

Life history variation in two populations of California Newt, *Taricha torosa*

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ABSTRACT.—California Newts (*Taricha torosa*) are common amphibians throughout much of California, yet their life history has been little studied. We examined *T. torosa* in 2 physically separated breeding locations, a farm pond and a nearby stream, between February and June 2015. We synoptically collected physical measurements on adults as well as tissue samples from a subset of the newts present in both locations throughout the time period. Stable isotopes of carbon and nitrogen were used to characterize the trophic niche space among newts of different locations and ages. Our results suggest differentiated breeding phenologies as well as unique trophic signatures in the 2 different locations. In our sampling, the pond group bred and developed a few weeks earlier in the season and ate at a higher trophic level, while the stream group bred and developed later and ate lower on the food chain. Taken as a whole, our results suggest that the newts in this area exhibit some degree of ecological and life history plasticity.

RESUMEN.—Los Tritón de California (*Taricha torosa*) son anfibios comunes en gran partes de California, pero sus historias de vida han sido poco estudiada. Examinamos *T. torosa* en 2 ubicaciones de reproducción separadas físicamente, un estanque de granja y un arroyo cercano entre Febrero y Junio de 2015. Recopilamos sinópticamente mediciones físicas en tritones adultos, así como muestras de tejido de un subconjunto de los tritones en ambas ubicaciones durante el periodo de tiempo. Se utilizaron isótopos estables de carbono y nitrógeno para caracterizar el espacio de nicho trófico entre los tritones de diferentes ubicaciones y edades. Nuestros resultados sugieren fenologías de reproducción diferenciadas, así como firmas tróficas únicas en cada de las 2 ubicaciones diferentes. El grupo del estanque se reproduce mas temprano en la temporada, se desarrolla más rápido y come a un nivel trófico más alto. Mientras, el grupo del arroyo se reproduce más tarde en la temporada, se desarrolla más lentamente y come mas baja en la cadena alimentaria. En general, nuestros resultados sugieren que los tritones en esta área exhiben rasgos ecológicos y de historias de vidas plásticos.

Newts in the genus *Taricha* (family Salamandridae) are distributed across the Pacific coast of North America and are often observed boldly moving over land during the rainy season. Part of this behavior comes from possessing poisonous skin secretions containing tetrodotoxin, one of the most toxic nonprotein substances known (Stebbins and Cohen 1995, Noguch and Arakawa 2008). During the winter and spring months, after rain events, adult newts can be seen heading toward their aquatic breeding sites. Although the species is distributed widely, the California Newt (*Taricha torosa*) has not been as intensively studied as some of the other amphibian species in California (e.g., California Tiger Salamander [*Ambystoma californiense*; Trenham et al. 2000] or

California Red-legged Frog [*Rana draytonii*; Hayes and Tennant 1985, Bishop et al. 2014]), with much of the research on newts having been carried out on Southern California populations (Kats et al. 1992, 1994, Kerby and Kats 1998, Bucciarelli et al. 2016, 2017).

As *T. torosa* adults begin to migrate, they make choices regarding where and when to breed. In Contra Costa County, California, near San Francisco, possible breeding locations include natural and man-made ponds, as well as seasonal and permanent streams. *Taricha torosa* shows similar breeding site fidelity and homing ability in comparison with other newts (Thomson et al. 2016), suggesting that individual newts are more likely to utilize one particular habitat when multiple

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Fig. 1. Sample and habitat locations of the 2 newt populations examined in this study. **A**, Turre Pond. **B**, Las Trampas Creek (Contra Costa County, CA).

habitats are present (Twitty et al. 1964). In the habitat around Moraga, California (Contra Costa County), a number of streams and farm ponds are available for breeding, oftentimes in close proximity to each other. Dr. Larry Cory, a retired herpetologist from Saint Mary's College of California, for years casually monitored 2 breeding groups of newts in Moraga, California, a pond-breeding group and a group that breeds in Las Trampas Creek (Fig. 1). Cory observed that the newts in the 2 locations consistently bred at different times of the year, which suggests that the animals are phenotypically plastic with respect to reproduction (L. Cory personal communication). It

is reasonable to assume that ecological or environmental factors coincide with the phenological differences in breeding and may be expressed in aspects of the newts' diets (Anthony et al. 2008).

One of the goals of trophic ecology is to understand how environmental variations influence an organism's diet (Polis and Strong 1996, Finlay et al. 2002, Layhee et al. 2014). Stable isotopes of carbon and nitrogen are frequently used to examine aspects of an organism's diet by plotting isotopic values from tissue samples in bivariate space (Fry 2006, Layman et al. 2012). Taken together, C and N isotope values provide indirect indicators of feeding

pathways (Layman et al. 2012), or a snapshot of an organism's trophic niche (Finlay et al. 2002, Fry 2006), which is often difficult to compile by using other means (Sepulveda et al. 2012).

Isotopic biplots provide information on both the base of a food web and trophic structuring (Fry 2006, Layman et al. 2012). For example, the specific ratio of heavy to light carbon isotopes (i.e., $^{13}\text{C}/^{12}\text{C}$) in a tissue sample can be used to identify the organism's source of organic carbon, which reflects what the organism has eaten. In lentic systems (e.g., ponds and lakes), smaller δ carbon values (i.e., more negative) indicate carbon that was fixed photosynthetically by pelagic organisms (e.g., floating algal cells), while larger values (i.e., less negative) indicate carbon fixation in a littoral zone (e.g., attached algae) (France 1995). In small lotic systems (e.g., streams), smaller δ carbon values indicate that the carbon was fixed by in situ organisms (e.g., algae), while larger values indicate carbon that originated outside the system (e.g., allochthonous inputs) (Finlay 2001). In addition, the isotopic carbon ratio is conserved in each feeding encounter, meaning that in terms of carbon isotopes, "you are what you eat" (Fry 2006). In a similar manner, the ratio of heavy to light nitrogen isotopes (i.e., $^{15}\text{N}/^{14}\text{N}$) is used to examine trophic placement of an organism. This ratio increases by approximately 3.4 units as one organism eats another, thereby increasing the δ nitrogen signature as an organism eats higher up the food chain (Fry 2006).

Because California Newts have a life cycle that is part terrestrial and part aquatic, their diet and feeding ecology should reflect distinct changes as they transition from one life stage to another (eggs, larvae, or adults) or reside in different locations (Davic and Welsh 2004). These changes should be evident for newts breeding in different habitats like ponds and streams, because these environments house very different aquatic communities (Wetzel 2001, Dodds and Whiles 2010).

This study aimed to examine the natural history and trophic relationships of the California Newt, *T. torosa*, with respect to how variation in habitat, season, sex, and life stage influence the ecology of the aquatic phases of the animal. Specifically, we were interested in examining the following question: Are there

measurable differences between pond- and stream-breeding newts in Contra Costa County, California, with respect to their phenology and trophic relationships? To this end we collected life history data on *T. torosa* individuals from a stream and a pond in northern California and utilized stable isotope geochemistry to examine their diets.

METHODS

All newts were collected from 2 sites, the first on Las Trampas Creek, a first/second-order seasonal stream, and the second a nearby permanent pond on the Turre Family property in Moraga, Contra Costa County, California (Fig. 1). The pond is reportedly a historically permanent natural feature on the property, but one that has been augmented by the construction of a low dam/berm on the outflow location. On the occasions when the pond has outflow, the water runs into an unnamed tributary of Las Trampas Creek, with the 2 sampling sites only 0.57 km away from each other. Collections at the stream and creek sites were always conducted within 2–3 d of each other. At each sampling event and location, we collected surface water temperatures using a digital thermometer. Newts at the 2 sites were surveyed every 2–3 weeks from February through late June of 2015. All adult newts were collected by hand, individual animals were visually sexed, and 2 physical attributes were recorded: snout–vent length (SVL; tip of snout to anterior of vent; digital calipers, ± 0.01 mm) and overall body weight (digital scale, ± 0.1 g). A 3-way analysis of variance ($\alpha = 0.05$) was used to compare snout–vent lengths of adults with respect to month (February and April), location (creek and pond), and sex (general linear model, Minitab 17.3.1). All 2-way interaction terms were included in the model. A 3-way ANOVA ($\alpha = 0.05$) was also used to examine adult newt weight with respect to month (February and April), location (creek and pond), and sex (general linear model, Minitab 17.3.1). All 2-way interaction terms were included in the model.

During 3 time periods (February, April, and June), 3–8 adult newts were randomly selected for stable isotope analysis. To collect tissue for isotope analysis, we removed a 5- to 7-mm piece of the end of each newt's tail and placed

TABLE 1. Three-way ANOVA results ($\alpha = 0.05$) for adult snout-vent length (SVL) versus month (February and April), location (pond and creek), and sex. Table includes degrees of freedom (df), the independent coefficient (Coef), the standard error of the coefficient (SE Coef), the F value, and the P value. All 2-way interaction terms are included in the model. Factors statistically significant at $\alpha = 0.05$ are in bold.

Source	df	Coef	SE Coef	F	P
month	1	-0.234	0.391	0.36	0.551
location	1	1.522	0.418	13.27	<0.001
sex1		0.456	0.417	1.20	0.276
month * location	1	0.439	0.380	1.34	0.249
month * sex	1	0.441	0.413	1.14	0.288
location * sex	1	-0.150	0.399	0.14	0.707
Error	166				
Total	173				

it in 70% ethanol for preservation. All adult newts were returned to their place of origin. In addition, during these time periods, small samples (2–7 individuals) of larval newts were collected, along with newt egg masses, in order to assess breeding site fidelity in the adults. In these cases, due to tissue sampling constraints, the whole organism was euthanized using MS222 prior to preservation in 70% ethanol.

Prior to stable isotope analysis, all tissue samples were individually dried at 60 °C for a minimum of 48 h and pulverized using a clean ceramic mortar and pestle. Between 0.5 mg and 1.5 mg of pulverized tissue was placed in a 5 × 9-mm tin capsule (Costech Analytical Technologies, Inc., Valencia, CA, USA). The capsules were crimped and loaded into a sterile 96-well plate and sent for isotopic analysis of carbon-13 and nitrogen-15 via a mass spectrometer at the UC Davis Stable Isotope Facility. Carbon and nitrogen ratios are both expressed as δ values and were calculated using the following formula:

$$\delta \text{ Isotope (\%)} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3.$$

In order to statistically compare isotopic niche space between pond and stream adult newts, 2 separate 3-way ANOVAs ($\alpha = 0.05$) were used to compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with respect to month (February and April—the only months during which adults were present), location (creek and pond), and sex (general linear model, Minitab 17.3.1; Verbarg et al. 2007, Layman et al. 2012). All 2-way interaction terms were included in the model. Due to sample size constraints and issues with sexing larvae, t tests ($\alpha = 0.05$) were used to compare the isotopic data ($\delta^{13}\text{C}$

and $\delta^{15}\text{N}$ values) for *Taricha* eggs and larval newts between pond and stream. To help with visualization of the data, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were also examined by plotting the mean values in a bivariate graph (Fry 2006, Layman et al. 2012, Layhee et al. 2014). When more than one individual or sample of a particular organism was graphed, standard error (SE) bars were added to indicate variability around the mean value.

RESULTS

Two hundred and one adult newts were captured and measured across both sites. Many more individuals could have been captured, but because the study was primarily designed to examine isotopic feeding relationships, the large-scale collection of all newts present was not undertaken. There were noticeable differences in when newts arrived at the pond versus at the stream. When first sampled on 15 February 2015, the pond already contained newt egg masses, indicating that some newts had been on-site for at least 1–2 weeks prior to our visit. In contrast, the first egg masses in the stream were observed on 2 March, suggesting a delay in timing between the 2 sites of approximately 2 weeks. This temporal delay was also seen in the first emergence of larval newts. In the pond, the first larvae were observed on 17 April, while in the stream, the first larvae were observed on 4 May but were likely present in the week prior, given their size.

The results of the 3-way ANOVA for adult SVL versus month (February and April), location (pond and creek), and sex can be seen in Table 1. The results indicate a significant effect of location, with the pond newts being longer than the creek newts. The results of

TABLE 2. Three-way ANOVA results ($\alpha = 0.05$) for adult weight versus month (February and April), location (pond and creek), and sex. Table includes degrees of freedom (df), the independent coefficient (Coef), the standard error of the coefficient (SE Coef), the *F* value, and the *P* value. All 2-way interaction terms are included in the model. Factors statistically significant at $\alpha = 0.05$ are in bold.

Source	df	Coef	SE Coef	<i>F</i>	<i>P</i>
month	1	16.433	0.244	0.35	0.556
location	1	0.137	0.232	13.33	<0.001
sex	1	-0.547	0.247	4.89	0.028
month * location	1	-0.301	0.225	1.79	0.183
month * sex	1	0.591	0.245	5.82	0.017
location * sex	1	-0.003	0.237	0.00	0.990
Error	166				
Total	173				

TABLE 3. Three-way ANOVA results ($\alpha = 0.05$) for adult newt δC values versus month (February and April), location (pond and creek), and sex. Table includes degrees of freedom (df), the independent coefficient (Coef), the standard error of the coefficient (SE Coef), the *F* value, and the *P* value. All 2-way interaction terms are included in the model. Factors statistically significant at $\alpha = 0.05$ are in bold.

Source	df	Coef	SE Coef	<i>F</i>	<i>P</i>
location	1	-0.273	0.135	4.09	0.057
sex	1	-0.018	0.197	0.01	0.927
month	1	0.629	0.176	12.71	0.002
location * sex	1	0.070	0.166	0.18	0.678
location * month	1	0.206	0.183	1.26	0.275
sex * month	1	-0.198	0.153	1.68	0.210
Error	20				
Total	26				

TABLE 4. Three-way ANOVA results ($\alpha = 0.05$) for adult newt δN values versus month (February and April), location (pond and creek), and sex. Table includes degrees of freedom (df), the independent coefficient (Coef), the standard error of the coefficient (SE Coef), the *F* value, and the *P* value. All 2-way interaction terms are included in the model. Factors statistically significant at $\alpha = 0.05$ are in bold.

Source	df	Coef	SE Coef	<i>F</i>	<i>P</i>
location	1	0.851	0.273	9.74	0.005
sex	1	-0.474	0.397	1.42	0.247
month	1	-0.907	0.356	6.48	0.019
location * sex	1	-0.241	0.336	0.51	0.481
location * month	1	-0.855	0.370	5.35	0.032
sex * month	1	0.130	0.309	0.18	0.679
Error	20				
Total	26				

the 3-way ANOVA for adult weight versus month (February and April), location (pond and creek), and sex can be seen in Table 2. The results indicate (1) a significant effect of location, with the pond newts weighing less than the creek newts; (2) a significant effect of sex, with the females weighing less than the males; and (3) a significant month * sex interaction.

The results of the 3-way ANOVA for adult newt δC values versus month (February and April), location (pond and creek), and sex can be seen in Table 3. The results indicate a significant difference between months: February

samples have fewer negative δC values than April samples do. The results of the 3-way ANOVA for adult newt δN values versus month (February and April), location (pond and creek), and sex can be seen in Table 4. The results indicate a significant effect of location, with (1) pond adults showing higher values than creek adults; (2) a significant effect of month, with April showing higher values than February; and (3) a significant location * month interaction.

The *t* tests comparing δC and δN values between ponds and streams for eggs and

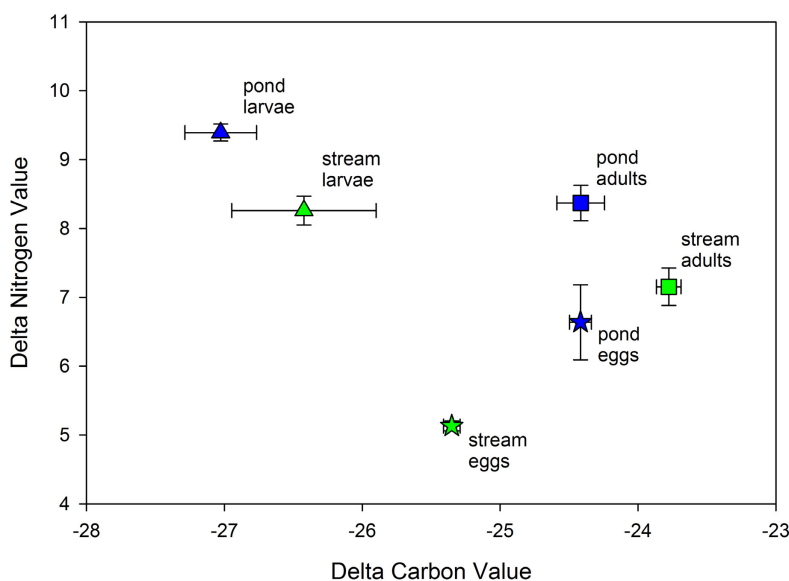


Fig. 2. Stable isotope biplots showing mean δN and δC values for the pond and stream newt adults, larvae, and egg masses that were sampled during the months of February, April, and June. Symbols for the biplot are as follows: blue symbols = pond individuals, green symbols = stream individuals, \square = newt adults, \triangle = newt larvae, \star = newt egg masses. Error bars represent standard error of the mean.

juveniles indicate no significant difference for δN egg values ($t = 2.13$, $df = 2$, $P = 0.167$), but they do indicate significant differences for δC egg values ($t = 7.85$, $df = 2$, $P = 0.016$), δC larvae values ($t = -2.67$, $df = 14$, $P = 0.018$), and δN larvae values ($t = 6.71$, $df = 21$, $P < 0.001$).

In order to visualize the results of the ANOVAs and compare the trophic niche space occupied by the pond and stream newts at all 3 life stages, we created an isotopic biplot (i.e., Fig. 2). This figure clearly demonstrates the differences between pond and stream animals: the pond adults show higher δN values and more negative δC values than the stream adults. A similar pattern is observed for the larval newts: the pond individuals show enriched δN values and more negative δC values. The t test for the egg data indicates no δN differences between stream and pond but does show a significant δC difference, with the stream eggs showing more negative δC values as seen on the biplot (Fig. 2). Taken as a whole, the different habitats and life stages occupy distinctly different biplot space, which supports the statistical results that we reported earlier, with the pond values having higher δN values and lower δC values, except in the case of the newt eggs.

DISCUSSION

Our data support the idea of 2 differentiated newt breeding phenologies with unique trophic interactions in the Moraga, California area: a pond group, which bred and developed a few weeks earlier in the season while eating higher on the food chain, and a stream group, which bred and developed slightly later while eating lower on the food chain. A number of features differentiate these 2 groups.

The first has to do with the adult life history variation that we observed between the pond and the stream. When comparing adults from the pond versus the stream, we found a significant pattern in that pond individuals had larger SVLs than their stream-breeding counterparts. It is unclear why this pattern exists. One possibility is that because the pond habitat is particularly constrained in its overall size, there is more intraspecific competition for within-pond breeding sites, which attracts and retains larger-bodied individuals with presumably higher competitive abilities. These larger individuals may also be older and more experienced.

Another possibility is that the pond itself presents a more benign physical environment

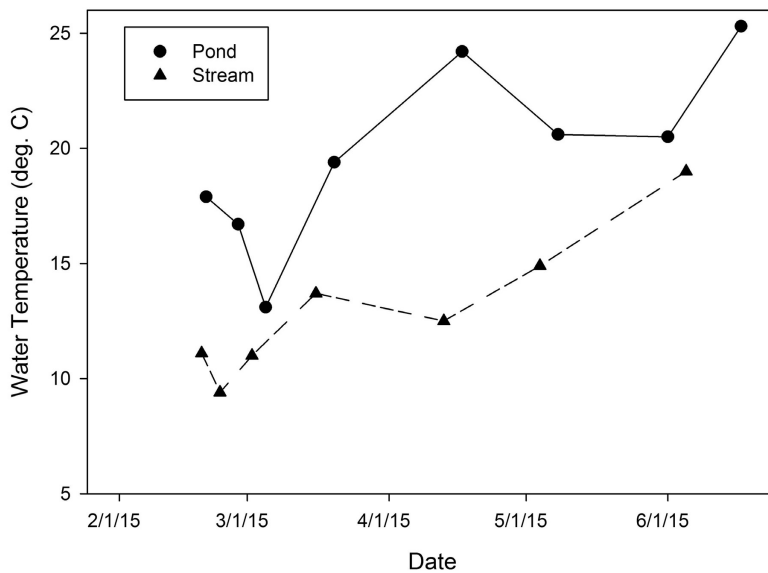


Fig. 3. Water temperature (°C) for surface waters of the pond and flowing water in Las Trampas Creek (Contra Costa County, CA) over the 5 months of the study (February–June 2015).

because it is warmer (Fig. 3), it holds an abundance of food (M.P. Marchetti personal observation), and its water is present year-round. This suite of ecological conditions provides a stable and predictable habitat throughout the breeding season. The stream on the other hand represents a more risky environment because its water is significantly cooler (Fig. 3), its food is significantly less plentiful (Marchetti personal observation), and its aquatic environment is more unpredictable in both the short term (i.e., floods/spates) and the long term (i.e., seasonal drying). The more stable pond environment may attract and retain larger, more competitive, or more experienced individuals than the riskier stream habitat does.

One way to examine the riskiness of the stream habitat would be to document over a number of years the date that surface flow ceases and determine how often the stream retains sufficient water for larvae to metamorphose and emerge. It may be that in any but the wettest years, the stream serves as a population sink for newt reproduction because it provides breeding conditions early in the year but fails to provide aquatic habitat long enough for transformation and emergence. If this is the case, the pond environment is the safer and more desirable habitat choice. Our observations of the drying times in the creek

over the last 7 years support this idea, as the creek often dries completely by mid- to late June, which is too early for the developing larvae to complete metamorphosis.

Another difference between the pond and stream is the spatial density of newts, eggs, and larvae, with the pond having much higher densities due to the limited extent of the habitat. This higher density in the pond likely impacts the diet choices of both adults and larvae by providing easier opportunities for conspecific predation. Cannibalism has been observed many times in *T. torosa* (Polis and Myers 1985, Elliott et al. 1993, Kats et al. 1994, Kerby and Kats 1998) and can be fairly common (Kats et al. 1992). Conspecific predation, if it were occurring, would have the effect of enriching δN values for the adults and larvae in the pond over individuals in the stream, similar to what is shown in Fig. 2. Future studies that examine the entirety of both aquatic communities and enumerate diet in more significant detail in the 2 locations may help elucidate the situation.

An additional difference between the 2 habitats has to do with the weight of the adult newts. The significant difference in weight observed between the pond and stream adults is likely due to the pond animals breeding approximately 2 weeks earlier than their stream

counterparts. By the time we sampled the pond adults in February, some individuals may have finished reproduction for the season, while many of the stream adults were at the beginning stages and therefore retained their terrestrial prereproductive weights. We also found that females were, in general, lighter than males, which also supports the idea that we measured the weight of some individuals post reproduction, as the females contribute more biomass to reproduction than males. Future work will need to record the reproductive status of the females.

Specific differences between the habitats can be seen in the overall trophic relationships displayed in Fig. 2. The adults and larvae have similar δN values within the ponds and streams, respectively, but very different δC values, suggesting that life stage has less effect on trophic position than on carbon source and diet choice. Adults entering the aquatic phase will carry the isotope ratio from their terrestrial food for 4–6 weeks, and it is known that δC sources differ significantly between terrestrial and aquatic foods (Bishop et al. 2014). In this study, it appears that larvae and adults are consuming different prey, but interestingly, the larvae have higher δN values than the adults. The larvae of *Taricha* are also known to be carnivorous (Petranka 1998), so one possible explanation for the enriched δN values is cannibalism by the larvae. Conspecific cannibalism could account for elevated δN levels among larvae, whereas the adult newts may be less likely to engage in this behavior because they leave soon after spawning, resulting in relatively lower trophic levels.

Conspecific predation is not the only possible explanation for the differential isotopic values. It is possible to get variation in isotope data if the newts are substantially changing their diets through time (Bardwell et al. 2007, Peterson et al. 2017), particularly with the pond individuals having about a 2-week head start in terms of development. This effect could be significant for the larvae because their diets are likely to change as they grow and as their gape and mobility increase (Bardwell et al. 2007). In addition, the underlying micro- and macroinvertebrate aquatic communities are also phenologically changing through time, which may have a significant influence on the diet of the newts (Peterson et al. 2017). In addition, the fewer negative δC values of

stream-dwelling newts suggest that some of their food derives its carbon from allochthonous inputs to the shady stream, whereas these inputs are not as available in the pond.

During this study, we were not able to sample the basal organisms in the stream or pond (periphyton and phytoplankton, respectively). This calls up the possibility that there were inherent isotopic differences between the 2 habitats and that the differences we observed were present at the base of the food chain rather than in trophic usage. While this possibility may be true for the larvae, the migrating adults coming to the 2 locations would ostensibly be drawn from the same terrestrial population and therefore not be as affected by it. Unfortunately, we are unable to rule out this possibility without future work on the system. Regardless, the differences we see in the trophic structure of the 2 systems and among life stages are interesting and suggest many avenues for further study.

It also appears that significant life history plasticity within *Taricha torosa* is reflected in the isotope variation, particularly when adult pond animals are compared with adults from the stream. At this time, it is unclear why differentiation among the adults would show up in trophic data if all of the newts were part of a single panmictic population. This question could be examined in more detail by using long-term demographic work through mark-recapture (Watters and Kats 2006, Bucciarelli et al. 2016) or by accurately aging individuals (e.g., skeletochronology) (Trenham et al. 2000).

In addition, it is worth noting that this work was completed at the end of a period of extreme drought in California (2011–2016). It would be interesting to compare the trophic niche space of all the newt life stages detailed here to the niche space in an average or a wet year in order to evaluate the impact of limited precipitation and groundwater recharge on newt diets in these systems. In general, ecologists have a fairly poor understanding of how trophic ecology changes in response to environmental shifts (Arribas et al. 2015), particularly for seasonal systems (Peterson et al. 2017). Along the same lines, it would be interesting to collect adult newt tissue before the newts enter the aquatic systems to breed, as the terrestrial portion of their diet is not well known (Thomson et al. 2016). Characterizing the terrestrial diet through stable isotopes

would involve significant methodological challenges in terms of collecting potential terrestrial prey items (Bishop et al. 2014). Future work on this species should also examine and compare egg size and the time to larval emergence between pond and stream, as some previous work has suggested that larger eggs metamorphose more quickly (Stebbins and Cohen 1995).

Taken as a whole, our results suggest that the newts inhabiting these 2 breeding locations exhibit a fair degree of ecological and life history plasticity, particularly with respect to their diets. It is possible that the newts in the 2 habitats represent independent and discrete genetic populations with rare interbreeding, although this scenario is unlikely given their proximity. More likely is the scenario that when breeding migrations are initiated, individual newts home to one of the 2 aquatic habitats in the area, resulting in 2 well-mixed populations. With this scenario in mind, it is interesting that we were able to both physically and trophically characterize the 2 groups of newts, suggesting that local ecological and environmental conditions have a large effect on the newt's life history. Appreciating the trophic plasticity of California Newts can help us understand the natural differences in freshwater ecosystems and assess the newt's ability to adjust to different environmental conditions (Arribas et al. 2015).

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LITERATURE CITED

ANTHONY, C.D., M.D. VENESKY, AND C.A.M. HICKERSON. 2008. Ecological separation in a polymorphic

terrestrial salamander. *Journal of Animal Ecology* 77: 646–653.

ARRIBAS, R., C. DÍAZ-PANIAGUA, S. CAUT, AND I. GOMEZ-MESTRE. 2015. Stable isotopes reveal trophic partitioning and trophic plasticity of a larval amphibian guild. *PLOS ONE* 10(6):e0130897. 19 pp.

BARDWELL, J.H., C.M. RITZI, AND J.A. PARKHURST. 2007. Dietary selection among different size classes of larval *Ambystoma jeffersonianum* (Jefferson Salamanders). *Northeastern Naturalist* 14:293–299.

BISHOP, M.R., R.C. DREWES, AND V.T. VREDENBURG. 2014. Food web linkages demonstrate importance of terrestrial prey for the threatened California Red-legged Frog. *Journal of Herpetology* 48:137–143.

BUCCIARELLI, G.M., D.B. GREEN, H.B. SHAFFER, AND L.B. KATS. 2016. Individual fluctuations in toxin levels affect breeding site fidelity in a chemically defended amphibian. *Proceedings of the Royal Society B, Biological Sciences* 283:art20160468. 9 pp.

BUCCIARELLI, G.M., H.B. SHAFFER, D.B. GREEN, AND L.B. KATS. 2017. An amphibian chemical defense phenotype is inducible across life history stages. *Scientific Reports* 7:art8185. 8 pp.

DAVIC, R.D., AND H.H. WELSH JR. 2004. On the ecological roles of salamanders. *Annual Review of Ecology, Evolution, and Systematics* 35:405–434.

DODDS, W.K., AND M.R. WHILES. 2010. *Freshwater ecology: concepts and environmental applications of limnology*. Academic Press, Burlington, MA. 811 pp.

ELLIOTT, S.A., L.B. KATS, AND J.A. BREEDING. 1993. The use of conspecific chemical cues for cannibal avoidance in California Newts (*Taricha torosa*). *Ethology* 95: 186–192.

FINLAY, J.C. 2001. Stable carbon isotope ratios of river biota: implications for energy flow in lotic food webs. *Ecology* 82:1052–1064.

FINLAY, J.C., S. KHANDWALA, AND M.E. POWER. 2002. Spatial scales of carbon flow in a river food web. *Ecology* 83:1845–1859.

FRANCE, R.L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Marine Ecology Progress Series* 124:307–312.

FRY, B. 2006. *Stable isotope ecology*. Springer, New York, NY. 308 pp.

HAYES, M.P., AND M.R. TENNANT. 1985. Diet and feeding behavior of the California Red-legged Frog, *Rana aurora draytonii* (Ranidae). *Southwestern Naturalist* 30:601–605.

KATS, L.B., J.A. BREEDING, K.M. HANSON, AND P. SMITH. 1994. Ontogenetic changes in California Newts (*Taricha torosa*) in response to chemical cues from conspecific predators. *Journal of the North American Benthological Society* 13:321–325.

KATS, L.B., S.A. ELLIOTT, AND J. CURRENS. 1992. Intraspecific oophagy in stream-breeding California Newts (*Taricha torosa*). *Herpetological Review* 23:7–8.

KERBY, J.L., AND L.B. KATS. 1998. Modified interactions between salamander life stages caused by wildfire-induced sedimentation. *Ecology* 79:740–745.

LAYHEE, M., M.P. MARCHETTI, S. CHANDRA, T. ENGSTROM, AND D. PICKARD. 2014. Impacts of aquatic invasive species and land use on stream food webs in Kaua'i, Hawai'i. *Pacific Conservation Biology* 20:252–271.

LAYMAN, C.A., M.S. ARAUJO, R. BOUCEK, C.M. HAMMER-SCHLAG-PEYER, E. HARRISON, Z.R. JUD, P. MATICH, A.E. ROSENBLATT, J.J. VAUDO, L.A. YEAGER, AND D.M. POST. 2012. Applying stable isotopes to examine

- food-web structure: an overview of analytical tools. *Biological Reviews* 87:545–562.
- NOGUCHI, T., AND O. ARAKAWA. 2008. Tetrodotoxin–distribution and accumulation in aquatic organisms, and cases of human intoxication. *Marine Drugs* 6:220–242.
- PETERSON, M.G., K.B. LUNDE, M.C. CHIU, AND V.H. RESH. 2017. Seasonal progression of aquatic organisms in a temporary wetland in northern California. *Western North American Naturalist* 77:176–188.
- PETRANKA, J.W. 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, DC. 587 pp.
- POLIS, G.A., AND C.A. MYERS. 1985. A survey of intraspecific predation among reptiles and amphibians. *Journal of Herpetology* 19:99–107.
- POLIS, G.A., AND D.R. STRONG. 1996. Food web complexity and community dynamics. *American Naturalist* 147: 813–846.
- SEPULVEDA, A.J., W.H. LOWE, AND P.P. MARRA. 2012. Using stable isotopes to test for trophic niche partitioning: a case study with stream salamanders and fish. *Freshwater Biology* 57:1399–1409.
- STEBBINS, R.C., AND N.W. COHEN. 1995. *A natural history of amphibians*. Princeton University Press, Princeton, NJ. 316 pp.
- THOMSON, R.C., A.N. WRIGHT, AND H.B. SHAFFER. 2016. California amphibian and reptile species of special concern. University of California Press, Oakland, CA. 390 pp.
- 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.
- TWITTY, V., D. GRANT, AND O. ANDERSON. 1964. Long distance homing in the newt *Taricha rivularis*. *Proceedings of the National Academy of Sciences of the United States of America* 51:51–58.
- VERBURG, P., S.S. KILHAM, C.M. PRINGLE, K.R. LIPS, AND D.L. DRAKE. 2007. A stable isotope study of a neotropical stream food web prior to the extirpation of its large amphibian community. *Journal of Tropical Ecology* 23:643–651.
- WATTERS, T.S., AND L.B. KATS. 2006. Longevity and breeding site fidelity in the California Newt (*Taricha torosa*): a long-term study showing the efficacy of PIT tagging. *Herpetological Review* 37:151–152.
- WETZEL, R.G. 2001. *Limnology: lake and river ecosystems*. Academic Press, San Diego, CA. 1006 pp.

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