. To estimate population size confidently, it is necessary to determine the probability that animals that were present escaped detection. Because the probability that an individual came to the pond and escaped capture during a given breeding season is presumably equal to the rate at which individuals crossed the fence without being captured, raised to the power of the number of capture opportunities, we calculated (1) observed inward and outward trespass rates for each year and (2) the mean minimum number of times each individual crossed the drift fence (Gill, 1985).

An example of an observed trespass would be an animal that was last released on the inside of the drift fence and next captured on the outside of the drift fence. Observed trespasses include all single, triple, etc., trespass events. We estimated annual trespass rates as the proportion of all recaptures that would have required the individual to cross the drift fence without being recaptured. Double, quadruple, etc., sequential trespasses are undetectable because individuals would be recaptured on the side of the fence where they were last released, but if such events are likely to occur frequently, they should be estimated. Assuming constant annual trespass rates, the probability of undetectable trespasses can be estimated as the square of the observed trespass rates. Because many individuals released outside the fence were leaving for the season, and thus invulnerable to recapture, only individuals that subsequently reentered the pond were included when calculating outgoing trespass rates.

We used each individual's annual history of captures to calculate the minimum number of times they had crossed the drift fence, assuming that (1) no undetected trespasses occurred and (2) all animals initially arrived from areas outside the drift fence. The mean number of crossings was also corrected for the influence of undetectable trespasses by multiplying the calculated mean number of crossings by the square of the observed trespass rate and adding this value to the calculated mean number of crossings. Based on the above assumptions, we estimated adult sampling efficiency as $e = [1 - (a + a^2)^c]$, where e = sampling efficiency, a = observed trespass rate, b = mean number of crossings, and $c = (b \cdot a^2)$.

Each year some of the newly emerged metamorphs also bypassed the fence without being captured. We often captured unmarked trespassers in cans on the outside of the fence along with individuals that had been captured and marked as they left the pond. We estimated each season's juvenile sampling efficiency as $e = [1 - (x/y)]$, where e = sampling efficiency, x = the number of unmarked juveniles captured on the outside of the drift fence, and y = the total number of marked and unmarked juveniles captured outside.

To investigate the timing and cues for breeding migrations, we calculated total weekly and monthly captures of arriving and departing males and females for each breeding season.

TABLE 1. BLOMQUIST POND DRIFT FENCE SAMPLING EFFICIENCIES FOR ADULT AND NEWLY METAMORPHOSED *Ambystoma californiense*. Trespass rate is the observed frequency at which individuals crossed the fence without being captured, number of crossings is the mean number of times individuals entered and exited the pond annually, and sampling efficiency is the probability that an individual that was present could escape capture completely. Juvenile sampling efficiency is based on the fraction of total juveniles captured on the outside of the drift fence that were marked. * juveniles had not yet emerged at time of writing.

	1992	1993	1994	1995	1996	1997	1998	Mean
Males								
Trespass rate	0.23	0.38	0.12	0.22	0.23	0.26	0.14	0.22
No. of crossings	3.8	3.3	3.9	3.3	3.2	2.7	2.3	3.2
Efficiency	0.99	0.91	1.00	0.99	0.99	0.96	0.99	0.98
Females								
Trespass rate	0.19	0.23	0.09	0.15	0.25	0.19	0.13	0.18
No. of crossings	3.0	2.9	2.9	2.5	2.5	2.8	2.5	2.7
Efficiency	0.99	0.98	1.00	0.99	0.95	0.99	0.99	0.98
Juveniles								
Efficiency	0.79	0.69	0.45	0.56	0.84	0.80	—*	0.69

Capture totals included only the initial entry and final exit for each individual in each year. We also calculated the following mean climatic variables for each time interval: total daily rainfall, maximum daily temperature, minimum daily temperature, mean daily relative humidity, and mean soil temperature at 50 cm. To account for the impact of trespasses, we corrected annual population totals for breeding males and females by dividing the census total by the annual sex-specific sampling efficiency (Table 1).

We captured unmarked metamorphs throughout the summer and during the following fall and winter. Therefore, we calculated total annual production as the number captured in the summer plus the number captured inside the drift fence during the following fall and winter. We excluded unmarked fall and winter animals captured outside the fence from census totals, because it is likely that some of these individuals were dispersing from nearby ponds (PCT, pers. obs.). To correct for trespasses, we divided census totals by the calculated juvenile capture efficiency (Table 1).

We calculated survivorship for cohorts of salamanders initially marked in the same year as either breeding adults or emerging metamorphs. The portion of the initial cohort surviving in each subsequent year was calculated as the number of individuals recaptured in that year and any later years, so as to account for survivors that may have skipped breeding opportunities. The number of years in which each individual was captured was also calculated to determine how many times individuals breed during their lives. Finally, we calculated the frequency at which known survivors skipped breeding opportunities for each cohort over all years.

RESULTS

Capture efficiency.—The observed rate of trespass calculated for adult recaptures over all seven years combined was 20% (Table 1). No difference was detected between in-coming and out-going trespass rates (paired *t*-test: $t = 0.33$, df = 6, $P = 0.75$), but trespassing males were detected at a higher rate than females (paired *t*-test: $t = 2.73$, df = 6, $P = 0.03$). Because we detected no consistent differences between in-coming and out-going rates, we calculated annual sex-specific trespass rates by pooling inward and outward movement data. The minimum number of times that individuals entered or exited the pond during a given breeding season ranged from 1 to 15 ($\bar{x} = 3.1 \pm 2.1$) and was generally higher for males than females (paired *t*-test: $t = 2.7$, df = 6, $P = 0.03$; Table 1). Because the probability that an individual will escape detection in a given year declines geometrically with an increasing number of capture opportunities, the tendency of *A. californiense* to enter and exit the pond multiple times during the breeding season minimized the impact of high trespass rates on population estimates. Even accounting for undetectable trespasses, more than 95% of the breeding population was captured in all but one year (Table 1).

Newly metamorphosed juveniles trespassed the drift fence in proportions roughly similar to the overall adult trespass rate (0.31 vs 0.21, respectively). However, because the vast majority of new metamorphs do not exit and reenter the

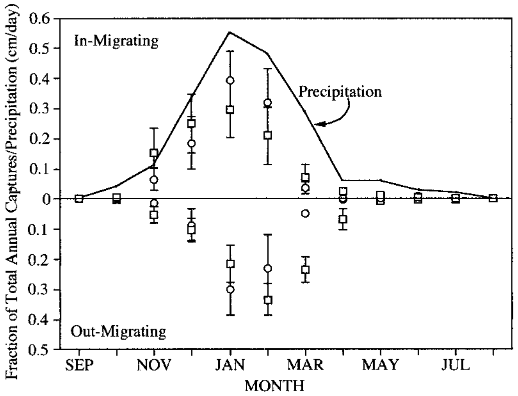

Fig. 1. Mean ± 2 SE monthly fraction of total annual captures of male (squares) and female (circles) *Ambystoma californiense* at Blomquist Pond over seven seasons (1992–1998). Line represents monthly precipitation means normalized to centimeters per day.

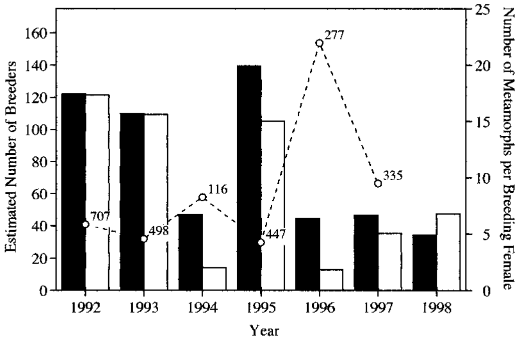

Fig. 2. Annual breeding activity and reproductive success of *Ambystoma californiense* at Blomquist Pond. Bars show numbers of total breeding males (solid) and females (open) corrected for sampling efficiency; line illustrates numbers of juveniles surviving to metamorphosis per breeding female; point labels are corrected estimates of total metamorph production.

drift fenced area, trespass has a more dramatic impact on estimates of total numbers of metamorphic juveniles (Table 1).

Breeding migrations.—Adults arrived at BP throughout the rainy winter months, but the largest numbers were always captured as the first soaking rains of the season filled the pond. A few adults arrived at the pond with the first fall rains in October or November, but the majority of adult immigration generally occurred from December to February (Fig. 1). Males primarily arrived at the pond in December and January and departed in February and March, whereas female arrival and departure both generally peaked in January. In stepwise regression analyses of the relationship between total weekly captures and all measured climatic variables, mean daily rainfall was the only variable to enter into the model for incoming males ($F_{1,302}$ = 148.4, $P < 0.001$) and females ($F_{1,302}$ = 230.6, $P < 0.001$), and outgoing females ($F_{1,303}$ = 129.1, $P < 0.001$); mean soil temperature ($F_{4,299}$ = 34.1, $P < 0.001$), mean minimum temperature ($F_{4,299}$ = 10.9, $P < 0.001$), and mean daily rainfall ($F_{4,299}$ = 8.0, $P < 0.001$) all entered the model for outgoing males. Males consistently arrived at the pond before females and remained four times longer within the area of the drift fence (days at pond: $\bar{x}_M = 44.7 \pm 32.5$; $\bar{x}_F = 11.8 \pm 15.2$; paired *t*-test: $t = -11.8$, df = 6, $P < 0.001$). Although males that arrived earlier in the season generally remained for longer periods, this pattern was much less striking for females (correlation: $r_M = -0.47$, n = 212; $r_F = -0.15$, n = 158).

Breeding population structure.—Estimated annual populations of breeding adults at BP varied from 57–244 (Fig. 2). Only in 1994 and 1996 did the sex ratio differ significantly from 1:1, with males outnumbering females more than three to one in these two years (χ^2, both $P < 0.005$). Male bias in annual sex ratios was related to the date that BP filled but not total annual rainfall (stepwise regression: variables entered = Julian date full, $F_{1,5}$ = 12.2, P = 0.02). This pattern resulted from a higher proportion of surviving females skipping breeding opportunities in years with later rainfall (see below). Even including years with strong male bias in breeding aggregations, the total numbers of individual adult males and females marked over all seven years of the study was not significantly different from 1:1 (M = 367; F = 342; χ^2 = 0.44, df = 1, $P > 0.05$).

Masses of incoming adults varied more than fivefold (14.2–80.5 g) and snout–vent length (SVL) of the largest individuals was almost twice that of the smallest (75–130 mm). Analysis of variance of the effects of year, sex, and status (i.e., new vs experienced breeder) on SVL, indicated significant effects of year and status and a significant interaction between these two variables (Table 2). These results suggest that year-to-year size variation is strongly affected by the proportion of the population breeding for the first time, although other data indicate that age structure alone cannot explain among-year size differences (see below).

Juvenile production.—Total annual production of metamorphic juveniles ranged from 122–775 ($\bar{x}$ = 421 ± 227), whereas mean juvenile produc-

TABLE 2. ANALYSIS OF VARIANCE OF THE EFFECTS OF YEAR, SEX, AND STATUS ON ADULT BODY SIZE (SVL). Year = breeding season, Sex = male or female, Status = new adult or recaptured adult marked in an earlier breeding season. Data from 1992 were excluded from the analysis because all individuals captured were "new" by definition. *** $P < 0.001$.

	F	DF
Year	9.4***	5,502
Sex	0.3	1,502
Year*Sex	1.8	5,502
Status	19.1***	1,502
Year*Status	5.3***	5,502
Sex*Status	0.0	1,502
Year*Sex*Status	1.1	1,502

tion per breeding female ranged from 4.7–21.9 ($\bar{x} = 8.5 \pm 6.1$). We used stepwise linear regression to evaluate the relationship among several abiotic and biotic independent variables (total rainfall, date BP filled, hydroperiod, estimated number of breeding females, and total female biomass) and annual variation in both total metamorph production and mean per-female metamorph production. Total female biomass was the only independent variable to enter the model for total metamorph production ($F_{1,4} = 27.8$, $P = 0.006$), whereas hydroperiod was the only variable to enter the model for per-female metamorph production ($F_{1,4} = 5.1$, $P = 0.09$).

Pitfall captures of the first metamorphic juveniles ranged from 2 May to 6 June, and juvenile captures always continued for some time after BP dried completely (Fig. 3). The timing of juvenile emigration varied significantly among years (ANOVA: $F_{5,1526} = 397$, $P < 0.001$; Fig. 3), and mean date of emigration was related directly to pond drying date (regression: $R = 0.78$, $n = 6$, $P = 0.004$; Fig. 3). Metamorph size at emergence ranged from 41–78 mm SVL ($\bar{x} = 60.3 \pm 6.5$ mm) and 2.2–17.4 g ($\bar{x} = 8.2 \pm 2.9$ g), and varied significantly among years (ANOVA: SVL: $F_{5,1526} = 143$, $P < 0.001$; mass: $F_{5,1526} = 145$, $P < 0.001$). Emigrating juvenile size generally declined throughout the summer and was positively related to the number of days prior to pond drying (regression: $R_{SVL} = 0.31$, df = 6, $P < 0.001$; $R_{mass} = 0.24$, df = 6, $P < 0.001$). Stepwise linear regression of mean metamorphic SVL on all annual biotic and abiotic variables revealed no significant relationships, but multiple regression on all possible combinations of these variables suggested that metamorphic size is dependent upon the contradictory influences of pond drying date and total seasonal rainfall ($F_{2,3} = 39.8$, $P = 0.007$). The regression equation for this relationship was SVL = 36.7 + 0.20 (Julian date dry) − 0.30 (cm total rainfall).

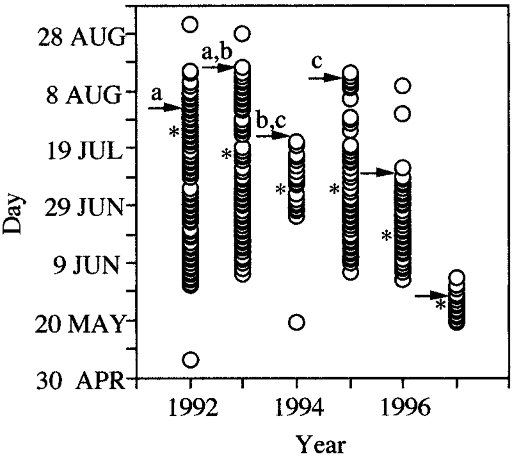

Fig. 3. Timing of summer captures of newly emerged metamorphic *Ambystoma californiense* at the Blomquist Pond drift fence. Asterisks indicate median date of "emergence," arrows mark the date on which the pond dried completely, and years marked with the same letter exhibited similar timing of emergence (all Sheffé's $P > 0.05$).

Age structure.—We recaptured 45 individuals that were marked as newly emerged metamorphs at BP returning as breeding adults. Minimum age at first breeding was two years for males and three years for females, but average age at first breeding was not significantly different between the sexes ($\bar{x}_M = 3.8 \pm 1.1$, $\bar{x}_F = 4.4 \pm 1.2$; unpaired $t = 1.5$, df = 43, $P = 0.15$). We found no significant relationship between size at emergence and age at maturity or size at maturity (mass and SVL), but a significant positive relationship between adult SVL and age was evident for females (regression: $F_{1,18} = 9.3$, $P = 0.007$).

Our age estimates based on skeletochronological preparations of 23 known-age samples did not differ significantly from actual ages, and estimated age was significantly correlated with known age (Table 3). The reproducibility of the technique was confirmed by blindly estimating ages for a set of 23 unknown-age samples on two separate occasions. For these duplicate efforts, there was no difference in the means or variances of estimates, and individual ages were significantly correlated between trials (Table 3).

Age estimates for samples of breeding *A. californiense* collected in 1992, 1996, and 1997 ranged from 3–11 yr for males and 2–11 yr for females (Fig. 4). Samples from 18 or more randomly chosen individuals of each sex were aged

TABLE 3. TESTS OF ACCURACY (KNOWN AGE) AND REPEATABILITY (UNKNOWN AGE) OF AGE ESTIMATION USING SKELETOCHRONOLOGY. Reported values are means ± SD. * $P < 0.05$.

Sample	n	Actual age	Estimate	*t*-paired	F	Z
Known age	23	4.26 ± 0.75	4.48 ± 0.90	1.15	0.70	2.0*
		(Trial 1)	(Trial 2)			
Unknown age	23	5.48 ± 1.59	5.48 ± 1.62	0.0	0.97	2.7*

for 1992 and 1997, and for both of these years, the age distributions of males and females were not detectably different (Kolmogorov-Smirov: both $P > 0.99$). There was also no difference in age distributions among years for total samples (Kruskal-Wallis: $H = 2.0$, $P = 0.4$). Four- and five-year-olds comprised more than half of each annual sample (Fig. 4). This observation, combined with the above reported ages at first breeding, suggests that in most years a high proportion of individuals captured at BP were breeding for the first time. There was a weak positive regression relationship between age estimates and SVL for both males ($F_{1,65} = 9.1$, $R = 0.35$, $P = 0.004$) and females ($F_{1,50} = 8.2$, $R = 0.37$, $P = 0.006$).

Survivorship.—A universal difficulty for estimating survivorship is differentiating migration from mortality. Of the individuals that we marked as new metamorphs or breeding adults at BP and recaptured in 1996, 1997, and 1998, roughly 20% were recaptured at a breeding pond 580 m from BP (Trenham, 1998). However, because our attempts to detect emigrants only began in 1996, we excluded recaptured emigrants from survival analyses. Of the new metamorphs that we marked and released in 1993, 1% of the PIT-tagged individuals and 5% of the toe-clipped individuals have been recaptured as adults. These results suggest that, for juveniles, PIT tags are either lost or induce mortality more commonly than toe clipping.

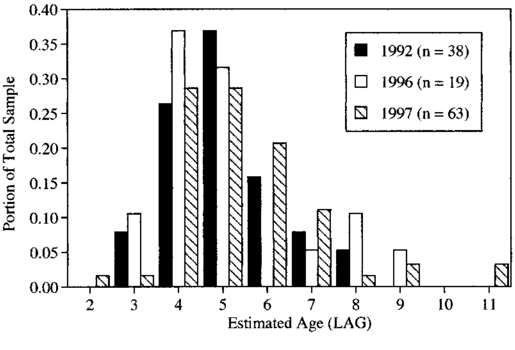

Fig. 4. Skeletochronological age structure profiles for breeding adult *Ambystoma californiense* at Blomquist Pond.

Both because the subadult period can be extremely protracted and because the 1992 season produced the greatest number of new metamorphs, we were best able to estimate survivorship to maturity for individuals that metamorphosed in the first year of the study. Of 495 metamorphs marked and released alive in the summer of 1992, only 3.4% have been recaptured as breeding adults. In comparison, 8.5% of the 130 individuals from this cohort that were captured during the following fall and winter have returned as adults. A similar pattern is evident for 1993 metamorphs (2.4% summer vs 11.6% fall and winter). This suggests that mortality of new metamorphs during their first summer is high (> 50%), which is not surprising given that daytime temperatures commonly exceeded 37 C and total monthly precipitation for August and September averaged less than 1 mm in all years.

The tendency of *A. californiense* adults to skip breeding in certain years makes precise determination of survivorship difficult. In Table 4, we report the percentages of each cohort known to be surviving in each subsequent year. The only detectable pattern was significantly lower survivorship in the first year following marking (unpaired *t*-test: $t = 3.0$, df = 34, $P = 0.005$). Mean estimated annual survivorship of females was slightly higher and more variable, than was male survivorship (Table 5). In contrast, recapture data indicated that on average males attempted to breed more times during their lives (unpaired *t*-test: $t = -3.7$, df = 571, $P < 0.001$; Table 5). Although only statistically significant in later rainfall years (unpaired *t*-test: $t = 0.3$, df = 5, $P = 0.05$), the observation that surviving females skipped breeding opportunities at a higher rate than males ($\bar{x}_F = 0.56 \pm 0.38$; $\bar{x}_M = 0.39 \pm 0.24$) explains much of this difference. For example, none of the 1992 females was recaptured during the later rainfall years of 1994 or 1996, but 22 and 10 of the 1992 males were captured in each of these years, respectively (Table 4). We found no relationship between size

TABLE 4. PERCENTAGES OF KNOWN SURVIVORS IN EACH YEAR FOLLOWING MARKING, FOR COHORTS OF BREEDING ADULT *Ambystoma californiense* INITIALLY CAPTURED IN THE SAME YEAR.

Year first marked		Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
1992	Males	55.5	31.9	22.7	11.8	5.0	3.4
	Females	42.1	15.7	15.7	7.4	7.4	2.5
1993	Males	33.3	25.5	9.8	5.9	3.9	
	Females	13.6	12.1	6.1	3.0	1.5	
1994	Males	38.1	19.0	4.8	0.0		
	Females	33.3	16.7	16.7	16.7		
1995	Males	32.0	26.0	12.0			
	Females	14.5	14.5	10.8			
1996	Males	19.0	4.8				
	Females	11.0	11.0				
1997	Males	6.9					
	Females	0.0					

at first capture and number of years captured, suggesting that mortality is not strongly dependent on size in adult *A. californiense*.

DISCUSSION

Population viability.—For a population to be stable, the lifetime reproductive output of an average female must yield one male and one female offspring that survive to breed. During this study, the average female bred 1.4 times and produced 8.5 young that survived to metamorphosis per reproductive event, resulting in roughly 12 lifetime metamorphic offspring per female. For juvenile production at this rate to maintain this population, survival from metamorphosis to breeding would have to be 18.2%. Because our best estimate of survival from metamorphosis to maturity is less than 5%, mean per-female reproduction was below simple replacement in all six years. Thus, it would appear that, in the absence of immigration or drastically fluctuating demographic parameters, this population would be doomed to local extinction. This diagnosis is consistent with the decline in numbers of breeding adults captured over the period of this study. However, because population turnover in this species often occurs on a time scale of 10 or more years, any conclusions about population stability would be premature (Connell and Sousa, 1983).

Prior studies of ambystomatid salamanders indicate that the demographic parameters calculated for *A. californiense* at BP are consistent with eastern species. Over 16 years, Semlitsch et al. (1996) observed annual juvenile production per breeding female ranging from 0 to 30 in *A. opacum*, *A. tigrinum*, and *A. talpoideum*. Studies at other localities reported similar reproductive outputs (*A. maculatum*, Shoop, 1974; Stenhouse, 1987; *A. californiense*, Loredo and VanVuren, 1996). The consistency of these rates is particularly striking given that these examples encompass species with highly variable reproductive capacities [maximum egg counts: *A. opacum* = 200 (Scott, 1994); *A. californiense* = 1340 (PCT, unpubl. data)]. Semlitsch et al. (1988) found 20% survivorship to breeding in a single cohort

TABLE 5. ANNUAL SURVIVORSHIP AND ESTIMATED NUMBER OF LIFETIME REPRODUCTIVE EVENTS OBSERVED FOR *Ambystoma californiense*. Values are means ± 1 SD. Mean survivorship was calculated using the data from Table 5, and numbers of reproductive events were calculated by totaling the number of years in which each individual was captured at BP.

	Annual survivorship			Number of years captured			
Cohort	n	Males	Females	n	Males	n	Females
1992	6	0.58 ± 0.10	0.60 ± 0.31	121	1.88 ± 0.98	119	1.57 ± 0.84
1993	5	0.55 ± 0.18	0.51 ± 0.27	66	1.39 ± 0.60	51	1.15 ± 0.40
1994	4	0.28 ± 0.21	0.71 ± 0.34	12	1.52 ± 0.75	21	1.58 ± 1.00
1995	3	0.53 ± 0.25	0.63 ± 0.44	83	1.36 ± 0.56	100	1.18 ± 0.47
Ave.	18	0.50 ± 0.20	0.60 ± 0.31	282	1.59 ± 0.81	291	1.36 ± 0.69

of metamorphic *A. talpoideum*, and over five years Scott (1994) documented return rates of 6% and 21% for *A. opacum* raised at high and low larval densities, respectively. Less lengthy studies have documented 4% of marked metamorphs breeding at two years for *A. californiense* (Loredo and VanVuren, 1996), and 1% returning at two years and 5% at three years for *A. tigrinum* in South Carolina (Semlitsch, 1983). Unfortunately neither of these studies reported data for later years. Other studies with estimates of adult survivorship also indicate that, even though ambystomatid salamanders can be long-lived, the vast majority of females breed only once or twice in their lifetimes (Husting, 1965; Williams, 1970; Raymond and Hardy, 1990).

Accepting that annual reproductive success of ambystomatid salamanders appears to be universally low (< 30 metamorphs produced per reproductive female), it seems likely that regulation of these populations may be more dependent upon terrestrial survival than previously suspected. It is difficult to assess the relative level of adult mortality at BP because of few comparable studies, but, relative to available published estimates, sexual maturity comes late and survivorship from metamorphosis to breeding is low. Although Loredo and VanVuren (1996) found 4% of 1992 juveniles returning at two years, we detected less than 0.5% of 1992 juveniles returning at two years, even though emerging metamorphs at BP were larger than those observed by Loredo and VanVuren (SVL: 64.0 ± 4.6 mm vs 58.0 ± 3.4 mm). Because we found no relationship between adult size and survivorship, there is no reason to suspect that mortality of subadults should differ markedly from adults. If we assume that survivorship of all metamorphs is 50% annually and that surviving individuals mature synchronously at four years, then only 6.5% (0.54) of the cohort would survive to maturity. Thus, low overall survival to maturity at BP may reflect the extended subadult stage at this site.

Taylor and Scott (1997) modeled the population dynamics of *A. opacum*, including the well-documented negative effects of high larval density on adult demographic parameters (Scott, 1994). This demographic model suggests that high survival of terrestrial phases (> 70% annually) is essential for maintenance of a completely isolated population. Previous mark-recapture studies of ambystomatids followed for at least three seasons have documented annual adult survivorship ranging from 10% to more than 90% with most averaging more than 60% (Husting, 1965; Whitford and Vinegar, 1966; Raymond and Hardy, 1990). At BP, apparent survivorship to year 1 (Table 4) was noticeably higher for the 1992 breeding cohort than for all subsequent cohorts, whereas survivorship to later years was similar among all cohorts. Because of the way in which cohorts were defined and survivorship was calculated, the 1992 cohort contained a mixture of first-time breeders and experienced breeders, whereas later cohorts were predominantly composed of first-time breeders. A similar pattern of survivorship was also observed by Husting (1965) and suggests elevated rates of mortality or emigration in first-time breeders, although in our case, alternative explanations such as PIT-tag-induced mortality or tag loss cannot be ruled out. This heterogeneity of survivorship suggests that demographic studies should be of sufficient duration to quantify the divergent demography of first-time and experienced breeders.

Breeding population structure.—Annual patterns of arrival for adult *A. californiense* at BP closely resemble those previously reported for other winter-breeding ambystomatid species (*A. tigrinum*, Semlitsch, 1983; *A. talpoideum*, Semlitsch, 1985), with significant migrations generally beginning in November or December and peaking in January. Weekly captures of in-migrating males and females were most strongly dependent upon rainfall. Although temperature also impacts migration activity, it is difficult to separate the effects of these two cues because the months during which temperatures are favorable for migration are also those in which almost all precipitation falls (Semlitsch, 1985). Early captures were always dominated by males, but individuals of both sexes arrived at the pond throughout the season.

Amphibian populations that exhibit consistently male-biased sex ratios appear to result from earlier maturation of males (Berven and Grudzien, 1990; Scott, 1994) and/or higher mortality of adult females (Husting, 1965). The BP population exhibited similar ages at maturity and overall rates of mortality between the sexes, and thus the approximately equivalent overall sex ratio is consistent with the maturation and survival interpretations of previous studies. We only observed significant sex ratio deviation in the two years when the pond filled late, and Loredo and VanVuren (1996) observed the identical pattern, with strong male bias in 1994 but not in 1993. Because large numbers of previously marked females often reappear in subsequent years, this phenomenon is apparently the result of higher proportions of females than males foregoing breeding in dry years (Semlitsch et al., 1996; present study).

Amphibian biologists have often attempted to draw inferences about population structure and historical recruitment events from size-frequency distributions (Bruce, 1976; Semlitsch, 1983), but highly variable growth rates and long lifespans challenge the validity of this approach for most species. We observed statistically significant variation in annual size distributions of breeding adults because of the large sizes of individuals in the 1993 and 1994 cohorts. Unfortunately, the majority of breeding adults captured during the course of these censuses emerged as metamorphs prior to the inception of this study; thus, determination of the cause(s) of size variation is impossible. The weak relationship between size and age for individuals of known age, as well as those for which ages were estimated using skeletochronology, cautions further against using size as a surrogate for age structure in breeding adults. Without marked individuals or independent age estimates, the only value of size data would seem to be for estimation of annual reproductive input, assuming body size and clutch size are positively correlated, or as a starting point from which to compare local populations and develop hypotheses regarding population regulation, assuming adult size and population density are correlated.

Skeletochronology is a potentially powerful tool and is undoubtedly more reliable than size distributions in many cases. However, without known age material for validation of this technique on a species-by-species basis, one must consider LAG counts to be no more than relative age estimates of questionable consistency (Hemelaar, 1985). Although in our study the overall accuracy and repeatability of the technique were high, only about half of the samples were assigned identical LAG counts upon successive inspections. However, more than 75% of those that varied between counts were within ± 1 LAG. Presently mark-recapture studies remain the most accurate means for aging amphibians, and skeletochronological studies should validate the method using known age material or other approaches (e.g., Kazmer, 1986).

Metamorph production.—Total juvenile production at BP was most strongly related to the total biomass of breeding females, which is an indicator of the total number of eggs deposited (Semlitsch, 1985; Scott, 1994; PCT unpubl. data). This is in sharp contrast to the extensive data of Semlitsch et al. (1996), indicating that juvenile production is primarily determined by hydroperiod. Separating the effects of hydroperiod and female biomass in the BP data is difficult because of the high degree of correlation between these two variables. The fact that BP is a deep pond that contains water long enough to support larvae to metamorphosis even in relatively dry years like 1994, whereas the pond studied by Semlitsch et al. (1996) frequently dried before any larvae metamorphosed, may explain this difference. Shallow natural vernal pools within 1 km of BP frequently dry before *A. californiense* reach sizes typical of metamorphs (PCT, HBS unpubl. data), and in these habitats, recruitment is probably more dependent on hydroperiod.

Explaining the influence of the combined effects of pond drying date and total annual rainfall on SVL at metamorphosis is more difficult. The positive influence of later pond drying dates on mean SVL is not surprising, but the negative relationship with annual rainfall would appear contradictory. Because there was no similar relationship between size and total number of females or number of metamorphic juveniles, this relationship does not seem to be the result of larval density dependence. We suspect that an unmeasured environmental variable(s) likely to influence larval growth rates and correlated with annual rainfall, such as water temperature or flow rate through the pond, is the most probable explanation. Because of high degrees of correlation between abiotic and biotic variables potentially influencing the larval environment, experimental manipulation is the only confident means to determine the relative contribution of environmental conditions to metamorph production and body size (Semlitsch, 1985; Scott, 1990).

In other species, the aquatic environment strongly influences larval survival and size at metamorphosis, which can in turn affect subsequent terrestrial survival and age at maturity (Semlitsch et al., 1988; Berven, 1990; Scott, 1994). In our samples, we found no relationship between metamorph size and age or size at first breeding. Our low overall return rates may limit our power to detect relationships that actually exist, or it may be that the postmetamorphic environment at this locality exerts a stronger influence on adult traits than the larval environment. The local distribution of *A. californiense* in Monterey County would appear to support this possibility. As one enters the Arroyo Seco drainage, just 8 km southeast of BP, the habitat becomes even hotter and drier, and this appears to constitute the regional distributional limit of the species (Stebbins, 1985). Certainly the extreme summer climate, with negligible precipitation and temperatures commonly exceeding

35 C from June to October, makes the terrestrial climate regime a potentially critical factor.

Management implications.—Demographic studies of this and other ambystomatid salamanders indicate that incidents of high reproductive success are relatively rare and that high survivorship of transformed individuals is critical for long-term viability of populations. Highly variable reproductive success also suggests that isolated populations would be vulnerable to stochastic local extinction, although long lifespans may reduce this threat. Metapopulation theory suggests that species occupying patchy habitats may exist in a balance between local extinction and recolonization (Levins, 1970) or that unproductive sink patches may be maintained by consistent immigration from source patches (Pulliam, 1988). Over the time scale of this study, BP apparently was a reproductive sink in all years. Source-sink dynamics have been suggested as explaining patterns of habitat occupancy for several amphibian species, although in these systems individual ponds appear to shift between source and sink status over time (Gill et al., 1983; Sinsch, 1992).

Although *A. californiense* still occurs throughout most of its historic range and can be locally common, there has long been concern about its future because of the widespread loss of its breeding habitat (Sorenson, 1994). Intensive human habitat alteration over the past 150 years has resulted in the loss of approximately 75% of the historic vernal pool breeding habitat of *A. californiense* (Holland, 1998). Because the remaining habitats are not formally protected and occur primarily on private property, loss and fragmentation of remnant vernal pool habitats continues. Our work indicates that without detailed study it may be impossible to differentiate sink and source habitats (Kadmon and Shmida, 1990; Watkinson and Sutherland, 1995). In the absence of specific knowledge of the contributions of individual breeding habitats to a regional population, protection of areas with multiple ponds would seem essential to the long-term viability of this species.

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