

# Delayed life history effects, multilevel selection, and evolutionary trade-offs in the California tiger salamander

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**Abstract.** Delayed life history effects (DLHEs) occur when fitness in one life stage affects fitness in subsequent life stages. Given their biphasic life cycle, pond-breeding amphibians provide a natural system for studying DLHEs, although these effects are not restricted to species with biphasic life histories. In this study, we used multiple mark–recapture techniques enabled by a large trapping array to monitor components of fitness and resulting DLHEs in a population of the endangered California tiger salamander (*Ambystoma californiense*). We found that DLHEs are prominent across all life stage transitions and that there is variation in whether selection acts primarily at the individual or cohort level. We also demonstrated that there is more than an order of magnitude variation in mean cohort fitness, providing tremendous variation for DLHEs to act upon. We documented an evolutionary trade-off between mass at emergence and date of emergence, which may play a role in maintaining the variation in mass (fitness) at emergence. A literature review revealed that such high levels of intercohort variation occur in many other pond-breeding amphibians, and that appropriately documenting the magnitude of intercohort variation requires long-term studies (roughly two population turnovers). Given the profound effect that DLHEs can have on population dynamics, quantifying intercohort variation in mean fitness and the level(s) at which selection acts will be very important for developing accurate models of population dynamics. In general, when developing models of population dynamics, more attention should be paid to variation in mean fitness and not just variation in total numbers.

**Key words:** *Ambystoma californiense*; California tiger salamander; contextual analysis; date of emergence; intercohort variation; Jepson Prairie Preserve, California, USA; mass at emergence; pond-breeding amphibian; population turnover; selection gradient.

## INTRODUCTION

Many taxa, but most notably holometabolous insects and many amphibians, have complex life cycles. Given the numerical dominance of such species on earth, it is important to understand how their populations are regulated. In particular, we would like to know whether density dependence occurs in one or many stages and how fitness in one stage affects fitness in subsequent ones. This latter problem constitutes the general purview of delayed life history effects (DLHEs; Beckerman et al. 2002), which are known to create limit cycles in population size (Leslie 1959, Prout and McChesney 1985). Such fluctuations have been observed in many amphibian populations, but they are usually attributed to climatic effects (Pechmann et al. 1991). In fact, DLHEs and climatic variation can act synergistically, as the population oscillations created by DLHEs can be

entrained by stochastic factors, such as climatic fluctuation (Leslie 1959). More generally, the lessons that can be learned from the study of DLHEs are not applicable solely to species with complex life cycles, as they have also been found in humans (Lummaa and Clutton-Brock 2002) and other mammals (Albon et al. 1987, Rose et al. 1998).

Although a great deal of the work that is relevant to DLHEs has involved amphibians, it has not been referred to as such in the literature. Many species of amphibians have an aquatic larval stage followed by a terrestrial adult stage, and the ecological consequences of selection in the larval stage on later terrestrial life provide an obvious question for life history theory. The main stumbling block in learning about DLHEs in amphibians has been lack of knowledge about the terrestrial adult stage, a consequence of the secretive, often fossorial, nature of post-metamorphic terrestrial amphibians. Breeding sites are generally much smaller than their associated terrestrial habitat (Semlitsch and Bodie 2003, Rittenhouse and Semlitsch 2007), and are the one concentrated area that many members of the

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population can be counted on to visit, often at a predictable time of year. Thus, most of what is known about DLHEs in amphibians has focused on the relationship between the fitness of dispersing metamorphs leaving the breeding site and the fitness of those same individuals when they return in subsequent years as sexually mature adults (Berven 1990, Scott 1994, Berven 2009). Little is known about the fitness relationships between metamorphs and juveniles, between the multiple years as terrestrial juveniles that many amphibians require to mature, and between juveniles and adults, and yet, such studies are critical if we are to piece together a complete analysis of DLHEs in nature.

Here, we use a dispersed drift fence array to study a population of the endangered California tiger salamander (*Ambystoma californiense*; CTS; see Plate 1) during the entire surface-active season. This allows us to examine fitness relationships not only between metamorphs and adults, but also across the poorly studied intervening age-class transitions. These DLHEs may be particularly important in light of the huge variation that we observe in fitness, not only between individuals, but also between whole annual cohorts. Studies of other pond-breeding amphibians have found variation in mean cohort fitness (Semlitsch et al. 1988, Scott et al. 2007, Berven 2009), but there has been little discussion of the impact of that variation on population dynamics. We also use contextual analysis (Heisler and Damuth 1987) to determine whether variation in fitness is better modeled at the individual or cohort level, because this will inform how subsequent models of population dynamics can best be developed (Taylor and Scott 1997).

## METHODS

### *Data collection*

Our study was conducted at the Jepson Prairie Preserve, Solano County, California, USA, one of the best remaining examples of native California prairie (Küchler 1977). The most prominent feature of the preserve is Olcott Lake, a 33-ha playa pool that serves as a breeding site for CTS. Olcott Lake is ephemeral and fills to a maximum depth of ~0.6 m. Our drift fence array is located along the northeast shore of Olcott Lake. The fences of the array are evenly distributed across the upland landscape, 10–1000 m from the shoreline. The shoreline fence is continuous, covering ~17% of the pond shoreline (390 m), with pitfall traps every 10 m. The remaining fences are 10 m long and separated from each other by 90-m gaps. Pitfall traps are relatively large, 3.78-L buckets that can accommodate >20 individuals, even of the largest size class. For a more detailed description of the array see Searcy and Shaffer (2011). During the fall of 2010, a second continuous 840 m long drift fence was installed 275 m from the shoreline.

The pitfall trap array was operated May 2005–July 2011. Traps were open every rainy night between October and March and for every night during the May–July emergence period, and were monitored daily (Searcy and Shaffer 2011). We recorded the body mass, trap location, age class, and a digital image for each salamander captured. On average, CTS reach sexual maturity at four years old; however, given a fast enough growth rate, some females have been known to reach sexual maturity in three years and some males in two years (Trenham et al. 2000). We observed a few individuals (both male and female) that were mature at one year old. The location of each drift fence was determined using a Tripod 200C Ranger (Tripod Data Systems, Corvallis, Oregon, USA) with an accuracy of  $\pm 2.1$  m.

Adult and juvenile recaptures were determined using a pattern recognition program custom designed for CTS (Searcy and Shaffer 2011). Metamorphs lack discrete spots (spots take several months to fully coalesce post-metamorphosis), so recaptures were determined using either VIAT (visual implant alphanumeric tags) or VIE (visual implant elastomer; Northwest Marine Technology, Shaw Island, Washington, USA) (Jerry et al. 2001). In 2005 and 2006, 2335 metamorphs were implanted with VIAT and in 2010 another 1289 metamorphs were implanted with VIE (Appendix A).

### *Analysis*

Throughout this study, we conduct two different types of analyses when making comparisons among the five possible age-class transitions (metamorph–juvenile, metamorph–adult, juvenile–juvenile, juvenile–adult, adult–adult). Within-year comparisons compare animals to other members of their own cohort, asking whether there is a survival advantage to being larger than animals captured in the same year from the same age class. Across-year comparisons pool across cohorts, asking whether there is an advantage to being larger than animals from the same age class, regardless of the year in which they were captured. Within-year comparisons statistically remove the effects of good and bad years (current population density, rainfall, and other climatic variables being the primary drivers), whereas across-year comparisons include those effects.

In many of the following analyses, we use recapture as a proxy for survival and, thus, fitness. Presumably, some (unknown) number of animals that were not recaptured did survive, and as long as the recaptured animals were a random subset of the survivors, it should not affect our interpretations (Appendix B). The alternative is to use survival estimates from MARK (White and Burnham 1999). We ran MARK for our data, and found that the survival estimates obtained were unrealistically low compared to those from another CTS population in Monterey County (P. C. Trenham, *unpublished data*). For example, MARK provided adult “survival” estimates of 0.24/yr (in 2007) and 0.28/yr (in 2008), which

are roughly one-third of those from Monterey County. We believe that this is because our Jepson drift fences are a largely open system, surrounding one-sixth of the breeding pond, and thus many animals migrate into and out of our study area. In the Cormack-Jolly-Seber model, on which our MARK analysis was based, emigrants are lumped with mortalities, thus decreasing the estimated survival rate. Given this, we feel that in the absence of emigration rates, estimated mortality schedules from MARK are both biased and unrealistically low for this system. A more detailed analysis of this issue will be presented elsewhere.

We used standard ANOVA and regression to test for selection on mass. This started with 10 ANOVAs looking at individual-level selection, half with a blocking term for year to measure within-year selection and the other half without a blocking term to measure across-year selection. One of each type was used for each of the five between- and within-age-class transitions. We tested for cohort-level selection on mass between the metamorph and juvenile stages, using a linear regression between mean cohort mass at emergence (ME) and percentage recaptured as first-year juveniles. A contextual analysis (Heisler and Damuth 1987) was used to test whether selection on mass between the metamorph and juvenile stages was better modeled at the individual or cohort level (i.e., as a function of individual mass or as a function of mean cohort ME).

We next examined the relationship between ME and date of emergence (DE). Because DE and ME are correlated in CTS (Trenham et al. 2000), we used a correlated selection approach (Lande and Arnold 1983) to investigate individual-level selection on both traits. This test was only run for the transition between metamorph and juvenile stages, as that was the transition most likely to be affected by DE. We then examined how these traits affect distance traveled as a metamorph. This analysis utilized an ANCOVA with DE and ME as covariates and year as a class variable. We used a separate ANCOVA to look directly at the relationship between ME and DE, with ME as the response variable, DE as the covariate, and year as the class variable. To place these selection analyses in the context of CTS life history, we used an ANCOVA to test the relationship between ME and mass as a first-year juvenile, with juvenile mass as the response variable, ME as the covariate, and year as the class variable. We also used a general additive model to describe the average mass trajectory for a CTS. Here, the number of days since emergence was used to predict factorial change in mass since emergence.

Because the importance of these mass-dependent effects depends critically on the amount of standing variation in ME, we also collected data on this variation from other studies of pond-breeding amphibians. We identified, to the best of our knowledge, all studies that included data on mean cohort mass across multiple years at the same breeding site. We summarized this

variation as the ratio between the mean mass of the largest cohort and the mean mass of the smallest cohort, and plotted this ratio as a function of the number of annual cohorts available for that site. We then compared the fit of a linear vs. a quadratic regression to ask how many years of data, on average, are needed to estimate the total variation in ME for a population. For a more detailed description of the methods, see Appendix B.

## RESULTS

### *Analyses across three years at Olcott Lake*

In total, 25 344 salamanders were captured: 4247 (spring 2005), 5582 (2005–2006), 1509 (2006–2007), 1078 (2007–2008), 314 (2008–2009), 2448 (2009–2010), and 10 166 (2010–2011). We detected DLHEs across all life stage transitions in CTS in the form of selection for increased mass (Table 1), although in some cases this was only true of the across-year and not the within-year selection. This difference between across- and within-year selection was greatest for the metamorph-to-juvenile transition, where within-year selection is either neutral or in the direction of smaller mass, but across-year strongly favors larger mass. This difference is driven by strong cohort-level selection for larger mass ( $P = 0.03$ ) that overwhelms weaker individual-level selection for smaller mass ( $P = 0.17$ ). Significant cohort-level selection for larger mass was detectable with only three marked metamorph cohorts due to the exceptionally strong relationship between recapture rate and mean cohort ME ( $R^2 = 0.998$ ; Appendix B: Fig. B.1). A contextual analysis (Heisler and Damuth 1987) revealed that selection on mass at emergence across the metamorph-to-juvenile transition was modeled significantly better at the cohort level than at the individual level (multiple linear regression;  $\beta_I$  [coefficient of partial regression on the individual character] =  $-0.02$ ,  $P = 0.17$ ;  $\beta_C$  [coefficient of partial regression on the cohort mean] =  $0.24$ ,  $P < 0.001$ ).

Although there was no individual-level selection for larger body size across the metamorph-to-juvenile transition, there was significant individual-level selection for earlier emergence. A selection analysis on correlated characters (Lande and Arnold 1983) revealed that, within years, there was significant selection for earlier emergence and marginally significant selection for smaller mass (multiple logistic regression; for DE,  $P = 0.01$ ; for ME,  $P = 0.07$ ; for year,  $P < 0.001$ ). In addition, metamorphs that emerged earlier traveled farther in the metamorph stage and thus had the opportunity to sample a larger area before selecting an over-summering refuge site. An ANCOVA revealed that metamorphs that emerged earlier traveled significantly farther, although there was also significant interannual variation in this effect (ANCOVA; for DE,  $P < 0.001$ ; for ME,  $P = 0.97$ ; for year,  $P < 0.001$ ; for DE  $\times$  year,  $P < 0.001$ ; for ME  $\times$  year,  $P = 0.01$ ). When analyzed within each cohort, earlier emergence was consistently associated

TABLE 1. Effect of mass (mean  $\pm$  SE) on survival of the California tiger salamander (*Ambystoma californiense*) from within- and across-year analyses of five age-class transitions.

Age-class transition	Mass before selection (g)		Mass after selection (g)		Mass change (%)		Within year		Across year	
	Within year	Across year	Within year	Across year	Within year	Across year	df	<i>P</i>	df	<i>P</i>
Metamorph to juvenile	9.92 $\pm$ 0.05	9.48 $\pm$ 0.06	9.62 $\pm$ 0.21	10.89 $\pm$ 0.29	-3.0	14.9	3, 2452	0.17	1, 2454	<0.001
Metamorph to adult	11.34 $\pm$ 0.08	9.48 $\pm$ 0.06	13.08 $\pm$ 1.00	12.51 $\pm$ 1.22	15.4	32.1	3, 2324	0.07	1, 2326	0.01
Juvenile to juvenile	8.97 $\pm$ 0.11	7.51 $\pm$ 0.08	11.56 $\pm$ 0.78	10.61 $\pm$ 0.85	28.8	41.2	3, 1449	<0.001	1, 1451	<0.001
Juvenile to adult	8.98 $\pm$ 0.11	7.51 $\pm$ 0.08	11.47 $\pm$ 0.97	11.25 $\pm$ 1.14	27.8	49.7	3, 1439	0.01	1, 1441	<0.001
Adult to adult	22.86 $\pm$ 0.21	23.43 $\pm$ 0.17	24.43 $\pm$ 0.83	25.33 $\pm$ 0.87	6.9	8.1	4, 1113	0.06	1, 1116	0.03

*Notes:* The within-year analysis includes a blocking term for year so that animals are only compared to individuals in the same age class that were captured in the same year. This controls for the different climatic conditions that animals experienced in different years. The across-year analysis compares animals to all individuals in the same age class, regardless of the year in which they were captured. Mean mass before selection is the mean mass of all animals in the age class before the transition; mean mass after selection is mean mass in the age class before the transition, calculated for those animals that were recaptured after the transition. All estimates of mean mass are least-square means taken from the ANOVA models, which explains why values are slightly different depending on the specific model. The larger discrepancy in mean metamorph mass before selection for the within-year analysis is due to the fact that, for the metamorph–adult transition, all data from the 2006 cohort had to be dropped because no members of that cohort had been recaptured as adults. Mass change expresses the difference between mean mass before and after selection as a percentage, and significance gives the *P* value for the ANOVA associated with that mass change.

with traveling farther, and it was only the extent of this effect that varied by year (Appendix B: Table B.1). Because none of the simple effects contradicted the main effect, we conclude that, in general, metamorphs that emerged earlier traveled farther.

Although there was no within-year selection for larger size as a metamorph, there was strong within-year selection for larger size as a juvenile (Table 1). ME was a strong predictor of mass when first captured as a juvenile (Fig. 1), implying that although there was not an immediate advantage to large size at emergence, there was an advantage to this larger size later in life. This made ME a classic example of a DLHE; there was no immediate advantage to a large ME, but larger ME was selected for through its positive correlation with mass as a first-year juvenile. There was also strong within-year selection for metamorphs to emerge both early and at a large size, creating a potential evolutionary trade-off, because early emergence necessarily means truncating the period of rapid larval growth. This within-year selection resulted in a negative correlation between ME and DE (Fig. 2), because the most fit larvae emerged both early and large and the least fit larvae emerged both late and small.

Fig. 3 shows the mass trajectory of the average CTS, providing a context for these sometimes conflicting fitness components. Mean DE at Jepson Prairie was 10 June. Over the course of that summer, when there was selection for early emergence but none on ME, the average salamander lost 36% of its body mass. Maximum loss registered on 2 October, just before the wet season “officially” begins on 26 October (Köppen 1936). As soon as the wet season began, salamanders were considered one-year-old juveniles and selection switched to favoring greater ME. This corresponded to a

period of rapid growth during which the average salamander returned to its ME by 5 March. Growth stalled again (2 May–26 September), again matching closely the dry season (17 April–26 October). Rapid growth continued during the second year as a juvenile, such that by 5 October of the third year, the average salamander had reached the mean adult size (23.43  $\pm$  0.17 g; all data reported as mean  $\pm$  SE) and was presumably ready to breed. Past this point in the third year, we have very little information, and can only note that salamanders appear to continue growing into their fourth year and possibly beyond, probably at a decelerating rate.

From the perspective of modeling population dynamics, the importance of these DLHEs will depend upon the amount of variation in ME that selection has to act upon. Over our study, there was substantial variation both in individual ME (range 3.7–21.0 g) and in mean cohort ME (range 7.1  $\pm$  0.1 g to 13.7  $\pm$  0.4 g). Thus, regardless of their size in terms of number of individuals, some cohorts will contribute almost no breeding adults to the population, whereas other cohorts will have very high survivorship to maturity.

#### *Patterns across California tiger salamander sites*

Olcott Lake is an enormous and somewhat unusual breeding site in terms of its size. To examine the generality of the variation in mean cohort ME that we found at Olcott, we summarize variation in ME from two other breeding sites over a range of years and hydroperiods in Fig. 4. Round Pond is a smaller, but still quite large, 3-ha breeding site 0.9 km from Olcott; Blomquist Pond is a more typical 0.07-ha breeding site in Monterey County adjacent to the Hastings Natural History Reservation that was studied with a single drift fence

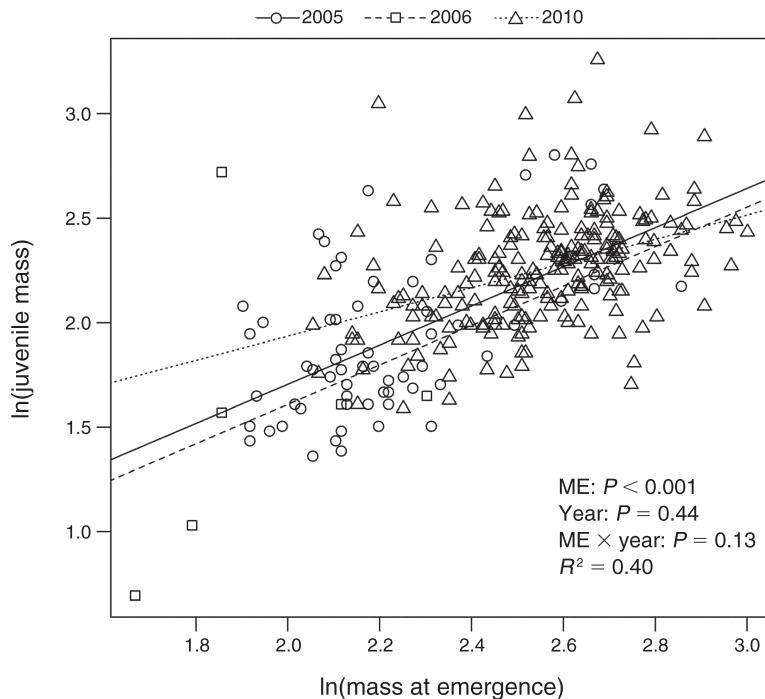


FIG. 1. Mass at emergence strongly predicts juvenile mass in the California tiger salamander (*Ambystoma californiense*). Data from all three years with metamorphs marked (2005, 2006, and 2010) are shown; factors are mean cohort mass at emergence (ME), year, and their interaction. Log-transformed mass was originally measured in grams.

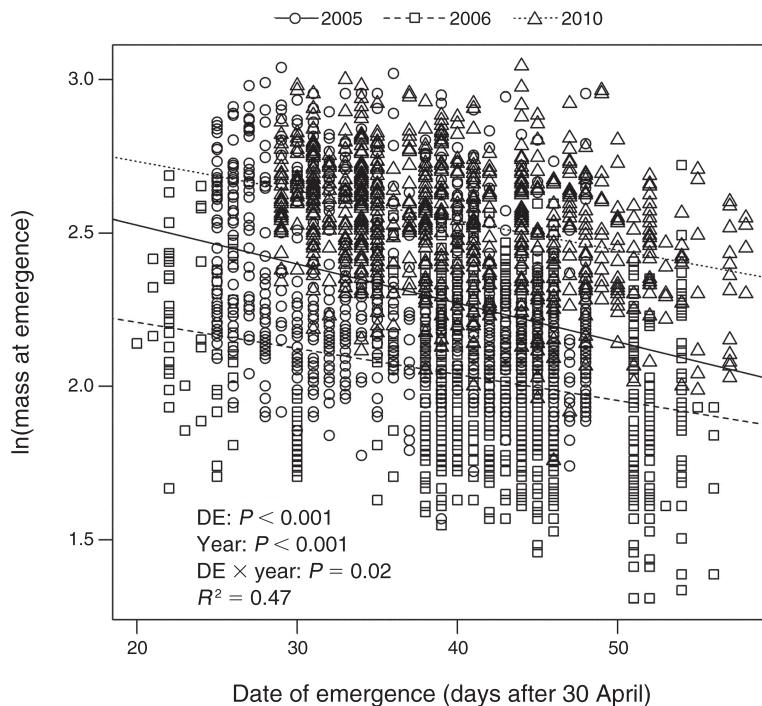


FIG. 2. Due to conflicting selection pressures, mass at emergence decreases with emergence date. Date is represented as the number of days after 30 April. Data from all three years with metamorphs marked (2005, 2006, and 2010) are shown; factors are date of emergence (DE), year, and their interaction. Log-transformed mass was originally measured in grams.

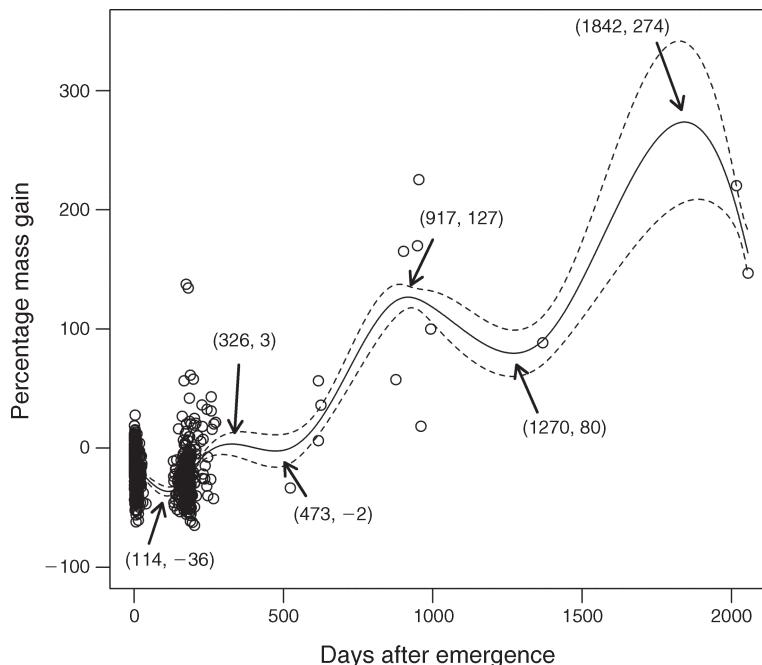


FIG. 3. Mass trajectory for California tiger salamanders (solid line, mean; dashed lines, SE). Each circle represents a recapture event. The line was fit using a general additive model. Numbers in parentheses are coordinates for each local minimum and maximum of the model. Values on the x-axis are days after date of emergence (mean date of emergence is 10 June); y values are the percentage increase or decrease in mass relative to mass at emergence (mean mass at emergence is 10.77 g). Thus, “100” on the y-axis represents a 100% increase in mass since emergence (i.e., 21.54 g for a salamander with the mean mass at emergence).

for nine years during the 1990s (Trenham et al. 2000). Variance among mean cohort ME is fairly similar between the three sites: for Blomquist, SD = 3.05 g; for Olcott, SD = 2.62 g; for Round, SD = 3.56 g. This suggests that substantial fitness variation for DLHEs to act upon will be common across CTS sites, regardless of

their size and location. We also note that Olcott Lake and Round Pond are in close proximity to each other and experience identical climatic conditions, yet the correlation in mean cohort ME between the two sites is low ( $r = 0.27$ ), indicating that the factors controlling mean cohort ME are not purely a function of local weather conditions.

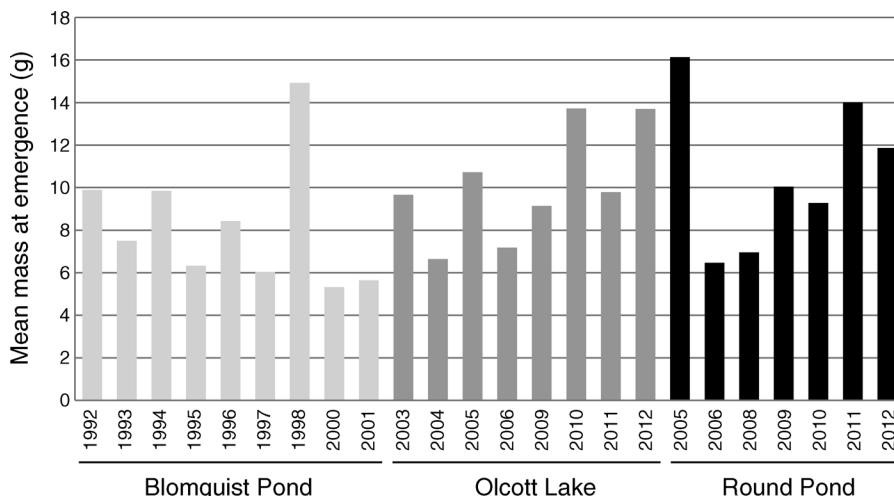


FIG. 4. Mean cohort mass at emergence for three different California tiger salamander breeding ponds across 7–9 years of study in California. Each breeding pond is represented by a different pattern: light gray, Blomquist Pond, Hastings Natural History Reservation, Monterey County; medium gray, Olcott Lake, Jepson Prairie, Solano County; black, Round Pond, Jepson Prairie, Solano County.

### *Patterns across pond-breeding amphibians*

Finally, to place the variation that we observed in ME into a broader context, we compiled a literature review of studies of pond-breeding amphibians that have documented mean cohort ME over multiple years from the same breeding site (Appendix B: Table B.2). We calculated among-cohort variation as the ratio of the largest to the smallest mean cohort ME. The variation ranges from 1.0 to  $>5.0$ , and the variation in mean cohort ME in CTS (2.8) falls in the middle of the variation observed in other species. As expected, the largest/smallest ME ratio increases with the number of cohorts that are investigated ( $P < 0.001$ ; Appendix B: Fig. B.2). Based on the available data, there is no indication that the range of variation is saturating with the number of measured cohorts (the quadratic term is not significant,  $P = 0.19$ ), even with the longest existing studies (22 and 23 annual cohorts).

### DISCUSSION

Delayed life history effects occur when life history traits (e.g., survival) depend on both current and previous environments (Beckerman et al. 2002). We have found pervasive evidence for delayed life history effects across the life history of CTS. At each stage in CTS's life cycle, greater mass, which must be governed in part by current and previous environments, leads to higher survival to the next stage (Table 1). Previous studies of pond-breeding amphibians have shown that variation in ME affects fitness of breeding adults (Berven 1990, Scott 1994, Berven 2009; but see Beck and Congdon 1999, Boone 2005, Gramapurohit 2009 for counter examples). However, none of these studies has been able to partition this large-size advantage at metamorphosis among the intervening life stage transitions. We found that larger size is advantageous at all life history stage transitions, although at the metamorph-to-juvenile transition, this selection advantage is better modeled at the cohort level than at the individual level. The metamorph-to-juvenile transition is particularly nuanced, and involves a potential trade-off between ME and DE, with earlier DE providing an immediate fitness benefit to metamorphs, whereas greater ME only provides a fitness advantage later in life.

#### *Delayed life history effects*

Models that incorporate DLHEs have proven to more accurately resemble true population dynamics in both plant and insect systems (Ginzburg and Taneyhill 1994, Crone 1997). It is thus essential that we understand how DLHEs operate if we want to build accurate population models for amphibians and other taxa. The pervasive DLHEs that we found in CTS, coupled with the substantial variation in mean cohort ME, clearly could have a large effect on population dynamics. In particular, the model for across-year selection on mass between the metamorph and adult stages suggests that

within a single breeding pond, terrestrial survival of the average metamorph in the heaviest cohort ( $14.9 \pm 0.3$  g) is up to 18.8 times that of the average metamorph in the lightest cohort ( $5.3 \pm 0.1$  g). Although this variation in average metamorph quality is not as great as the variation that has been detected in metamorph quantity (which ranges over four orders of magnitude; see Searcy et al. 2013), it will have a large effect on population dynamics.

Unfortunately, we still do not fully understand which environmental factors are governing fluctuations in mean metamorph mass. None of the environmental factors that we tested (e.g., number of metamorphs, number of breeding females, mean temperature, annual precipitation) was significantly correlated with mean cohort ME. What we do understand is the tremendous level of variation in mean cohort ME in CTS populations, and that similar levels of variation are found in virtually all pond-breeding amphibians that have been studied to date. Fig. B.2 (Appendix B) suggests both that the range of variation in mean cohort ME is very large (5.42 times in *Ambystoma talpoideum*; D. E. Scott, unpublished data) and that accurately estimating the range of variation will require monitoring a population for a very long time (over 20 years). Average turnover period for these species is  $\sim 10$  years (e.g., Gibbons and Semlitsch 1991, Taylor and Scott 1997, Trenham et al. 2000), and our literature review is consistent with Connell and Sousa (1983), who concluded that, as a good rule of thumb, populations should be followed for two full turnover periods (see also Blaustein et al. 1994, Pechmann and Wilbur 1994).

#### *Multilevel selection*

Our analysis points to selection acting at both the individual and cohort level, and each may be important contributors to the total selection on a population over time. Other studies have shown that there is a significant correlation between mean cohort ME and survival (Berven 1990, Scott 1994), but did not utilize a contextual analysis (Heisler and Damuth 1987) to partition the cohort-level relationship into individual-level (within each cohort, a higher percentage of large individuals survive) or cohort-level (a random sampling from within each cohort survive, but a higher percentage are from cohorts with a larger mean size) selection. Our contextual analysis reveals that across the critical metamorph-to-juvenile transition, selection for larger mass is better represented as cohort-level selection. This will play an important role in how selection on mass is modeled for a population, because predictions made by models based on cohort vs. individual level selection diverge as the intrinsic rate of population growth increases (Taylor and Scott 1997).

It is also important to keep in mind that this is a purely correlational analysis. It is hard to conceive of a mechanism by which a focal metamorph's survival probability would be increased by being surrounded by



PLATE 1. Adult California tiger salamander (*Ambystoma californiense*) at the Jepson Prairie Preserve, Solano County, California, USA. Adult and juvenile California tiger salamanders are only surface-active in the terrestrial habitat on rainy nights during the fall and winter. Individuals travel hundreds of meters between their breeding pond and refuge sites (rodent burrows), where they are protected from California's hot, dry summers. Photo credit: Vide Ohlin.

other large metamorphs. It seems more likely that there is some environmental factor, or suite of correlated environmental factors, that both improves the quality of the aquatic environment, thereby increasing mean cohort ME, and simultaneously ameliorates mortality pressures in the terrestrial environment, thereby increasing subsequent over-summer survivorship. One factor that could potentially fill this role is the number of cohort mates, because competition with other individuals in the same cohort for both aquatic prey and terrestrial burrows would decrease both mean ME and terrestrial survival. Although we did not detect a significant relationship between number of metamorphs and mean cohort ME (see preceding section), and survival over the first summer was better predicted by mean cohort ME ( $R^2 = 0.998$ ) than by number of metamorphs ( $R^2 = 0.88$ ), this does not preclude the possibility that a data set with more across-year replication would detect a significant contribution of number of metamorphs to both of the other metrics.

When considering the mean mass trajectory depicted in Fig. 3, it is difficult to believe that individual selection on mass is not operating across the metamorph-to-juvenile transition. During this transition, the average salamander loses 36% of its mass. Larger salamanders presumably have larger fat and water stores, and thus should be better able to tolerate this mass loss. For example, it has been shown that larger mass increases time to dehydration in a desert-adapted anuran (Newman and Dunham 1994), and should therefore be an

important component of survival over central California's hot, rainless summer. However, it may be the case that the threat of dehydration is so severe that such an effect is outweighed by the over-summering site that a salamander selects, because even a high-quality salamander will die in a low-quality retreat. This may explain why early emergence, which is correlated with sampling a larger area as a metamorph and thus having a larger range of over-summering sites to choose from, is such an important component of fitness.

#### *Optimal size at metamorphosis*

Fig. 2 reveals a negative correlation between ME and DE. If this relationship is driven by selection on ME alone, as was assumed in classic models of amphibian metamorphosis (Wilbur and Collins 1973, Werner 1986), it requires that the optimal value of ME decreases over time. Under the Wilbur and Collins (1973) model, this would require the body size at which larval growth rate slows to decrease over time, as this decreasing larval growth rate is the postulated trigger initiating metamorphosis. This could be the case if larger larvae require a higher rate of prey capture than smaller ones to maintain the same size-specific growth rate. Given that CTS are sit-and-wait predators that swallow their prey whole, the profitability of prey may be governed solely by search time, which is linearly correlated with prey density. Prey density may well decrease linearly over the course of the emergence period, consistent with a linear decrease in optimal ME. From the perspective of the

Werner (1986) model, early metamorphosis at a larger size can be explained if the aquatic  $\mu/g$  (mortality/growth) curve moves upward over the course of the emergence period, shifting its intersection with the terrestrial  $\mu/g$  curve to a lower mass. This upward movement of the aquatic  $\mu/g$  curve could occur if either  $\mu$  increases or  $g$  decreases. Both of these seem plausible, since  $\mu$  presumably increases dramatically as pond-drying reduces the volume of water, and  $g$  may decrease as the density of aquatic prey decreases. However, a simpler explanation for the negative correlation between ME and DE results if we consider that both traits are under selection simultaneously, and that there is a trade-off between them.

#### *Evolutionary trade-offs*

Agrawal et al. (2010:245) define a multi-trait trade-off as occurring “when two or more traits, which are both under directional selection to increase, share a limiting resource.” Our analyses demonstrate that, in CTS, both ME and DE are under directional selection (ME for larger size and DE for earlier time). We posit that the shared limiting resource is time. Clearly, individuals that emerge from the pond earlier are sacrificing time in the aquatic environment. As long as extra time in the aquatic environment would also lead to greater ME, then the limiting resource is shared. Although the first metamorphs emerge in late May, other larvae remain in the aquatic environment for another month. If there are enough resources to sustain the growth of these later-emerging metamorphs, then there is every expectation that the early-emerging metamorphs, which must have had a higher rate of resource acquisition to obtain their early size advantage, would continue to grow if they remained in the aquatic environment.

We postulate that an evolutionary trade-off between ME and DE can easily explain the negative correlation between these two critical life history features. Clearly, the optimal strategy in this situation is to emerge both early and large. Larvae with a high rate of resource acquisition may be close to this optimum and have the luxury of making small sacrifices in both ME and DE as part of their trade-off. Larvae with lower rates of resource acquisition will also be forced into a trade-off between DE and ME, and due to their slow growth rate, will emerge with an even lower ME, despite making a larger sacrifice in DE. An advantage to early emergence seems to be a common theme across amphibian species (Smith 1987, Semlitsch et al. 1988, Altwegg and Reyer 2003), suggesting that this trade-off may be common, and may maintain variation in both metrics (Berven and Gill 1983) within and across cohorts.

#### *Conclusions*

Previous work has shown that: (1) if they exist, DLHEs will play an important role in population dynamics (Leslie 1959); (2) that DLHEs are common in pond-breeding amphibians (Berven 1990, Scott 1994,

Berven 2009); and (3) that there is substantial inter-cohort variation in metamorph quality for DLHEs to act upon (Semlitsch et al. 1988, Scott et al. 2007, Berven 2009). Although this inter-cohort variation in metamorph quality has been documented, its potential impact on population dynamics and its partitioning among terrestrial life history phases have received very little attention. We demonstrate that in CTS, inter-cohort variation in average metamorph quality substantially impacts population dynamics. We have also shown that accurately documenting inter-cohort variation in metamorph quality requires data for at least two complete population turnovers, that DLHEs are prominent across all life stage transitions, and that there is variation in whether selection is primarily at the individual or cohort level. All of these empirical observations affect how population models should be developed (Taylor and Scott 1997). Given that DLHEs are common across diverse taxa, not just pond-breeding amphibians (Rose et al. 1998, Beckerman et al. 2002, Lummaa and Clutton-Brock 2002), our observations on the importance of variation in quality as well as quantity and how it interacts with DLHEs are widely applicable to the understanding of population dynamics.

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#### LITERATURE CITED

- Agrawal, A., J. K. Conner, and S. Rasmann. 2010. Tradeoffs and negative correlations in evolutionary ecology. Pages 243–268 in M. A. Bell, D. J. Futuyma, W. F. Eanes, and J. S. Levinton, editors. *Evolution since Darwin, the first 150 years*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Albon, S. D., T. H. Clutton-Brock, and F. E. Guinness. 1987. Early development and population dynamics in red deer. 2. Density-independent effects and cohort variation. *Journal of Animal Ecology* 56:69–81.
- Altwegg, R., and H. Reyer. 2003. Patterns of natural selection on size at metamorphosis in water frogs. *Evolution* 57:872–882.
- Beck, C. W., and J. D. Congdon. 1999. Effects of individual variation in age and size at metamorphosis on growth and survivorship of southern toad (*Bufo terrestris*) metamorphs. *Canadian Journal of Zoology* 77:944–951.
- Beckerman, A., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. Population dynamic consequences of delayed life-history effects. *Trends in Ecology and Evolution* 17:263–269.
- 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. 2009. Density-dependence in the terrestrial stage of wood frogs: evidence from a 21-year population study. *Copeia* 2009:328–338.

- Berven, K. A., and D. E. Gill. 1983. Interpreting geographic variation in life-history traits. *American Zoology* 23:85–97.
- Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology* 8:60–71.
- Boone, M. D. 2005. Juvenile frogs compensate for small metamorph size with terrestrial growth: overcoming the effects of larval density and insecticide exposure. *Journal of Herpetology* 39:416–423.
- Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. *American Naturalist* 121:789–824.
- Crone, E. E. 1997. Parental environmental effects and cyclical dynamics in plant populations. *American Naturalist* 150:708–729.
- Gibbons, J. W., and R. D. Semlitsch. 1991. Guide to the reptiles and amphibians of the Savannah River Site. University of Georgia Press, Athens, Georgia, USA.
- Ginzburg, L. R., and D. E. Taneyhill. 1994. Population cycles of forest Lepidoptera: a maternal effect hypothesis. *Journal of Animal Ecology* 63:79–92.
- Gramapurohit, N. P. 2009. Catch-up growth during juvenile life can compensate for the small metamorphic size in *Euphylyctis cyanophlyctis*. *Current Science* 97:1243–1246.
- Heisler, I. L., and J. Damuth. 1987. A method for analyzing selection in hierarchically structured populations. *American Naturalist* 130:582–602.
- Jerry, D. R., T. Stewart, I. W. Purvis, and L. R. Piper. 2001. Evaluation of visual implant elastomer and alphanumeric internal tags as a method to identify juveniles of the freshwater crayfish, *Cherax destructor*. *Aquaculture* 193:149–154.
- Köppen, W. 1936. Das geographische system der klimate. Pages 1–44 in W. Köppen and R. Geiger, editors. *Handbuch der Klimatologie*. Verlag von Gebrüder Borntraeger, Berlin, Germany.
- Küchler, A. W. 1977. The map of the natural vegetation of California. University of Kansas, Lawrence, Kansas, USA.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Leslie, P. H. 1959. The properties of a certain lag type of population growth and the influence of an external random factor on a number of such populations. *Physiological Zoology* 32:151–159.
- Lummaa, V., and T. Clutton-Brock. 2002. Early development, survival and reproduction in humans. *Trends in Ecology and Evolution* 17:141–147.
- Newman, R. A., and A. E. Dunham. 1994. Size at metamorphosis and water loss in a desert anuran (*Scaphiopus couchii*). *Copeia* 1994:372–381.
- Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253:892–895.
- Pechmann, J. H. K., and H. M. Wilbur. 1994. Putting declining amphibian populations in perspective: natural fluctuations and human impacts. *Herpetologica* 50:65–84.
- Prout, T., and F. McChesney. 1985. Competition among immatures affects their adult fertility: population dynamics. *American Naturalist* 126:521–558.
- Rittenhouse, T. A. G., and R. D. Semlitsch. 2007. Distribution of amphibians in terrestrial habitat surrounding wetlands. *Wetlands* 27:153–161.
- Rose, K. E., T. H. Clutton-Brock, and F. E. Guinness. 1998. Cohort variation in male survival and lifetime breeding success in red deer. *Journal of Animal Ecology* 67:979–986.
- Scott, D. E. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. *Ecology* 75:1383–1396.
- Scott, D. E., E. D. Casey, M. F. Donovan, and T. K. Lynch. 2007. Amphibian lipid levels at metamorphosis correlate to post-metamorphic terrestrial survival. *Oecologia* 153:521–532.
- Searcy, C. A., E. Gabbai-Saldate, and H. B. Shaffer. 2013. Microhabitat use and migration distance of an endangered grassland amphibian. *Biological Conservation* 158:80–87.
- Searcy, C. A., and H. B. Shaffer. 2011. Determining the migration distance of a vagile vernal pool specialist: how much land is required for conservation of California tiger salamanders? Pages 73–87 in D. G. Alexander and R. A. Schlising, editors. *Research and recovery in vernal pool landscapes*. Studies from the Herbarium, Number 16. California State University, Chico, California, USA.
- Semlitsch, R. D., and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* 17:1219–1228.
- Semlitsch, R. D., D. E. Scott, and J. H. K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. *Ecology* 69:184–192.
- Smith, D. C. 1987. Adult recruitment in chorus frogs: effects of size and date at metamorphosis. *Ecology* 68:344–350.
- Taylor, B. E., and D. E. Scott. 1997. Effects of larval density dependence on population dynamics of *Ambystoma opacum*. *Herpetologica* 53:132–145.
- Trenham, P. C., H. B. Shaffer, W. D. Koenig, and M. R. Stromberg. 2000. Life history and demographic variation in the California tiger salamander (*Ambystoma californiense*). *Copeia* 2000:365–377.
- Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *American Naturalist* 128:319–341.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 Supplement:120–138.
- Wilbur, H. M., and J. P. Collins. 1973. Ecological aspects of amphibian metamorphosis: nonnormal distributions of competitive ability reflect selection for facultative metamorphosis. *Science* 182:1305–1314.

## SUPPLEMENTAL MATERIAL

### Appendix A

Description of methods for determining which capture events are recaptures ([Ecological Archives E095-007-A1](#)).

### Appendix B

Detailed description of regression and ANOVA analyses mentioned in the text with supplemental tables and figures, plus additional analyses providing evidence that recaptured animals are a random subset of those that survived ([Ecological Archives E095-007-A2](#)).