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Coexistence within an endangered predator-prey community in California vernal pools

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Abstract

- 1. Globally endangered ecosystems, such as ephemeral wetlands, are often critical habitat for multiple interacting imperilled species. To conserve this biodiversity, managers must consider both species-specific resource requirements and mechanisms for endangered species coexistence under variable habitat conditions.
- 2. We examined communities native to California playa pools, ephemeral wetlands that have declined by >90% from their historic extent. Specifically, we describe the diet of a federally Threatened amphibian (Ambystoma californiense), and characterise interactions between this amphibian and two federally Endangered macrocrustaceans (Branchinecta conservatio and Lepidurus packardi) across three rain years to understand how these imperilled species coexist. We examined the dietary preferences of A. californiense larvae, metamorphs, juveniles, and breeding adults, and determined how prey electivity by larval A. californiense differs between natural playa pools and human-modified stock ponds.
- 3. Within playa pools, both breeding adult and larval A. californiense preyed extensively on L. packardi, whereas fully terrestrial juveniles had relatively empty stomachs. We provide evidence for size-moderated optimal foraging by larval A. californiense, and show that larval prey differed dramatically between playa pools and stock ponds. Additionally, an ontogenetic progression from smaller to larger prey gave the relatively large, endangered macrocrustaceans an earlyseason temporal refuge, during which they reached maturity in all three rain years.
- 4. Consistent with complex life cycle theory, our results suggest that ephemeral wetland habitat offers abundant food resources for A. californiense relative to terrestrial habitat. Our findings also suggest that diet flexibility facilitates the persistence of this imperilled amphibian in human-modified stock ponds. Temporal offsets in prey maturation rates and ontogenetic shifts in predator diets are likely to facilitate coexistence among the focal endangered species.
- 5. We highlight the importance of accounting for spatial and temporal variation in interspecific interactions when predicting the effects of environmental change on biodiversity, particularly in highly threatened ecosystems.

KEYWORDS

Ambystoma californiense, Branchinecta conservatio, diet, electivity, Lepidurus packardi

1 | INTRODUCTION

Understanding how species persist and coexist under variable environmental conditions is fundamental to ecology (Connell, 1975; MacArthur, 1970; Paine, 1966) and biodiversity conservation (Harley, 2011; Shochat et al., 2010; Wernberg et al., 2013). This information is critical for effectively managing declining ecosystems that harbour communities of interacting endangered species (Noss & Scott, 1995; Platt et al., 2001; Tiner, 2003). Conservation strategies aimed at protecting suites of imperilled species must account for both species-specific biological requirements and interspecific ecological interactions to identify environmental threats to population and community resilience (Decker et al., 2017; Ho et al., 2018).

Ephemeral (i.e. non-perennial) wetlands are becoming increasingly rare due to anthropogenic landscape modification and climate change (Dahl, 2014; Dalu et al., 2017; Sofaer et al., 2016). These wetlands can feature high endemism (Tiner, 2003), serve as important nodes within healthy metapopulations of wetland-dependent species (Gibbs, 1993), and act as critical stepping-stone habitat for migratory animals (Xu et al., 2019). Wetland fragmentation, degradation, and loss are often associated with population and biodiversity declines (Lehtinen et al., 1999; Simovich, 1998; Xu et al., 2019), and ephemeral wetland protection remains controversial and often extremely limited (Calhoun et al., 2017).

Wetland-dependent amphibians are relatively well-studied animals that have suffered declines due to several factors including habitat loss (Stuart et al., 2004). Many of these at-risk species have complex life cycles, with larvae occupying ephemeral wetlands, post-metamorphic juveniles and non-breeding adults restricted to terrestrial uplands, and metamorphosing juveniles and breeding adults briefly exploiting either or both habitat types (Wilbur, 1980). Complex life cycle theory posits that such a biphasic life history will be evolutionarily advantageous when: (1) ephemeral wetlands provide abundant resources that facilitate rapid larval growth and development; and (2) the transient nature of these ecosystems selects for a bet hedging strategy in which later life stages take refuge in the more stable terrestrial environment (Wassersug, 1975; Wilbur, 1980; Wilbur & Collins, 1973). Studies comparing resource consumption across all of the life stages of biphasic amphibians are lacking, leaving both room to test complex life cycle theory and a need to better identify the resource requirements of amphibians across habitat types. The latter is particularly important for declining species that require management interventions.

In this study, we describe the diet of an imperilled complex life cycle salamander, and investigate interactions between it and two endangered macrocrustaceans in ephemeral playa pools characteristic of California grassland ecosystems. The California grassland/ vernal pool ecosystem has declined by >90% from its original extent due to agricultural conversion and urbanisation (Holland, 2011), leading to concomitant declines in virtually all components of its native flora and fauna. We focus on three at-risk members of this vernal pool ecosystem: the Central distinct population segment (DPS) of the California tiger salamander (Ambystoma californiense; state and federally Threatened; Figure 1a,b; USFWS, 2004; CDFW, 2021), vernal pool tadpole shrimp (Lepidurus packardi; federally Endangered; Figure 1c; USFWS, 1994), and conservancy fairy shrimp (Branchinecta conservatio; federally Endangered; Figure 1d; USFWS, 1994). Although these species often coexist in playa pools, each species can also occupy wetlands that lack the other species (CDFW, 2020).

Ambystoma californiense has largely been extirpated from California's Central Valley due to intensive agricultural practices (Holland, 2011). Most extant populations are confined to California's Coast Range and the Sierra Nevada foothills (Fisher & Shaffer, 1996; USFWS, 2004), which are more topographically complex than the Central Valley, largely lack *B. conservatio* and *L. packardi* populations, and are dominated by human-modified stock ponds routinely used for cattle watering. Remnant *A. californiense* populations are now federally protected as three DPSs: Central (Threatened), Santa Barbara (Endangered), and Sonoma (Endangered; reviewed in USFWS, 2004). Given that all three of these DPSs demonstrate



FIGURE 1 Ambystoma californiense adult (a), A. californiense larva (b), Lepidurus packardi adult (c) and Branchinecta conservatio adult female with egg case (d). Images are not to scale. Ambystoma californiense larva photographed at Ohlone Wilderness; all other specimens photographed at Olcott Lake. Photos by Adam G. Clause

similar habitat use, comparing larval A. *californiense* diet between playa pools and stock ponds for the Central DPS should reveal the range of variation in prey communities tolerated by this imperilled, declining amphibian across its range.

In wetlands where all three focal species are found, salamander larvae and macrocrustaceans may compete for zooplankton soon after hatching, when members of all three species are small (Anderson, 1968; Pennak, 1989; Rogers, 2001). However, as they grow A. californiense larvae increasingly feed on larger prey (Anderson, 1968), probably including B. conservatio and L. packardi. In addition, differences in adult body sizes between B. conservatio and L. packardi (Eng et al., 1990; Rogers, 2001) may result in L. packardi predation on B. conservatio (Alexander & Schlising, 1997). Mechanisms that allow this suite of imperilled species to coexist as a tri-species trophic network despite negative species interactions (i.e. competition and predation pressures) remain unknown, yet may be a key to their continued persistence as a community.

Numerous mechanisms may facilitate the coexistence of the three focal species. One commonly reported mechanism in related systems is phenological asynchrony, where potentially negative interspecific interactions are mitigated by temporal offsets in species' life histories (Godfray et al., 1994; Harding et al., 2015; Rudolf, 2019). Associated with such temporal offsets are potentially stabilising ontogenetic shifts in habitat use, prey handling ability, or prey preferences that can alter predation timing and intensity (Graeb et al., 2006; Lind & Welsh, 1994). Other ambystomatid salamanders have shown shifts in dietary preferences (Sih & Petranka, 1988), suggesting that temporal offsets may be an important promoter of coexistence between A. californiense and its prey. Non-random diet electivity, in which salamanders disproportionately consume larger prey that provide a higher energetic return than smaller available prey, is another recurring observation in other ambystomatids (Denoël et al., 2007; Whiteman et al., 1996) that is consistent with optimal foraging theory (Persson & Brönmark, 2002). Non-random electivity may also serve to stabilise populations of large-bodied prey species via top-down control, and may provide non-preferred populations respite from negative interactions with either the shared predator or preferred prey species (Murdoch, 1969). Elucidating the dietary preferences of A. californiense across larval body sizes and life stages should shed light on the mechanisms that facilitate the coexistence of the three imperilled study species.

We tested three hypotheses in this study. First, frequent salamander breeding activity in human-modified stock ponds led us to postulate that larval *A. californiense* possess high dietary flexibility across habitats and prey availabilities. We tested this by comparing larval *A. californiense* diet and prey electivity between natural playa pools and human-modified stock ponds. Second, we hypothesised that larval *A. californiense* would consume more prey biomass relative to their body size than post-metamorphic life stages, reflecting greater prey availability in vernal pools compared to surrounding terrestrial habitat. The most stringent test of this hypothesis is to compare larvae with exclusively terrestrial juveniles. To accomplish this, we examined relative stomach content mass across *A. californiense* life stages using individuals sampled from playa pools and terrestrial upland habitat. Third, we hypothesised that phenological asynchrony in growth and predation facilitates larval *A. californiense* coexistence with *B. conservatio* and *L. packardi*. We tested this by quantifying *A. californiense*, *B. conservatio*, and *L. packardi* phenology and ontogeny in a natural playa pool across three field seasons to identify potential coexistence mechanisms.

2 | METHODS

2.1 | Life history of study species

Adult A. californiense migrate to wetlands during winter rain events (typically November-January; Searcy & Shaffer, 2011) to breed and deposit aquatic eggs (Storer, 1925). Aquatic larvae hatch after a minimum of 14 days, grow and develop over the following 3-6 months, metamorphose, and leave the wetland as metamorphs (Petranka, 1998). They spend an average of 4 years as fully terrestrial juveniles before reaching sexual maturity as adults, after which they typically survive for an additional 2-3 years (Trenham et al., 2000). Adults are terrestrial outside of the breeding season, but females and males spend an average of 12 and 45 days in wetlands when they return to breed, respectively (Trenham et al., 2000). Thus, from a habitat/diet perspective, the life cycle has four distinct phases: larvae that are strictly aquatic, metamorphs that transition from the aquatic to the terrestrial environment, juveniles that are strictly terrestrial, and adults that are generally terrestrial but return to the water for mating and egg-laying. Hereafter, we use the term postmetamorphic to collectively refer to the metamorph, juvenile, and adult life-stages of A. californiense.

Although also tightly linked to winter rains, life history timing differs for each of the playa pool macrocrustaceans. Branchinecta conservatio hatch as pools begin to fill from winter rains and tend to dramatically decline in abundance by April, possibly due to pool warming (Helm, 1998), an increase in predation (e.g. by wading birds; predatory insects are rare in natural playa pools; Table 1), senescence, or some combination thereof. At least 14 days after hatching (Pyke, 2005), B. conservatio mature (at body lengths of 1.5-2.8 cm) and begin reproduction (Eng et al., 1990). Adults deposit desiccation-resistant eggs (cysts) into egg cases, which are briefly held by the adult, and subsequently dropped or deposited on the pool bottom, where they enter dormancy and hatch when the pool refills (Brendonck, 1996; Hairston & Cáceres, 1996). Lepidurus packardi hatch from similarly durable cysts when pools fill with winter rain, but require a minimum of 25 days to reach sexual maturity (Pyke, 2005), and attain larger adult body sizes (1.5-8.6 cm) than B. conservatio before depositing cysts into egg cases (Rogers, 2001). Adult L. packardi often live until their pool dries completely, and some cysts can hatch after an abbreviated (8-20-day) dormancy, leading to discrete size and age cohorts within a single vernal pool (Ahl, 1991; Brendonck, 1996; Simovich, 1998).

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TABLE 1 Biomass of available prey and of larval Ambystoma californiense stomach contents from four wetlands in California, U.S.A.

		Wetland							
		Olcott		Round		Ohlone		Sunol	
Class	Order or family	Available	Diet	Available	Diet	Available	Diet	Available	Diet
Clitellata	Hirudinea	-	-	-	-	-	_	0.01	-
Gastropoda	Lymnaeidae	10.17	3.54	4.62	0.84	-	-	-	-
	Physidae	-	-	_	-	-	-	1.40	0.03
	Planorbidae	_	-	-	-	16.82	_	_	-
Arachnida	Acarina	-	-	-	_	-	0.01	0.11	0.004
	Araneae ^a	_	-	_	_	-	0.003	-	_
Branchiopoda	Chydoridae	0.14	0.002	0.3	0.001	-	-	-	-
	Daphniidae	37.55	1.51	14.61	0.09	0.18	0.01	5.37	0.54
	Macrothricidae	0.02	-	_	-	-	-	-	-
	Cyzicidae	0.002	-	0.51	0.45	19.05	_	_	_
	Triopsidae	32.2	94.76	15.07	98.39	-	_	-	-
Hexanauplia	Diaptomidae	19.61	0.01	62.72	0.04	0.34	0.0002	13.38	0.003
	Cyclopoida	_	-	0.29	0.02	_	_	0.64	0.002
Malacostracea	Amphipoda	-	-	_	-	-	_	-	0.06
Ostracoda	Podocopida	0.27	0.09	1.67	0.01	0.01	0.0003	0.37	0.01
Entognatha	Collembola ^a	-	0.0003	-	-	-	-	-	-
Insecta	Dytiscidae	0.01	_	_	_	0.02	0.01	0.005	0.004
	Chaoboridae	-	_	-	_	0.02	0.03	0.37	0.04
	Chironomidae	0.03	0.001	0.2	_	0.03	0.04	0.40	0.05
	Dipteraª	_	0.01	_	0.002	-	_	_	-
	Baetidae (nymph)	_	_	_	_	0.006	0.0003	0.28	0.03
	Aphididae ^a	_	0.001	_	_	-	0.001	_	-
	Corixidae	-	-	_	0.13	0.002	0.03	0.03	0.26
	Hemipteraª	-	-	-	_	-	0.65	-	_
	Notonectidae	0.02	0.08	-	0.04	8.05	1.3	2.34	0.98
	Coenagrionidae (nymph)	-	_	-	-	-	-	0.03	0.01
	Lestidae (nymph)	_	-	_	-	1.01	0.79	_	_
	Libellulidae (nymph)	_	—	_	_	_	—	0.20	_
Amphibia	Bufonidae or Hylidae (larvae) ^b	-	-	-	-	54.31	96.41	55.57	86.5
	Salamandridae (larvae)	-	-	-	-	0.16	0.72	19.49	11.48

Note: Entries are percentages of the total prey either available or consumed by larvae in a given wetland. Prey life stage is noted if only a single life stage was present in the samples.

^aPrey that are terrestrial.

^bBufonidae and Hylidae are indistinguishable once partially digested, and thus we combined them for analyses at the one wetland where both taxa occur.

2.2 | Study area

We studied four ephemeral wetlands located in California, U.S.A.: two playa pools at the Jepson Prairie Preserve in Solano County (Olcott Lake [33 ha; 38.271°N, 121.825°W] and Round Pond [3 ha; 38.259°N, 121.831°W]), one stock pond in the Ohlone Wilderness (0.03 ha; 37.535°N, 121.685°W), and one stock pond in the Sunol Regional Wilderness (0.08 ha; 37.528°N, 121.830°W), both in Alameda County (Figure 2). Olcott Lake and Round Pond are remnant examples of the large, natural playa pools that were common across much of the Central Valley grasslands. Olcott Lake is the largest remaining A. californiense breeding wetland, and the uplands surrounding it **FIGURE 2** Study wetland locations in California, U.S.A. sampled for *Ambystoma californiense* and aquatic prey communities



and Round Pond are among the most intact remaining examples of California's Central Valley grassland habitat (Küchler, 1977; Searcy et al., 2013). Macrocrustaceans, including *B. conservatio* and *L. packardi*, occur in both Olcott and Round. The only other documented amphibian at these pools is the ubiquitous Pacific tree frog, *Hyliola regilla*, which occurs at apparently low abundances. In contrast, the Ohlone and Sunol wetlands are human-modified stock ponds located in the oak-dominated Coast Range. Like most of the Coast Range, Ohlone and Sunol largely lack macrocrustaceans (including *B. conservatio* and *L. packardi*, although Cyzicidae are present) but contain a greater diversity of potential amphibian prey taxa, including *Anaxyrus boreas*, *Hyliola regilla*, Rana draytonii, and Taricha torosa.

2.3 | Prey availability

We collected aquatic samples using three methods to ensure broad coverage of prey types and wetland microhabitats: 2-m long surface plankton tows (17 cm diameter; 153- μ m mesh), 1-m D-net sweeps (25 cm net height; 900- μ m mesh), and 5-m long seine hauls (0.3cm mesh). We collected plankton tows and D-net samples at four widely separated locations across each breeding wetland. We collected four seine hauls each at Olcott Lake and Round Pond (both on 19 April 2010), three at Sunol (12 May 2010), and two at Ohlone (25 June 2010; see full sampling schedule in Table S1 of Supporting Information). These seine hauls covered a large portion of the surface area of the Sunol and Ohlone ponds when sampled, and coefficients of variation for prey types across seine hauls suggest that sampling was representative of the aquatic prey available at Olcott Lake and Round Pond, which are larger, shallower, largely unvegetated, and appear to have little habitat heterogeneity (see Supporting Information for additional discussion of the coefficients of variation). Although the sampling date differed among our study wetlands (Table S1), all four were sampled when A. californiense were at approximately the same point in their development (see below), and prey sampled at each site appeared representative of each wetland community based on previous observations. We weighed and released all captured vertebrates and endangered macrocrustaceans $(n \le 20 \text{ individuals per species, after which we only counted addi$ tional individuals; see Supporting Information for further detail). We preserved all other taxa in 95% ethanol, identified prey items to the lowest taxonomic level possible using standard references (Johnson & Boyer, 2005; Merritt et al., 2008; Thorp & Covich, 2009), dried them on filter paper, and weighed each to the nearest microgram (see Supporting Information for additional detail).

To acquire terrestrial samples of available prey, we opened four pitfall traps within 300 m of Olcott Lake's shoreline for 1 week. These traps were part of a drift fence array used in a long-term ⁶ WILEY - Freshwater Biology

mark-recapture project at Olcott Lake (Searcy et al., 2014, 2015; Searcy & Shaffer, 2016). We filled each 1-gallon trap with a 2.5-cm layer of antifreeze to attract insects (Ni et al., 2014), and covered the trap with 1-cm mesh screen to prevent A. californiense capture. We collected terrestrial samples on 19-26 February and 18-25 May 2010 (Table S1). We did not collect terrestrial samples at Ohlone or Sunol since we lacked drift fences at those sites. Round Pond has a relatively small adult A. californiense breeding population (Searcy et al., 2013) and is only a few hundred metres from the much more robust Olcott population, so we concentrated our terrestrial sampling solely at Olcott Lake.

2.4 Stomach flushing

Stomach flushing is a more accurate method for identifying prey selection in amphibians than faecal analysis (Costa et al., 2014), and we followed the procedures used by Mahan and Johnson (2007). We used a small catheter (1 mm internal diameter) and a large catheter (1.6 mm) to stomach flush larval and postmetamorphic A. californiense, respectively. We attached the catheter to a 60-ml syringe filled with tap water, inserted the free end (with its tip removed) through the mouth to the stomach, and then flushed the stomach until all food was regurgitated into an enamel tray. We determined this to be an effective method based on a pilot study using 10 captive adult A. californiense from the University of California, Davis (UC Davis) breeding colony, where we fed each salamander a cricket and stomach flushed it the next day. In all cases, stomach flushing captive animals caused regurgitation of the cricket, with no short- or long-term ill-effects on the salamander. However, one adult and five larval A. californiense died following stomach flushing in the field. After flushing, we immediately stored stomach contents in 95% ethanol and identified prey items to the lowest taxon possible using standard references (Johnson & Boyer, 2005; Merritt et al., 2008; Thorp & Covich. 2009).

When we sampled available prey, we also stomach flushed each A. californiense life stage/sex class found in that habitat (Table S1). To minimise any negative effects of stomach flushing, we sampled pools when the mean larval size reached the observed minimum for metamorphosis (50 mm snout-to-vent length [SVL]). We collected larvae using a minnow seine, and flushed 23 larvae from Round Pond (mean $SVL = 51.7 \text{ mm} \pm 5.2 \text{ SD}$) on 18 April 2010, 20 larvae from Olcott Lake (SVL = 58.9 mm \pm 5.0) on 19 April 2010, 20 larvae from Sunol $(SVL = 53.1 \text{ mm} \pm 3.8)$ on 10 May 2010, and 20 larvae from Ohlone $(SVL = 59.5 \text{ mm} \pm 11.7)$ on 26 June 2010. We also measured SVL and released larvae at the point of capture. Holomuzki and Collins (1987) showed that sampling 9-10 larvae of an ecologically similar congener (Ambystoma mavortium) is sufficient to thoroughly describe the diversity of taxa being eaten by larvae within a wetland. By doubling this sampling effort, we are confident that our larval A. californiense sample sizes were adequate to determine the range of prey types consumed in our study wetlands.

We captured post-metamorphic A. californiense at our drift fence array at Olcott Lake either 10, 100, 200, or 300 m from the pool's shoreline. We stomach flushed six juveniles, 15 adult females, and 18 adult males captured 13 January-4 March 2010, when the majority of adult salamanders were migrating away from the pool following breeding and terrestrial juveniles were surface active (Table S1). On 17 May 2010, we detected the first emerging metamorphs from the pool and stomach flushed 20 metamorphs on 17-19 May (Table S1). We weighed all post-metamorphic salamanders to the nearest 0.1 g using a hand-held digital scale (HH 120D, Ohaus Corp.), took a digital image of juvenile and adult dorsal spot patterns to ensure that all sampled individuals of these life stages were unique captures (Searcy & Shaffer, 2011), and immediately released all post-metamorphic individuals into appropriate rodent burrows near the point of capture.

Statistical analysis of diet samples 2.5

We used an electivity index to measure each A. californiense larva's preference for different prey taxa relative to those prey taxa's availability in the environment (Dodd, 2010). We guantified the relative abundance (by biomass) of prey items found in larval stomach contents (i.e. proportion of prey type [k] in an individual's stomach contents $[r_{\nu}]$ and in the environment (p_{ν}) , and calculated an electivity index (D) for different prey taxa by each salamander using equation 12 from Jacobs (1974):

$$D_k = \frac{r_k - p_k}{r_k + p_k - 2r_k p_k}$$

Electivity ranged from 1 (complete selection of prey type) to -1 (complete avoidance of prey type), with $D_k = 0$ indicating consumption in equal proportion to prey availability in the environment (Jacobs, 1974). We statistically compared electivity values for the four most abundant prey types in each study wetland (i.e. those that comprised the greatest percentage of total prey biomass available in the environment, calculated from standardised volumes of water sampled, field counts of prey captured, and mean dry mass measurements; see Supporting Information for further details). In each case, these four taxa accounted for >93% of the available prey biomass.

Because electivity values were not normally distributed, we performed non-parametric Kruskal-Wallis tests to determine dietary preferences of larval A. californiense in each of the four study wetlands. We included individual larval identity as a blocking effect and conducted a post hoc Steel-Dwass test to determine which prey categories were most selected. We also used a Kruskal-Wallis test to identify whether mean electivity for the largest prey type (i.e. the prey species with the largest mean body size) found in each study wetland at the time of sampling differed between wetlands. There was high variance in electivity among larvae, which we postulated was partially due to variation in larval body size and the inability of smaller larvae to feed on the largest available prey. To test for this

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effect, we binned individual larval electivity values for the largest prey type in each wetland as avoided = 0 when electivity <0, and se*lected* = 1 when electivity >0. We then conducted a logistic regression between binned electivity for the largest prey type and larval SVL. To further examine the relationship between larval body size and the importance of large prey in the diet, we conducted a linear regression between larval SVL and number of large prey (>20 mg dry mass) in stomachs

Differences in the prey consumed by larval A. californiense among study wetlands may have implications for larval growth and survival. To begin addressing this possibility, we calculated body condition as a proxy for larval fitness and compared larval body condition between natural and human-modified wetlands. We calculated body condition across all sampled larvae by taking the residuals from a linear regression of log-body mass versus log-SVL (Jakob et al., 1996). We then performed a linear mixed model with larval body condition as the response, wetland type (natural or human-modified) as the predictor, and wetland identity as a random effect.

Stomach contents of post-metamorphic A. californiense did not fully overlap with the invertebrates collected in the four pitfall traps, indicating that we incompletely sampled the terrestrial prey community. Therefore, we did not calculate electivity for the post-metamorphic life stage/sex classes. To examine variation in resource acquisition across life stages, we divided stomach content dry mass by salamander body mass (live weight pre-flushing) and shuffled this ratio 1,000 times to determine whether the observed proportion of individual body mass accounted for by stomach content differed between life stage/sex classes more than expected by chance. Since we only collected post-metamorphic life stages from Olcott Lake, we excluded larvae from other wetlands in this comparison. We conducted all statistical analyses in either JMP Pro 14.0 (SAS Institute Inc., 2019) or R Software v. 4.0.0 (R Core Team, 2020).

2.6 Tri-trophic phenology and ontogeny

Preliminary diet analysis suggested an important trophic connection between A. californiense, L. packardi, and B. conservatio. To understand the temporal dynamics of this relationship, we measured the growth of these three species during three rain years from 2010 to 2013 (Table S1). Based on 1893-2017 climate records from Vacaville, CA (Lawrimore et al., 2011), the 2010-2011 rain year had above-average precipitation (125% of mean) and Olcott remained inundated from 22 November throughout the A. californiense larval period. The 2011-2012 rain year had below-average precipitation (79% of mean) and Olcott initially filled on 21 January, dried completely by 10 March, and refilled starting 15 March. Precipitation in 2012-2013 was also below-average (71% of mean), but Olcott held water from 1 December-20 May. We seined the same 30-m section of Olcott every 7-14 days while the pool held water in all three years to document mean body sizes over time for A. californiense, L. packardi, and B. conservatio. Because the aquatic stages of each

species typically persist over multiple months (see Life History of Study Species subsection), we considered this an adequate sampling interval to document changes in mean body sizes. For each sampling event, we haphazardly selected up to 20 individuals of each of our three target species, measured length to the nearest 1 mm using a ruler, and recorded whether macrocrustaceans had cysts in their egg cases. We visually compared growth curves of our focal species through time using the LOESS method via the stat-smooth command from the ggplot2 package in R (Wickham, 2016).

3 RESULTS

3.1 | Dietary characteristics of A californiense

Larval A. californiense diet included prev from 30 different families (11 families in the two playa pools and 16 or 17 families in each of the two stock ponds; Table 1). In three of the four wetlands, a single prey type comprised \geq 95% of the diet. In the playa pools, this predominant prey item was L. packardi, which composed 95% and 98% of larval diet in Olcott Lake and Round Pond, respectively. In the stock ponds, the predominant prey items were tadpoles: H. regilla comprised 96% of the Ohlone diet, while a combination of H. regilla and A. boreas comprised 87% of the Sunol diet. Despite different diets, larval body condition did not differ between the natural and human-modified study wetlands (p = 0.51).

At each site, A. californiense larvae exhibited significant variation (p < 0.0001) in their electivity indices for the four most common prey types (Figure 3). In each case, the prey type with the largest body size was the most preferred, and mean electivity for the largest prey did not differ among the study wetlands (p = 0.11). The probability of selecting the largest prey increased with larval body size (p = 0.007). Specifically, the largest prey types were avoided by larvae with SVL < 44 mm, whereas larvae that exceeded this minimum size increasingly selected the largest prey (Figure 4a). Larger larvae were also more likely to have eaten a greater number of large prey (p < 0.0001; Figure 4b). Together, these results indicate that A. californiense larvae select the largest prey available in the wetland once they are no longer limited by gape size.

Diets of post-metamorphic A. californiense included prey from 22 different families (10 aquatic and 12 terrestrial). Lepidurus packardi was again the most common prey item for the three life stage/ sex classes that had recently been in the aquatic environment (91%, 94%, and 71% of metamorph, adult male, and adult female diets, respectively). Other important aquatic prey were Lymnaeidae and Daphniidae, which accounted for 6% and 3% of the metamorph diet, respectively. The most important terrestrial prey items were Carabidae (11% of juvenile diet), larval Noctuidae (22% of juvenile diet), Raphidophoridae (4% and 11% of adult male and adult female diet, respectively), Scolopendridae (13% of adult female diet), and Tipulidae (66% and 3% of juvenile and adult female diet, respectively). No other prey items accounted for > 1% of the diet of any life stage/sex class.



FIGURE 4 Relationships between *Ambystoma californiense* larval body size and (a) binned electivity for the largest available prey item, where *avoided* = 0 and *selected* = 1, and (b) number of large (>20 mg dry mass) prey items found in the stomach. Both panels display the pooled data from four wetlands in California, U.S.A. Circles represent individual larvae, and are jittered in panel (a) by a factor of 0.3 to improve the visibility of overlapping points. These results illustrate the ontogenetic shift in larval *A. californiense* as they switch to consuming large-bodied prey (a) and more of them (b) once they are no longer gape/size limited

The proportion of total salamander mass comprised of stomach contents varied significantly across A. *californiense* life stages (p < 0.0001; Figure 5). Larval stomach contents comprised the greatest proportion of total mass, and zero of 20 larvae sampled at Olcott Lake had empty stomachs. Metamorphs, juveniles, and adult males had the smallest proportions of body mass comprised of their stomach contents. Eleven of 20 sampled metamorphs had empty stomachs, indicating that most A. *californiense* were not feeding (or were unable to capture prey) during this morphological and ecological transition.

3.2 | Tri-trophic phenology and ontogeny

Our 2010–2011 temporal sampling of the size distributions of cooccurring *A. californiense*, *B. conservatio*, and *L. packardi* at Olcott Lake revealed that *B. conservatio* was largest until mid-March, when it was surpassed by *L. packardi* (Figure 6). During mid-March sampling, 12 of the 20 measured *L. packardi* were actively consuming a *B. conservatio*. Prior to this sampling, we found only one of the 200 measured *L. packardi* eating a *B. conservatio*. This suggests that *L. packardi* must achieve a relative size advantage over *B. conservatio*



FIGURE 6 Growth curves of Ambystoma californiense larvae, Branchinecta conservatio, and Lepidurus packardi measured every 7-14 days at Olcott Lake, California, U.S.A. from 22 November 2010-1 July 2011. This was a normal rain year (125% of the 124-year average precipitation) when rainfall patterns resulted in continuous pool inundation. We considered B. conservatio and L. packardi sexually mature once at least 50% of females or 50% of hermaphrodites, respectively, were observed to be carrying egg cases with cysts. Macrocrustaceans of this tri-trophic food chain reach sexual maturity before the next-largest species gains a size advantage over them and begins to consume them as prey. Branchinecta conservatio and L. packardi sizes are total lengths, while A. californiense sizes are larval snout-to-vent lengths

before preying successfully on B. conservatio. By the next sampling period in late March, the B. conservatio population had declined to <40% of that in mid-March and never recovered. However, the

majority of B. conservatio matured by mid-January and deposited cysts well before L. packardi predation began. Stomach flushing of A. californiense larvae indicated that they also must reach a size

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threshold (SVL c. 47 mm) before they can eat *L. packardi*. Most *A. californiense* larvae reached this size threshold in late April. There was no discernible change in the *L. packardi* population in mid-May, but by late May it started to decline and *L. packardi* were exceptionally rare by early June. However, the majority of *L. packardi* were mature and carrying cysts by mid-March, well before the onset of intense *A. californiense* predation.

The relative growth patterns observed among our three focal species in 2012-2013 were similar to those observed during the 2010-2011 rain year despite lower total precipitation (Figure S1). However, this was not the case during the unusual precipitation pattern of 2011-2012. Although all three species demonstrated some hatching success following pool refill, *L. packardi* and *A. californiense* never reached the minimum relative size advantage needed to eat *B. conservatio* and *L. packardi*, respectively (Figure S2). Despite reduced predation by *L. packardi*, *B. conservatio* still demonstrated a rapid decline in abundance comparable to the other two study years (Figure S2). No *A. californiense* metamorphs were recruited in 2011-2012 because the pool dried before larvae reached the minimum body size required for metamorphosis.

4 | DISCUSSION

Our study provides the first comprehensive view of *A. californiense* diet within and across life stages, and the first detailed investigation of a tri-trophic food chain in this imperilled ephemeral wetland community. Because our primary focus was from the top-down perspective of *Ambystoma* larval feeding ecology, we first discuss *A. californiense* diet in the context of our first two study hypotheses, followed by our third hypothesis regarding the more complex three-species interactions as they relate to endangered species coexistence.

4.1 | Dietary characteristics of A. californiense

Two previously unrecognised aspects of larval A. *californiense* predation—their flexibility with respect to prey species and consistent electivity for large prey—are important for understanding their basic ecology and conservation.

A species' ecological success and conservation options are in part determined by its ability to tolerate variation in environmental conditions (Calosi et al., 2008; Razgour et al., 2019). Although natural *A. californiense* habitat has dramatically declined due to agricultural conversion and urbanisation (Davidson et al., 2002; Holland, 2011), well-known *A. californiense* breeding activity in human-modified stock ponds, coupled with our extensive field observations that the prey base of such ponds is very different from that in natural playa pools, led us to hypothesise that larval *A. californiense* possess high dietary flexibility that facilitates their persistence in this altered breeding habitat. Our findings support this hypothesis. In natural playa pools, *L. packardi* was strongly preferred by larval A. californiense, comprising ≥95% of the diet of later-stage larvae. However, L. packardi are mostly absent from pools in the Coast Range, Sonoma and Santa Barbara Counties, and many of the remaining playa pools in the Central Valley. In stock ponds at Ohlone and Sunol, larval A. californiense maintained their preference for the largest prey items, demonstrating comparable mean electivity values to larvae from natural playa pools, but shifted to anuran tadpoles in the absence of L. packardi. Dietary shifts between different invertebrate species have also been observed in ambystomatid salamanders in disturbed versus undisturbed stream reaches (Ruiz-Martinez et al., 2014). The comparable electivity for alternate large prey and the observed equivalency of body conditions suggest that the observed vertebrate-rich larval diet in human-modified wetlands may be nutritionally equivalent to that based on large invertebrate prey. However, additional studies of how these very different prey communities might affect A. californiense growth. survival. and reproduction are needed to fully uncover potential fitness consequences of this dietary shift.

The feeding ecology of most wetland-breeding amphibians includes both larval and post-metamorphic life stages. This complexlife-cycle strategy led to our second hypothesis: the aquatic phase provides an opportunity for rapid growth and development supported by an abundant prey base, and larval A. californiense thus consume more prey biomass relative to their body size than the post-metamorphic life stages. Again, our empirical results support this hypothesis. Larval A. californiense had much fuller stomachs than metamorphs and fully terrestrial juveniles. Over 50% of metamorphs had empty stomachs as they entered the terrestrial phase of their life cycle. This suggests that metamorphosing salamanders either dramatically reduce foraging effort during this energetically costly transition (Pandian & Marian, 1985), become inefficient at foraging, potentially due to reduced buccal pressure for carrying out aquatic suction feeding as has been experimentally demonstrated in the closely related A. mavortium (Lauder & Shaffer, 1986), or experience reduced food availability during the water-to-land transition. Stomach contents of A. californiense juveniles, the only fully terrestrial life stage, were similarly limited, suggesting relative prey scarcity or foraging inefficiency within the terrestrial environment, and illustrating the ecological advantage of a complex life cycle that includes the ephemeral aquatic environment (Wassersug, 1975; Wilbur, 1980; Wilbur & Collins, 1973). Such advantages of complex life cycles have been demonstrated by comparing aquatic and terrestrial salamander species (Jaeger, 1981), but we know of no other studies comparing intraspecific diets across aquatic and terrestrial salamander life stages. The observed differences in stomach biomass between larvae and juveniles may account for the much faster growth of larvae, which double in mass every c. 2 weeks during c. 4.5 months in the aquatic environment, whereas terrestrial juveniles typically triple in mass over c. 2.5 years (Searcy et al., 2014).

Because consuming larger prey has been hypothesised to be energetically advantageous for gape-limited predators (Forsman, 1996), our finding that larval *A. californiense* preferentially consume prey taxa with the largest body sizes is consistent

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with expectations from optimal foraging theory. In keeping with gape limitation documented in congeners (Smith & Petranka, 1987), our few samples from larval A. *californiense* <44 mm SVL suggest that these larvae were restricted to smaller prey items, and thus that larger prey had a size refuge early in the inundation period. Although we were unable to safely flush the stomachs of smaller larvae, our results agree with ontogenetic changes in prey size observed in other *Ambystoma* species (Bardwell et al., 2007; Sarma et al., 2017; Whiles et al., 2004).

Diet of adult A. californiense during the relatively brief aquatic breeding period has never been documented before. We found that adult A. californiense leaving the pool following breeding had proportional stomach content masses intermediate between those of larvae and juveniles, with adults again consuming primarily the largest aquatic invertebrates (particularly *L. packardi*). This result suggests that adults also exploit the rich aquatic food resources available during the breeding season. However, like metamorphs, adults may be less efficient at capturing aquatic prey than larvae (Lauder & Shaffer, 1986, 1988; Shaffer & Lauder, 1988), or are less voracious given the lower energetic demands of reduced growth rates (Searcy et al., 2014). Post-metamorphic A. mavortium also exploit aquatic resources to obtain high-energy prey items (Denoël et al., 2007; Whiteman et al., 1994, 1996). Although poorly understood, foraging in wetlands may be an important part of breeding adult energy budgets. Abundant aquatic prey resources may therefore contribute to adult body condition, larval growth, and size at metamorphosis, all of which increase fitness in the terrestrial environment (Scott, 1994; Searcy et al., 2014).

It is possible, but unlikely, that we missed soft-bodied prey that digest rapidly. We found little unidentifiable material in *A. californiense* stomach contents, suggesting that the consumption of softbodied prey was infrequent, or its passage was extremely rapid. We do not expect that the relatively soft-bodied *B. conservatio* would have degraded in this manner, because fairy shrimp have been regularly identified in the stomach contents of *A. mavortium* (Denoël et al., 2007; Whiteman et al., 1994, 1996), suggesting that they are retained long enough for identification if they are eaten. Future research involving genetic sequencing of stomach contents or faecal matter would help settle these issues (Unger et al., 2020).

Because our results indicate that both adult A. *californiense* at Olcott Lake and larval A. *californiense* at all four study wetlands preferentially feed on large-bodied prey, managing breeding wetlands to sustain abundant communities of such prey is likely to support local A. *californiense* population viability. Our findings indicate that A. *californiense* populations are likely to persist where *L. packardi* become extirpated as long as an alternative large-bodied prey source is available. However, in natural playa pools such as those found at Jepson Prairie, where anuran larvae are scarce, the loss of *L. packardi* could negatively affect both larval and breeding adult A. *californiense* fitness, possibly leading to population declines. We encourage conservationists to consider these important aspects of A. *californiense* biology when managing natural, created, and restored breeding pools to benefit this imperilled predator.

4.2 | Tri-trophic phenology and ontogeny

Our final hypothesis stated that phenological asynchrony in resource use promotes the coexistence of larval A. californiense, B. conservatio, and L. packardi. Supporting this hypothesis, our regular aquatic sampling during three consecutive rain years revealed that the coexistence of imperilled A. californiense, B. conservatio, and L. packardi at Olcott Lake (and presumably in other remnant California playa pools) is facilitated by temporal offsets in growth and reproduction, and consequent ontogenetic prey shifts, among these species. This system is best described as one with early arrival advantage and size-mediated priority effects, both of which are common properties of wetland ecosystems (Fukami, 2015: Rasmussen et al., 2014). In those years when the pool held water continuously through A. californiense metamorphosis (2010-2011 and 2012-2013), B. conservatio largely escaped predation by L. packardi until mid-March, when the majority of females had already bred and deposited their durable cysts. In 2011, after L. packardi exceeded B. conservatio in size, we observed a dramatic increase in L. packardi predation of B. conservatio and subsequent decline in B. conservatio densities, consistent with population-level effects of *L. packardi* predation. However, a similar decline of B. conservatio observed in the 2011-2012 rain year when predation by L. packardi was limited illustrates the existence of alternative drivers of decline, such as water temperatures exceeding the thermal tolerance of *B. conservatio* (Helm, 1998), increases in other sources of predation, or senescence. The first generation of L. packardi also had a size refuge from predation by A. californiense until mid-to-late April, by which time most L. packardi were carrying cysts. Cysts were thus available within the pool to give rise to the next generation of L. packardi both within the same wet season and in future years (Ahl, 1991). Based on diet samples, the body size threshold for L. packardi predation by A. californiense was a larval SVL of c. 47 mm, and an increase in A. californiense predation throughout the larval period presumably contributed to the decline in L. packardi abundance starting in late May 2011. This balance between reproductive timing in both macrocrustacean prey species and growth of their relevant predator is likely to be the result of strong selective pressures under historic habitat conditions. Evidence from other wetland communities similarly suggests that the presence and phenology of larval Ambystoma is a powerful selective agent on prey growth rates and body sizes (Urban, 2007).

Predation pressures probably also shape the number of generations produced by each prey species per inundation period (one for *B. conservatio* and sometimes multiple for *L. packardi*). *Branchinecta conservatio* has large range overlap with *L. packardi*, coexisting with that species across 86% of its known populations (CDFW, 2020). The predation exerted by *L. packardi* later in the inundation period probably selects for a single, intense bout of early *B. conservatio* reproduction. *Lepidurus packardi*, on the other hand, has limited range overlap (19% of recorded observations) with *A. californiense* (CDFW, 2020), and may be a top aquatic predator in many wetlands that it occupies. Multi-generation breeding within a single inundation period by *L. packardi* may therefore be beneficial across much WILEY Freshwater Biology

of its range, although less often favoured in the presence of A. *californiense*. Throughout our sampling, we observed a unimodal body size distribution for *L. packardi*, suggesting that a second generation either never hatched or unsuccessfully recruited in the presence of *A. californiense* predation.

The contrast between the atypical 2011-2012 rain year, when Olcott Lake prematurely dried in March, and the years when Olcott Lake remained inundated throughout the spring, underscores the roles of phenology and ontogeny in this system. Although cysts of both macrocrustaceans were able to hatch upon pool refill in 2012 and some A. californiense adults successfully bred during the refill period, L. packardi adults and A. californiense larvae never achieved body sizes required to exert significant predation pressures on *B. conservatio* or *L. packardi*, respectively. Moreover, A. californiense larvae failed to recruit at Olcott Lake in 2011-2012 because the pool redried before larvae attained the minimum body size required for metamorphosis. These results suggest that truncating development time before summer dry down-due either to inconsistent/insufficient rainfall or more rapid wetland drying (e.g. under increased temperatures)-may negatively affect A. californiense population viability and limit the energetic resources available to L. packardi. Unfortunately, forecasted higher mean temperatures and less predictable precipitation patterns in California (Vaghefi et al., 2017) will probably lead to greater frequencies of shortened and interrupted wetland hydroperiods. This climate change will be likely to shift hatch dates and growth trajectories of all three species (Shin & Kneitel, 2019), but not relative arrival timing given the shared cue of wetland filling. Our data from the 2011-2012 rain year suggest that increasingly frequent and intense drought years with shortened hydroperiods should favour species with short generation times (like B. conservatio) over those requiring long, consistent inundation (such as A. californiense). Developing a comprehensive view of the long-term consequences of altered predator-prey dynamics in California's playa pools under climate change will require obtaining species-specific growth rates and survivorship curves (Ewald et al., 2013), presenting a fascinating, but challenging system for future ecological modeling and conservation management alike.

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AUTHOR CONTRIBUTIONS

A.M. was primarily responsible for writing the manuscript and producing figures, and contributed to statistical analyses. C.S. and A.C. led the collection of field data. Additionally, A.C. processed samples and contributed to figure design and production. S.C. contributed significantly to laboratory data collection, analyses, and writing the Materials and Methods. H.B.S. and C.S. were primarily responsible for experimental design. C.S. performed and supervised statistical analyses, and contributed significantly to the writing of the Materials and Methods and Results. All coauthors contributed substantially to revisions of the submitted documents.

DATA AVAILABILITY STATEMENT

The data and R scripts that support the findings of this study are openly available on Dryad at https://datadryad.org/stash/dataset/ doi:10.5061/dryad.zpc866t7x (Messerman et al., 2021).

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SUPPORTING INFORMATION

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