dynamics of a top predator, *Ambystoma tigrinum nebulosum* (Caudata, Ambystomatidae) in a lentic community. Copeia 1987:949-957.
Holycross, A.T., T.C. Brennan, and R.D. Babb. 2022. A Field Guide to Amphibians and Reptiles in Arizona. Second Edition. Arizona Game and Fish Department, Phoenix, AZ.
Hossack, B.R., E. Muths, J.C. Rorabaugh, J.A. Lemos Espinal, B.H. Sigafus, T. Chambert, G. Carreón Arroyo, D. Hurtado Felix, D. Toyos Martinez, and T.R. Jones. 2016. Notes on distribution of tiger salamanders (presumed *Ambystoma mavortium stebbinsi*) in Sonora, Mexico. Herpetological Review 47:177-180.
Jones, T.R., and F.R. Hensley. 2020. *Thamnophis cyrtopsis* Black-necked Gartersnake. Pp. 388-400 *in*: A.T. Holycross and J.C. Mitchell (eds.). Snakes of Arizona. ECO Publishing, Rodeo, NM.
Jones, T.R., M.J. Ryan, T.B. Cotton, and J.M. Servoss. 2020. *Thamnophis eques* Mexican Gartersnake. Pp. 418-432 *in*: A.T. Holycross and J.C. Mitchell (eds.). Snakes of Arizona. ECO Publishing, Rodeo, NM.
Lannoo, M.J., and C.A. Phillips. 2005. *Ambystoma tigrinum* (Green, 1826), Tiger Salamander. Pp. 636-639 *in*: M.J. Lannoo (ed.). Amphibian Declines, the Conservation Status of United States Species. University of California Press, Berkeley, CA.
Long, C.A. 1964. The badger as a natural enemy of *Ambystoma tigrinum* and *Bufo boreas.* Herpetologica 20:144.
Petranka, J.W. 1998. Salamanders of the United States and Canada. Smithsonian Institute Press, Washington and London.
Powell, R., R. Conant, and J.T. Collins. 2016. Peterson Field Guide to Reptiles and Amphibians of Eastern and Central North America. Fourth Edition. Houghton Mifflin Harcourt, Boston, MA, and New York, NY.
Rossi, J.V., and R. Rossi. 2003. Snakes of the United States and Canada: Natural History and Care in Captivity. Krieger Publishing Company, Malabar, FL.
Shaffer, H.B., and M.L. McKnight. 1996. The polytypic species revisited: differentiation and molecular phylogenetics of the tiger salamander *Ambystoma tigrinum* (Amphibia: Caudata) complex. Evolution 50:417-433.
Snyder, J.D., T.J. Maret, C.A. Raney, and J.P. Collins. 1996. Exotic predators and altered disturbance regime control salamander distribution in arid lands. Department of Zoology, Arizona State University, Tempe, AZ.
Webb, R.G., and W.L. Roueche. 1971. Life history of the tiger salamander (*Ambystoma tigrinum mavortium*) in the Chihuahuan Desert. Great Basin Naturalist 31:193-212.

NATURAL HISTORY NOTE

Larval Ecomorph Mouthparts in the Western Spadefoot

Nicole Kleponis, Independant Researcher, Pleasanton, CA; *nicolekleponis@gmail.com*

Jeff A. Alvarez, The Wildlife Project, PO Box 188888, Sacramento, CA; *jeff@thewildlifeproject.com*

Members of the New World spadefoot family Scaphiopodidae are known for their larval plasticity, having the ability to change their physical features to adapt to their specific environments (Morey 1998, Morey and Reznick 2004, Ledon-Rettig 2008, Martin and Pfennig 2009). Such larval plasticity includes the ability to extend the timing of metamorphosis, depending upon their natal pools (Morey 1998, Morey and Reznick 2004, Ledon-Rettig 2008, Martin and Pfennig 2009), and the formation of a specialized diet (Ledon-Rettig 2008, Ledon-Rettig et al. 2008, Martin and Pfennig 2009, Paull et al. 2012). Species of the genus *Spea* have been documented to have a carnivore (sometimes referred to as cannibal) larval ecomorph (Orton 1954, Bragg and Bragg 1958, Martin and Pfennig 2009, Ledon-Rettig et al. 2008, Levis et al. 2018, Levis and Pfennig 2019, Alvarez et al. 2024). The hormones triiodotyrosine and corticosterone are associated with both the creation of the carnivore morph and metamorphosis (Ledon-Rettig et al. 2008) as the carnivore morph is thought to be an adaptation to short-duration pools and crowded conditions with intra-specific competition (Pfennig 1990, 1992). Based on their genetics (Bragg and Bragg 1958, Ledon-Rettig et al. 2008) and environmental conditions (Martin and Pfennig 2009), carnivore larvae develop large jaws and sharp keratinized jaw sheaths (Orton 1954, Bragg and Bragg 1958 Martin and Pfennig 2009, Ledon-Rettig et al. 2008, Levis et al. 2018, Levis and Pfennig 2019). These mouthparts are specialized for hunting macroscopic prey such as Branchiopoda shrimp (Ledon-Rettig et al. 2008, Levis and Pfennig 2019) or other tadpoles, including those of their own species and cohort (Pfenning 1990, Ledon-Rettig et al. 2008, Alvarez et al. 2024).

In the carnivore morphs of the related Plains Spadefoot (*Spea bombifrons*) that were found in sympatry with Mexican Spadefoot (*S. multiplicata*) a

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novel physical trait was described: a keratinized palate spike descending from the upper palate (Levis et al. 2018). Levis and Pfennig (2019) suggested this palate spike aids in spearing prey (Levis et al. 2018), and a significantly reduced spike was observed in omnivore morphs of the Plains Spadefoot (Levis, pers. comm.). Herein we show that these physical traits are also present in the Western Spadefoot (*S. hammondii*) carnivore and omnivore morphs. Further, we show the phenotypic comparison between carnivore and omnivore larval morph characteristics in Western Spadefoot.

We carefully examined the first 50 individuals of a similar size and Gosner stage from a total capture of 251 individual larval Western Spadefoot, while in the field, and collected photographic record of the mouthparts of each, when possible, using an iPhone 7 camera. A single photo also captured the dorsal surface of the larva to document any potential observed or reported morphological differences among Western Spadefoot larvae (Hansen and Shedd 2024). Following Ledon-Rettig and Pfenning (2011), we collected additional photos of mouth parts that were used to examine the mouth parts of individual larvae that we characterized as carnivore, omnivore, or a specimen showing a range of both characteristics.

We found a wide range of morphological differences among individuals of the same or similar Gosner stage (Gosner 1960) and size cohort, although carnivore morphs were often larger. We characterized individuals with an absence of pointed upper jaw sheath, a shallow lower jaw notch, and a reduced palate spike as omnivore morphs (Fig. 1A and B), and characterized carnivore morphs by cuspated upper jaw sheaths (i.e., resembling a beak), and lower jaw sheaths with a deep center notch and sharp peaks on either side and a well-developed palate spike (Fig. 2A and B). A minority of individuals sampled showed an intermediate level of these characteristics (Fig. 3).

Intermediate morphs face greater intra-species competition (Bragg and Bragg 1958, Martin and Pfenning 2009, Paull et al. 2012), a form of disruptive selection (Martin and Pfenning 2009), and are most common among young larvae (Martin and Pfenning 2009, pers obs.). We observed several larvae with intermediate variability of their mouthparts (Fig. 3). This intermediary morph was characterized by the upper jaw sheath having a point, though not as exaggerated as the carnivore morph. The lower jaw sheath in the intermediary morph is visually thicker than the omnivore morph and includes a deep notch but lacks the sharp peaks of the carnivore morph (Fig. 3).

The degree to which the carnivore trait is expressed can make distinguishing carnivorous morphs from intermediate morphs difficult. The larval diet phenotypic expression is best described as a spectrum with omnivores and carnivores on opposing ends (Fig. 4). Larval head shape can be an indication of jaw shape, and in this species, it can range between the two extremes. The omnivore jaws are unpronounced, creating a tear-drop body shape from the dorsal view, progressing to oval in those with wider jaws. The opposite end of the spectrum is a carnivore morph with jaws wider than the posterior portion of the body.

The Western Spadefoot faces challenges in successful breeding due to climate variation and localized drought throughout its range (Morey 1998, Thomson et al. 2015), exacerbated by the species' preference for shallow, temporary pools. Droughts, long-term patterns of declining rainfall, or shifts in the timing of rainfall may result in limited or insufficient hydroperiods for natal pools. This can increase larval interactions within natal pools, which

Previous research, with the Mexican Spadefoot, showing a directional shift towards favoring carnivores eventually led to a switch favoring omnivores as competition for prey decreased carnivore fitness, although the omnivore morph required longer hydroperiods for successful metamorphosis (Pfennig 1992, Martin and Pfennig 2009).

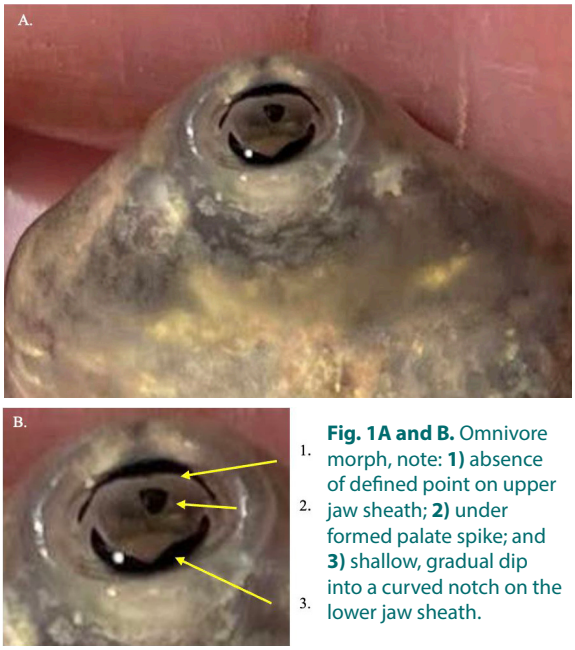

Fig. 1A and B. Omnivore morph, note: **1)** absence of defined point on upper jaw sheath; **2)** under formed palate spike; and **3)** shallow, gradual dip into a curved notch on the lower jaw sheath.

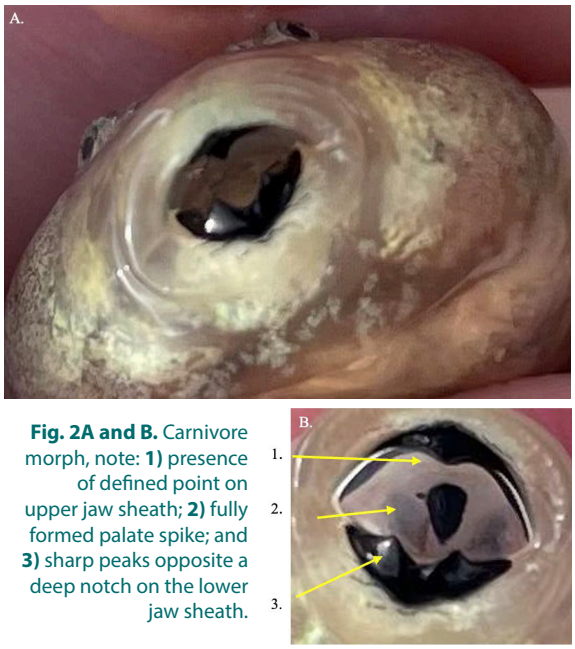

Fig. 2A and B. Carnivore morph, note: **1)** presence of defined point on upper jaw sheath; **2)** fully formed palate spike; and **3)** sharp peaks opposite a deep notch on the lower jaw sheath.

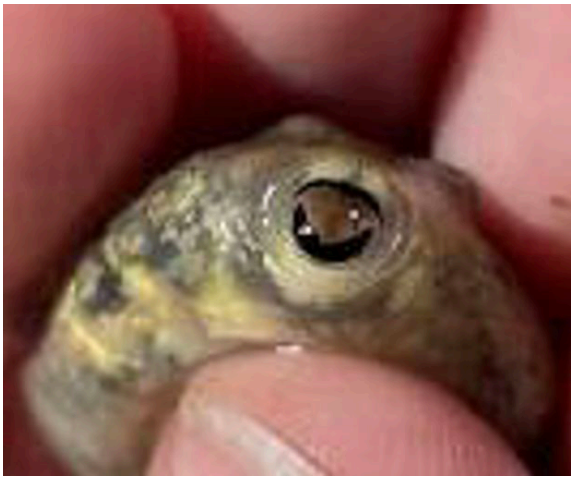

Fig. 3. Larval mouthparts showing intermediate variability of the mouthparts.

may also increase the probability of the carnivore morph presence and favor this adaptation. This shift would be a change to the currently observed disruptive selection, which favors both carnivores and omnivores over intermediates. Previous research, with the Mexican Spadefoot, showing a directional shift towards favoring carnivores eventually led to a switch favoring omnivores as competition for prey decreased carnivore fitness, although the omnivore morph required longer hydroperiods for successful metamorphosis (Pfennig 1992, Martin and Pfennig 2009). This could be detrimental to the Western Spadefoot if shorter, less predictable hydroperiods are responsible for the initial shift favoring carnivores, reducing their fitness as well as putting additional predation pressure on intermediary and omnivore morphs. The presence of the carnivore ecomorph likely represents an evolutionary advantage for the larvae that are capable of metamorphosis at a larger size, or during a shorter time-period, allowing for successful metamorphosis, even when habitats are rapidly shrinking and drying. The dietary plasticity in the Western Spadefoot shows this species' adaptations towards varying ecological and environmental conditions which may prove to be advantageous as human-caused climate changes become more extreme.

The dietary plasticity in the Western Spadefoot shows this species' adaptations towards varying ecological and environmental conditions which may prove to be advantageous as human-caused climate changes become more extreme.

Fig. 4. Larval diet phenotypic expression described as a spectrum with omnivores and carnivores on opposing ends. Note that jaws increase in size with an increase in carnivorous characteristics, exceeding the width of the posterior portion of the body.

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Literature Cited

Alvarez, J.A., A. Peralta-García, and J. H. Valdez-Villavicencio. 2024. Putative cannibalism in the western spadefoot (*Spea hammondii*) in northern Baja California Mexico. Sonoran Herpetologist 37:96-97.

Bragg, A.N., and W.N. Bragg. 1958. Variations in the mouth parts in tadpoles of *Scaphiopus* (*Spea*) *bombifrons* Cope (Amphibia: Salientia). The Southwestern Naturalist 3:55.

Gosner, K.L. 1960. A simplified table for staging Anuran embryos and larvae with notes on identification. Herpetologica 16:183-190.

Hansen, R.W., and J.D. Shedd. 2024. California Amphibians and Reptiles, Princeton University Press, Princeton, NJ.

Ledón-Rettig, C.C., and D.W. Pfennig. 2011. Emerging model systems in eco-evo-devo: The environmentally responsive spadefoot toad. Evolution & Development 13:391-400.
Ledon-Rettig, C.C., D.W. Pfennig, and N. Nascone-Yoder. 2008. Ancestral variation and the potential for genetic accommodation in larval amphibians: Implications for the evolution of novel feeding strategies. Evolution & Development 10:316-325.
Levis, N.A., A.J. Isdaner, and D.W. Pfennig. 2018. Morphological novelty emerges from pre-existing phenotypic plasticity. Nature Ecology & Evolution 2:1289-1297.
Levis, N.A., and D.W. Pfennig. 2019. Phenotypic plasticity, canalization, and the origins of novelty: Evidence and mechanisms from amphibians. Seminars in Cell & Developmental Biology 88:80-90.
Martin, R.A., and D.W. Pfennig. 2009. Disruptive selection in natural populations: The roles of ecological specialization and resource competition. The American Naturalist 174:268-281.
Morey, S.R. 1998. Pool duration influences age and body mass at metamorphosis in the western spadefoot toad: Implications for vernal pool conservation. Pp. 86-91 *in*: C.W. Witham, E.T. Bauder, D. Belk, W.R. Ferren, Jr., and R. Ornduff (eds). Ecology, Conservation, and Management of Vernal Pool Ecosystems – Proceedings from a 1996 Conference. California Native Plant Society, Sacramento, CA.
Morey, S.R., and D.N. Reznick. 2004. The relationship between habitat permanence and larval development in California spadefoot toads: Field and laboratory comparisons of developmental plasticity. Oikos 104:172-190.
Morey, S., and D. Reznick. 2001. Effects of larval density on post-metamorphic spadefoot toads (*Spea hamonndii*). Ecology 82:510-522.
Orton, G.L. 1954. Dimorphism in larval mouthparts in spadefoot toads of the *Scaphiopus hammondi* Group. Copeia 1954:97.
Paull, J.S., Martin, R.A., and DW. Pfennig. 2012. Increased competition as a cost of specialization during the evolution of resource polymorphism: Competition and resource polymorphism. Biological Journal of the Linnean Society 107:845-853.
Pfennig, D. 1990. The adaptive significance of an environmentally-cued developmental switch in an anuran tadpole. Oecologia 85:101-107.
Pfennig, D.W. 1992. Polyphenalism in spadefoot toad tadpoles as a locally adjusted evolutionarily stable strategy. Evolution 46:1408-1420.
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.

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