ECOLOGICAL CONTEXT OF SIZE EXTREMES AT METAMORPHOSIS IN THE CALIFORNIA TIGER SALAMANDER (*AMBYSTOMA CALIFORNIENSE*)

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ABSTRACT—Our goal was to determine the minimum and maximum size at which California tiger salamanders (*Ambystoma californiense*) metamorphose. We analyzed museum specimens, a subset of larval salamanders collected in our own fieldwork, and data reported in the literature. Our data suggest that California tiger salamanders enter or complete metamorphosis at sizes smaller and likely larger than previously reported. This wide range in metamorph body size may be an adaptation for living in unpredictable regions of the arid West, where hydroperiods of aquatic breeding sites can range from vernal to perennial, and that historically understudied perennial reservoirs may account for the recently observed maximum size at metamorphosis.

RESUMEN—Nuestro objetivo fue determinar el tamaño mínimo y máximo en el que las larvas de salamandras tigre de California (*Ambystoma californiense*) experimentan metamorfosis. Analizamos especímenes de museos, un subconjunto de larvas de salamandras recolectadas en nuestro propio trabajo de campo y datos reportados en la literatura. Nuestros datos sugieren que las salamandras tigre de California inician o terminan la metamorfosis en tamaños más pequeños y posiblemente más grandes de lo reportado anteriormente. Esta amplia distribución de tamaños corporales de los metamórficos puede ser una adaptación para vivir en regiones impredecibles del oeste árido, donde los hidroperiodos en los sitios acuáticos de reproducción pueden variar de temporal a perenne y que reservas perennes históricamente poco estudiadas pueden explicar los tamaños máximos recientemente observados en la metamorfosis.

In the complex life cycles of amphibians, metamorphosis is the transition from an aquatic larval stage to a terrestrial adult stage. Although amphibian metamorphosis has been well studied, many aspects remain relatively enigmatic. Size at metamorphosis is highly relevant to fitness; larger individuals have considerable developmental advantages over smaller larvae (Calef, 1973; Morin, 1983; Hecnar and M'Closkey, 1997). Several factors contribute to metamorphic size and timing in amphibians. Some, such as hormonal cues, are intrinsic (inherent, or internal). Others, including larval density (crowding), water temperature, and pond hydroperiod (days per year that an area of land is wet), are extrinsic pressures, which can be wide-ranging and variable (Gilbert and Frieden, 1981; Semlitsch et al., 1988; Duellman and Trueb, 1994; Stebbins and Cohen, 1995; Ryan and Semlitsch, 1998). Wilbur (1980) reported that species that experience uncertain extrinsic conditions appear to exhibit a wider range of possible sizes at metamorphosis. He further stated that larval density alone has a demonstrable and predictable effect on metamorphic size and timing (see also Morin, 1983). When not overcrowded, larvae grow quickly and metamorphose early. Conversely, Wilbur and Collins (1973) and Wilbur (1980) found that at higher densities, competition for food influences the size at and timing of metamorphosis, favoring faster-growing larvae. In a simple, sensitive model that fits many pond-breeding amphibians, they established a predicted upper and lower threshold for body size and timing of metamorphosis relative to larval density. This predictive model has held up to testing by many researchers (e.g., Gilbert and Frieden, 1981; Scott, 1994; Stebbins and Cohen, 1995; Ryan and Semlitsch, 1998; Morey and Reznick, 2000), and some researchers have even expanded its use to predict how larval-stage development affects fitness and survival in the adult life stage (Semlitch et al., 1988; Taylor and Scott, 1997).

Wilbur (1980) argued that predation risk for amphibian larvae is size dependent because larvae can outgrow most of their insect predators and often transition to land before predation by aquatic insects becomes a limiting factor. This timing dependence may be true for early breeders like the California tiger salamander (*Ambystoma californiense*), which are among the earliest breeders and lay comparatively large eggs compared with their insect predators, giving them a developmental head start (Storer, 1925). Studies have concluded that anuran larvae attain a size threshold at which predation is suddenly escaped (sensu Calef, 1973; Morin, 1983). Beneath that threshold, predation may reduce density-dependent food limitation, releasing survivors from competition and allowing a faster growth rate (Wilbur, 1980). We know of no research that has investigated a threshold in the relationship between insect predators and larval California tiger salamander, but within ephemeral ponds, California tiger salamander is often the largest predator in the community, sometimes cannibalizing smaller larvae (pers. observ.).

The duration of metamorphosis differs among amphibian species. Anuran larvae undergo substantial changes in development (i.e., external and internal morphologic, physiologic, and anatomic changes) and require commensurate time to metamorphose (Gilbert and Frieden, 1981). Urodeles such as California tiger salamanders, however, develop their limbs within a few days after hatching (Anderson, 1968; Salthe and Mecham, 1974). Successive metamorphic stages unfold rapidly, with the resorption of gills and tail fin, development of pigments and glands, and the further development of leg muscles (Etkin, 1964; Harrison, 1969). In essence, their morphology is already adultlike shortly after hatching, and full transformation—after the cue to metamorphose—usually occurs within a few days, a distinct advantage for exploiting ephemeral ponds for reproduction.

Some amphibians have adapted to exploit transient opportunities for growth or dispersal such as ephemeral aquatic environments in the arid western United States (Wilbur, 1980; Shaffer et al., 2004). The California tiger salamander, which occurs in a north-south distribution from Yolo County to Santa Barbara County, within the Sierra Nevada Foothills, the North and South Coast Range, and portions of the Central Valley, is an upland salamander—spending 9–11 months of the year in upland areas, typically in rodent burrows (Loredo and Van Vuren, 1996; Stebbins and McGinnis, 2012). They make migratory movements toward aquatic breeding habitat in winter, where adults remain for weeks to months, before moving back into uplands (Jennings and Hayes, 1994; Alvarez et al., 2021).

The California tiger salamander has adapted to reproducing in ephemeral vernal pool habitats of California (Anderson, 1968; Shaffer et al., 2004), but its size extremes at metamorphosis have historically been understudied. Our purpose here is to report new minimum and maximum thresholds for size at metamorphosis in California tiger salamanders and to establish a link between newly reported upper thresholds and the recent discovery that this urodele takes advantage of perennial, human-made water bodies as part of its reproductive strategy.

Materials and Methods—We reviewed information from peer-reviewed published data, museum collections, and our own unpublished personal observations. Field data were also collected from ephemeral ponds at the Blue Oak Ranch (BORR), Santa Clara County, California (37°22′54.0912″N, 121°44′14.2584″W, 675 m). The BORR is a 1,300-acre reserve owned and operated by the University of California, Berkeley. The site is a mixed oak woodland with annual grasslands and is located approximately 8 km east of the southern portion of San Francisco Bay. It falls within the California Floristic Province at an elevation of between 550 and 920 m. For a more complete site description of BORR, see Wilcox et al. (2004). We collected California tiger salamanders with hand-held dip nets and temporarily maintained them in plastic 19-L buckets filled halfway with pond water from the site. We measured the live specimens we handled to the nearest 1.0 mm and museum specimens to the nearest 0.5 mm to compensate for possible desiccation. We released all animals alive at the site of capture.

The California tiger salamander is endemic to California, and all our data refer to locations in this state. We differentiated California tiger salamanders from nonnative barred tiger salamanders (*Ambystoma mavortium*) on the basis of previously conducted genetic analysis that reported that the populations we examined included California tiger salamanders and did not include nonnative tiger salamanders or admixed individuals (Wilcox et al., 2015). Further, we note that the nonnative hybrid swarming that was once believed to occur through much of central California has recently been greatly contracted to a region that includes portions of western Santa Clara and northern Monterey and San Benito counties, thus greatly limiting the concern of the influence of the nonnative species on our populations (Shaffer et al., 2020).

Results—*Peer-Reviewed Publications*—The published literature yielded few measurement data from which to conclusively determine a minimum size at which California tiger salamanders can metamorphose. We noted that researchers reported either total length (TL) or snout–vent length (SVL), but rarely both (Table 1). The limited reported data indicated that California tiger salamanders can grow to 180 mm TL (summarized by Altig and McDiarmid, 2015). Jennings and Hayes (1994) reported that California tiger salamander larvae reached a weight of 10 g at metamorphosis but provided no other measurements. Loredo and Van Vuren (1996) monitored metamorphosing California tiger salamanders for 3 years in Concord, Contra Costa County, and reported their smallest specimen at 56 mm SVL and their largest at 80 mm SVL, but no TL was recorded. Trenham et al. (2000) conducted work in a livestock reservoir in Monterey County, where they collected metamorphosing California tiger salamanders. Those specimens ranged from 41 to 78 mm SVL (Table 1), but again, no TL was recorded. Holland et al. (1990) collected postmetamorphic salamanders that measured 56–69 SVL that they believed recently left the aquatic habitat, with no TL reported.

TABLE 1—California tiger salamander (*Ambystoma californiense*) minimum and maximum size at metamorphosis, as reported in the literature or measured in the field. Measurements are for total length (TL) and snout–vent length (SVL) in millimeters. Habitat types are vernal pool (VP), ephemeral stock pond (EP), and perennial stock pond (PP).

County	TL	SVL	Habitat type	Source
Minimum				
Contra Costa	—	56	EP	Loredo and Van Vuren, 1996
Fresno	60[a]	—	VP	Anderson, 1968
Monterey	—	41	EP	Trenham et al., 2000
San Joaquin	55.7	33.3	VP	MVZ 09208[b]
San Joaquin	56.5	35.5	VP	MVZ 206877[b]
San Joaquin	60	—	VP	Storer (Field Notes 1925)
San Luis Obispo	—	56	VP[c]	Holland et al., 1990
Santa Clara	57	34	EP	This study
Santa Clara	61	37	EP	This study
Santa Clara	61	38	EP	This study
Santa Clara	63	38	EP	This study
Santa Clara	66	39	EP	This study
Santa Clara	72	44	EP	This study
Santa Clara	78	45	EP	This study
Santa Clara	76	47	EP	This study
Sonoma	83	—	VP	Edwards, 2018
Maximum				
Unreported location	180	—	—	Altig and McDiarmid, 2015
Contra Costa	—	80	EP	Loredo and Van Vuren, 1996
Contra Costa	144	84	EP	Alvarez, 2004
Fresno	141	—	VP	Anderson, 1968
Monterey	—	78	EP	Trenham et al., 2000
Santa Clara (type I)[d]	158	70	PP	Wilcox et al., 2015
Santa Clara (type II)	241	122	PP	Wilcox et al., 2015

[a] Values reported as average TL and SVL. Estimated length inferred from Figure 3 of Anderson (1968).
[b] Raised in the laboratory through metamorphosis (30 days) by T. I. Storer. Data collected from field notes curated at the Museum of Vertebrate Zoology.
[c] Reported as a lake, by Holland et al. (1990), that dried in June annually.
[d] Type I and type II refer to two distinct phenotypes reported by Wilcox et al. (2015).

Edwards (2018) reported his smallest larva from a vernal pool at the Alton South Preserve, Sonoma County to be that of a California tiger salamander measuring 83 mm TL.

Museum Collections—At the Museum of Vertebrate Zoology (MVZ) at the University of California, Berkeley, we examined postmetamorphic specimens collected separately in San Joaquin County by Storer (in 1922) and H. Snook (described in the field notes of T. Storer in 1923). Storer raised one of several collected larvae to metamorphosis over 30 days; after transforming on 8 May 1922, it measured 56.5 mm TL (no SVL was reported; Table 1). The transformed metamorph was raised an additional 31 days and then euthanized and preserved (MVZ 206877; Fig. 1). Storer also reported (in field notes) that one captive larva from San Joaquin County was measured by Storer and reported as 60 mm TL at metamorphosis. A specimen collected by Snook (13 May 1923; MVZ 09208) from the vicinity of Stockton, San Joaquin County, measured 55.7 mm TL (Table 1; Fig. 1). We conducted additional SVL measurements of the two museum specimens (Table 1). Although they had been stored in ethyl alcohol for at least 95 years and experienced some level of shrinkage, our figures take into account the original reported measurements as recorded in Storer's field notes for both specimens, which are curated at the MVZ.

Field Observations—We collected approximately 50 California tiger salamander larvae from Basin Pond, a small reservoir on the BORR, on 23 May 2006. Although previously present, Pacific treefrogs (*Hyliola regilla*) were no longer present but larval California tiger salamanders were visually detectable at the site after the pond water level had dropped by approximately 65% over 17 days. At the time we collected specimens, maximum pond depth was 12 cm and the surface area was ≤ 15 m^2. J.A.A. measured a random subset of 8 of the 50 specimens; we classified all as metamorphosing larvae on the basis of the developmental changes they exhibited, including size, pigment density (i.e., darkened background color), resorption stage of gills and tail fin, and full use of all four legs. The 8 specimens measured 57–78 mm TL (mean = 66.7 mm TL) and 34–47 mm SVL (mean = 40.6 mm) (Fig. 1). On 15 November 2008, also at the BORR, while draining Eagle Lake (37°24′24.213″N, 121°43′58.7244″W), we collected 28 California tiger

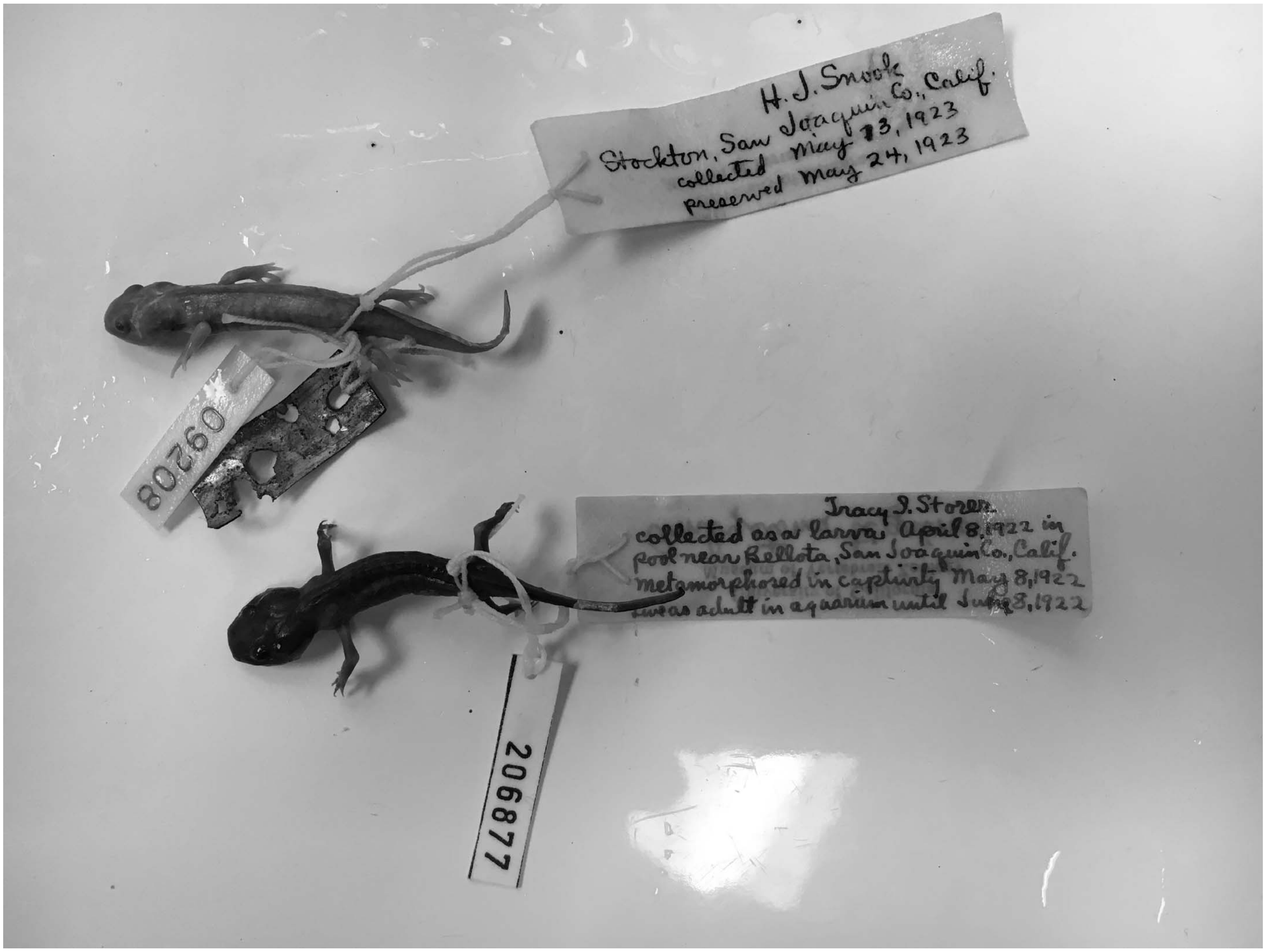

FIG. 1—Postmetamorphic specimens of California tiger salamander (*Ambystoma californiense*) collected by Storer (1922) and Snook (1923) and maintained at the Museum of Vertebrate Zoology, Berkeley, California. Museum tag = 19 × 74 mm, for scale. Photographed by J. Wilcox.

salamander larvae of two distinct size cohorts. The maximum SVL and TL for phenotype I ($n = 23$) were 70 and 158 mm, respectively; the maximums for phenotype II ($n = 5$) were 122 and 241 mm, respectively (Fig. 2). These specimens were genetically determined to be California tiger salamanders (see Wilcox et al., 2015).

DISCUSSION—Although published data provide an approximate minimum and maximum reported size threshold for metamorphosis in California tiger salamanders, these limited data omit the wider range of size that exists in the field.

Minimum Thresholds at Metamorphosis—The individuals collected by Snook (MVZ 09208) and by Storer (MVZ 206877) likely represent the best estimates of the lower threshold. Our field data from Santa Clara County (minimum = 57 mm TL) support this. It is possible, of course, that the minimum size threshold at metamorphosis is smaller yet, and further investigation is needed.

Maximum Thresholds at Metamorphosis—The potential maximum TL is difficult to determine in natural conditions; in any given water body, transformations are likely happening along a continuum. In part because the hydroperiod of aquatic breeding habitat in California (particularly vernal pools) is highly variable, metamorphosis in natural populations of California tiger salamander is challenging to monitor, and the exit event (and therefore the timing and size) of transitioned salamanders is seldom witnessed. It is now known, however, that this species also commonly uses anthropogenic perennial reservoirs for reproduction (Alvarez, 2004; Alvarez et al., 2013; Wilcox et al., 2015). The advantage of such stable environments is that larvae are not subject to the kinds of erratic hydroperiod pressures they would encounter in natural water bodies, and can therefore develop with fewer constraints, referenced by Whiteman (1994) and Whiteman et al. (1996) as facultative pedomorphosis. Whiteman et al. (1996) suggested that environmental

FIG. 2—Premetamorphic California tiger salamander (*Ambystoma californiense*) larva from Eagle Lake, Santa Clara County, California (see Wilcox et al. [2015] for genetic evaluation of this specimen). We released the specimen (122 mm snout–vent length, 242 mm total length) immediately after we recorded measurements. Photographed by J. Wilcox.

conditions, such as perennial water bodies created for cattle, may drive or support facultative pedomorphosis. It may not be surprising, therefore, that the largest reported size to date of a California tiger salamander before metamorphosis is that of a specimen (122 mm SVL; 241 mm TL) collected from a perennial pond (Wilcox et al., 2015). We predict that as these anthropogenic ponds are further investigated, the maximum reported threshold will increase.

The ability of California tiger salamanders to metamorphose quickly—like several species of spadefoot—may be an evolutionary response to unpredictable and varied climate, as well as to local site conditions (Stebbins and McGinnis, 2012). Anderson (1968) reported that California tiger salamanders that he studied in vernal pools metamorphosed in as few as 7 days. Although we did not directly monitor the physical transition through metamorphosis, our anecdotal observations during the period of study reported here suggest that a larva can transform from fully aquatic to fully terrestrial in as few as 4 days (J. Alvarez, unpubl. data). This is slightly longer than that suggested by Etkin (1964), who stated that some species of urodeles can complete transformation in 2 days.

Wilbur and Collins (1973) predicted that amphibian larvae are capable of metamorphosis after reaching a set minimum body size but often remain in the larval state beyond that threshold. Morey and Reznick (2000) interpreted this variability as a measure of phenotypic plasticity, or adaptability, that favors either early escape from a deteriorating larval environment or persistence in a favorable one.

Although the variables for larval body size and growth rate predicated on work by Wilbur and Collins (1973) address only intrinsic and extrinsic cues, predation also factors into metamorphic rate and size. Predation of larvae by aquatic insects, conspecifics, or nonnative game fish may relieve the pressures of larval density and competition, permitting faster growth and larger size at metamorphosis (Wilbur, 1980; Morin, 1983). In ephemeral ponds, urodeles such as California tiger salamanders are often the largest predator in the community, sometimes cannibalizing smaller larvae (Morin, 1983; pers. observ.).

From fieldwork, museum collections, and an examination of the available literature, we determined that minimum size at metamorphosis in California tiger salamanders can occur at approximately 56 mm TL (MVZ 09208), and ranges from an SVL of approximately 33 mm (MVZ 09208) to 122 mm (Wilcox et al., 2015) (Table 1). Although we released the large larvae we collected from Eagle Lake, preventing firm conclusions about maximum metamorphic threshold, their sizes suggest that California tiger salamander larvae can attain a premetamorphic size of up to 241 mm TL and 122 mm SVL before metamorphosis—far beyond the upper limit reported by Storer (1925) or Altig and McDiarmid (2015).

Research Implications—In California tiger salamanders, the first few months after transitioning are the most precarious. Populations may not suffer long term, however, because this species appears to be long lived (Trenham et al., 2000). Multigenerational studies are recommended to determine how size at metamorphosis determines population fitness over time (Scott et al., 2007; Searcy et al., 2014). Future research should also explore the relationship between the speed of California tiger salamander larval development and the presence of predators such as aquatic insects. To better understand climate change impacts, we urge researchers to compare the growth and development of California tiger salamander larvae in ephemeral ponds with those in perennial ponds. We speculate that anthropogenic perennial ponds may provide much-needed breeding habitat if precipitation rates decline long term.

Management Implications—Multiple variables complicate the ability to predict metamorphosis in a given California tiger salamander population at a given site during a particular year. This does include the persistence of nonnative barred tiger salamanders within the state and the influence of these genes on the native population (Johnson et al., 2011; Ryan et al., 2013; Wilcox et al., 2015). Recently, however, Shaffer et al. (2020) confirmed that the geographic extent and genetic influence of these introduced animals is far more contracted that previously reported and may have less to very little influence on the ability of the California tiger salamander to express facultative pedomorphosis since the genetic influence appears to be restricted to Monterey and San Benito counties.

Size at metamorphosis may be the simplest gauge of breeding success (Whiteman et al., 1996). To increase the likelihood of witnessing larval size at or near metamorphosis and improve the predictability of a successful breeding year, we suggest that managers establish weekly field surveys in California tiger salamander habitat (including perennial ponds) beginning in April of each year. Given the ability of urodele larvae to transform in the space of a few days (Etkin, 1964; pers. observ.) and at less than 60 mm TL (MVZ 09208; MVZ 206877; this study), consistency is key; inconstant pond surveys may erroneously conclude that water bodies devoid of larvae were never occupied or that reproduction failed, when in fact recruitment may have occurred even if the pond hydroperiod was brief. Further, to assure larvae the time needed to reach their largest potential size at metamorphosis, we strongly encourage land managers and restoration specialists to create or manage for aquatic breeding habitat that accommodates the full potential range of metamorphic size. This may involve dredging silted ponds or repairing failing dam structures on perennial ponds. Aquatic habitats formerly considered unsuitable (e.g., creeks, including those with fish) have recently proven to be felicitous for reproduction by this species (Alvarez et al., 2021) and should be treated as viable habitat. In some areas, it will likely be necessary to eliminate exotic game fish for California tiger salamander populations to persist. We also urge (per Alvarez, 2004; Alvarez et al., 2013; Wilcox et al., 2015; this study) that perennial ponds be managed for the California tiger salamander when those structures fall within its range.

We express our gratitude to the late T. I. Storer, who collected data and curated those data, along with his field notes, at the MVZ, Berkeley, California. His work remains invaluable nearly 100 years later. We are equally grateful to C. Spencer, MVZ, for access to the specimens. N. Parizeau gave us extremely helpful and constructive comments on the manuscript that greatly improved its readability and usefulness. G. Padgett-Flohr supplied difficult-to-find references, for which we are grateful. We are also grateful to two anonymous reviewers who improved the manuscript greatly. Live California tiger salamanders were handled under a United States Fish and Wildlife Service Recovery Permit (TE-068745).

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