Illustrated review of Mormon cricket *Anabrus simplex* (Tettigoniidae, Tettigoniinae) embryonic development

Robert B. Srygley[1], Laura B. Senior[1]

1 Pest Management Research Unit, Northern Plains Agricultural Research Laboratory, USDA-Agricultural Research Service, 1500 N. Central Ave., Sidney MT 59270, USA.

Corresponding author: Robert B. Srygley (robert.srygley@ars.usda.gov)

Academic editor: Tony Robillard | Received 13 December 2022 | Accepted 13 November 2023 | Published 11 March 2024

https://zoobank.org/99977F28-A7D9-4632-BD7C-757B7E047AF4

Citation: Srygley RB, Senior LB (2024) Illustrated review of Mormon cricket *Anabrus simplex* (Tettigoniidae, Tettigoniinae) embryonic development. Journal of Orthoptera Research 33(1): 87–93. https://doi.org/10.3897/jor.33.98763

Abstract

Mormon crickets *Anabrus simplex* Haldeman, 1852 are a pest of crops and rangeland in the western United States, but little is known about their development in the egg stage. Mormon crickets have multiple states at which they may diapause and thus affect population growth. Consequently, a series of photographs of Mormon cricket embryonic stages was organized using published research on Old World katydids. Earlier stages were more difficult to distinguish without removing the chorion. However, where possible, features that can be seen through the chorion are indicated with the expectation that these will be useful in characterizing development in living embryos. As with other Orthoptera, the timing of development varied greatly among individuals, but at a minimum, embryos filled approximately half the egg in six weeks, whereas they required 12 weeks from oviposition to reach the final stage before their obligate winter diapause.

Keywords

diapause, environment, hatching, katydid, ontogeny

Introduction

In the temperate zone, shield-backed katydids (Orthoptera: Ensifera: Tettigoniidae) spend most of their life cycle in the egg. During much of this time, the embryo may be quiescent or in diapause and not growing. Diapause may occur at multiple stages during embryonic development and last for differing amounts of time (Hartley and Warne 1972). As a result, embryonic morphogenesis can vary greatly in its temporal pattern both among individuals and species. Due to this temporal variation, external morphology of embryos is a more reliable means than age (i.e., time from oviposition) for classifying embryonic development (Van Horn 1966, Donoughe and Extavour 2016).

General embryology of shield-backed katydids was described by Warne (1972). Based on the location of the primordial cells that give rise to the embryo (embryonic primordium) and the movement of the embryo within the egg, Warne (1972) identified four classes of embryonic development in the Tettigoniidae. Having examined European specimens from 10 of the 21 subfamilies, Warne concluded that development was conserved phylogenetically such that each subfamily was represented by only a single developmental class.

Relative to other Orthoptera, members of Tettigoniidae remain underrepresented in descriptions of their external embryological morphology. Even though some species, such as the spiny bush cricket *Acanthoplus discoidalis* Walker, 1869 (Bradyporinae) and the Mormon cricket *Anabrus simplex* Haldeman, 1852 (Tettigoniinae: Platycleidini), are economically important (Srygley and Jaronski 2019, Mviha et al. 2022), little is known about their embryology due to the difficulty of rearing them in the laboratory. Mormon crickets are flightless katydids of the western United States. They frequently reach densities that result in significant economic impacts on the grazing industry and force livestock selloffs, especially during droughts when forage is scarce (Cowan and Shipman 1947). Mormon cricket outbreaks are characterized by the formation of dense bands of later-instar nymphs or adults moving directionally as a group (Simpson et al. 2006) and serve as a model for nymphal locust behavior on other continents (Buhl et al. 2006, Srygley 2016). Commonly found on rangeland, Mormon cricket bands also migrate into crops where they can cause major damage (Wakeland 1959).

Adult females lay eggs individually in soil ca. 2.5 cm beneath the surface. Eggs have a facultative diapause stage that may occur early in development. In that state, the embryonic primordial tissue may remain for multiple growing seasons and winter periods (Srygley 2020a). The nearly fully developed embryo has an obligate diapause stage that requires a cold vernalization period to terminate. In the spring when the soil warms, the nearly fully developed embryos complete development and the nymphs hatch (Pfadt 2002).

Cowan and Shipman (1940) fixed Mormon cricket eggs in cupric-phenol fixative (Petrunkevitch 1933) and photographed them to create a series of embryonic stages of the Mormon cricket. This early study was not published. The utility of creating a series of photographs of external morphology of the embryo and

relating the development to more modern treatises of katydid development (e.g., Warne 1972, Ingrisch 1984) became evident as we learned more about the multiple states in which quiescence, diapause, or aestivation can occur in *A. simplex*. Both environmental conditions experienced by the parent (Srygley 2020a) and by their eggs (Srygley 2020b) can prolong the time that the eggs remain in diapause in the soil (i.e., egg banks).

The series of photographs by Cowan and Shipman (1940) indicated that the location of the embryonic primordium and movement of the embryo within the egg were similar to that described by Warne (1972) for the dark bush cricket *Pholidoptera griseoaptera* (De Geer, 1773), which is in the same subfamily as *A. simplex*. In a subsequent study, Ingrisch (1984) made several changes to the embryonic stages for *P. griseoaptera* and described in greater detail the embryonic development of the wart-biter *Decticus verrucivorus* (Linnaeus, 1758) (Tettigoniinae).

In this paper, we document stages of embryonic development for *A. simplex* organized in accordance with Ingrisch (1984). We use features visible without dissection with the expectation that revelation of stages that are clearly defined through the egg shell and those that are less clearly defined will be useful to field and lab biologists who study Mormon cricket development. A consistent embryonic staging system is needed in some developmental studies, particularly in cases where the developmental progress of a living embryo is being monitored. If the stage of an embryo can be identified without removing it from its eggshell, by examining its external appearance, the embryo can continue its development rather than being terminated during the staging process (Donoughe and Extavour 2016). Our technique relies primarily on the examination of undissected embryos and could lead to better identification of stages without dissection.

Materials and methods

Mormon cricket male and female 7th instar nymphs were collected on Paint Rock Road in the Bighorn Mountains, WY (44°27'52"N, 107°27'33"W, 2653 m.a.s.l..) on July 9, 2015 and brought to the lab in Sidney, Montana. Females were set up in nylon mating cages (30 × 21 × 21 cm BugDorms, Megaview Science Co., Ltd., Taiwan) on the day that they molted to adult. If an adult male was available, it too was added to the cage on the same day. Otherwise, a male was added following eclosion. Mating pairs were placed in either long-day (15:9 h day:night) or short-day (12:12 h day:night) treatments with the temperature cycle—warming to 30°C during the day and cooling to 15°C at night—the same in both chambers (Srygley 2020a). They had continuous access to equal parts by volume of hulled sunflower seeds, mixed wild bird seed, dried tropical fish flakes, and half and half wheat germ and wheat bran as well as ad lib access to water in a stoppered bottle with a cotton wick. Fresh organic Romaine lettuce was offered daily. On the floor of the cage was an aluminum pan (20 × 20 cm) filled with autoclaved sand (2.5 cm deep) for oviposition. To collect the eggs, the sand was sieved weekly. Combined eggs from all mating pairs were evenly divided into two sets of 12 groups (Table 1). Each group of eggs was buried approximately 1.3 cm in sand moistened to 25% saturation with water in a 265 ml cup with a lid. One set was placed into an Associated Environmental Systems (AES) chamber (Acton, Massachusetts, model SD-505) at the beginning of a 12-week variable cycle:variable thermoperiod (VC:VT) temperature profile that is the best currently available for Mormon cricket egg development, diapause, and hatching (see Srygley and Senior 2018, suppl. table S2). The second set was placed into an AES chamber running a constant daily temperature cycle and constant thermoperiod (CC:CT, Srygley and Senior 2018, suppl. table S1) that cycled between a maximum of 30°C during the day and a minimum of 15°C at night for 10 weeks followed by a two week cooling period. Embryos incubated in CC:CT diapause more intensely and require 18 weeks in subzero temperatures to hatch relative to those incubated in VC:VT, which require only 6 weeks (Srygley and Senior 2018).

Table 1. Parental treatments and incubation of eggs preserved for observation of embryonic development.

Population, Year	Parental photoperiod, temperature	Incubation environment	N eggs preserved	N embryos portrayed
WY, 2015	15:9 h, 30:15°C	VC:VT**	169	4
WY, 2015	15:9 h, 30:15°C*	CC:CT	104	9
WY, 2015	12:12 h, 30:15°C	VC:VT	156	1
WY, 2015	12:12 h, 30:15°C*	CC:CT	65	2
WY, 2018	15:9 h, 30:15°C	VC:VT	195	4
OR, 2018	15:9 h, 30:15°C	VC:VT	365	2

*Thermoperiod was the same although photoperiod varied (Srygley 2020a).
**Incubation environments after Srygley and Senior (2018).

In 2018, additional *A. simplex* were collected in the field and set up in mating pairs for egg collection. Males and females were collected from Cedar Spring Road and from Montague Road near Arlington OR on May 28, 2018 (coordinates for Arlington: 44°40'39"N, 120°12'41"W, 87 m) and sent to the lab in Sidney. Others were reared in cages in the Bighorn Mountains, WY (44°49'35"N, 107°49'41"W, 2773 m) and brought to the lab on August 28, 2018. An adult male and female from the same location comprised a mating pair. Mating pairs were treated the same as those collected in 2015 except only the long day photoperiod (15:9 h) was used. Moreover, to provide a more precise starting time for embryonic development, the sand in each mating cage was sifted daily and the eggs recovered were sorted into 12 groups and set up simultaneously in the 12-week VC:VT temperature profile.

In both years, for each population and incubation treatment, one cup of eggs in sand was removed from the environmental chamber weekly for 12 consecutive weeks following the date of sifting. Thus, in total, for each population and incubation treatment, 12 groups of eggs were removed: one group at the end of each week for each of the 12 weeks in the egg development profile. Immediately upon removal, the eggs were placed in a refrigerator at 4°C to minimize further development. As soon as possible thereafter, the eggs were sifted out of the sand and then cleared and fixed using a slightly modified version of the Hogan (1959) protocol. The eggs were soaked for 30 min in distilled water at room temperature and any clinging sand particles were gently removed. The moist eggs were transferred to a scintillation vial and soaked for 30–45 minutes in a 2:2:1 by volume mixture of glacial acetic acid, chloroform, and absolute ethanol at 37°C. After soaking, they were transferred to 1:1 by volume solution of glycerol and 70% ethanol for storage. In addition to stabilizing the tissues, the fixation process increased the transparency of the chorion (Hogan 1959).

For review and photography of the egg stages, the eggs were removed from the storage solution and reviewed using a stereomicroscope (Leica model M205C), a camera (Leica model DMC 4500), imaging software (Leica Application Suite version 14.13.10), and dark field. For each stage, an image was selected that best represented the characters of a described stage and clearly

differentiated the stage from the subsequent and preceding stages in the developmental series. For some stages, the embryo was photographed from more than one perspective, and for some stages, the chorion was removed to better display the characters.

Embryonic development of Tettigoniidae is separated into seven phases based on orientation and movement of the embryo. Within each phase, stages of development are differentiated morphologically. Phase 0, which includes the first three stages of blastoderm formation, is not included in this study because it was not visible with our methods nor those of Warne (1972) or Ingrisch (1984). Those authors follow Chapman and Whitham (1968) and separate this phase into Stage 1: No blastoderm; Stage 2: Blastoderm covers half the yolk, and Stage 3: Blastoderm covers the whole yolk. For orientation, micropyles are ventrally located near the posterior end of the tettigoniid egg (Warne 1972).

Results and discussion

Phase and stage descriptions.—**Phase I:** Formation and differentiation of the embryonic primordium (Fig. 1).

Stage 4: Embryonic primordium circular, appearing as a disc of tissue when the broad side of the disc is oriented facing the viewer (see also, Suppl. material 2: fig. S1). The disc is difficult or impossible to discern when viewed in other orientations. The embryonic primordium lies on the yolk at the posterior end of the egg (slightly off-center). Cowan and Shipman (1940) portray the embryonic primordium in their Fig. 1 (see Table 1).

Stage 5: Growth has begun, and the embryonic primordium has become pear shaped and lies on the yolk at the posterior end.

Stage 6: Differentiation into protocephalic (i.e., head) and protocormic (i.e., thoracic and abdominal) regions. Protocormic region begins to elongate but still quite short, although clearly more defined than in Stage 5. The stodomodeum (rudimentary mouth) appears (Ingrisch 1984) but is difficult to see through the chorion. The embryo lies with the anterior end toward the posterior end of the egg (i.e., antero-posterior orientation).

Stage 6 transitioning to Phase II (Anatrepsis) Stage 7: Segmentation, which is difficult to discern in these images, is developing in the gnathal and thoracic regions whereas abdominal segmentation has not begun. The protocorm is still relatively short, while the protocephalon has widened (see also Suppl. material 2: fig. S2). Stage 7 marks the start of Anatrepsis.

Phase II: Anatrepsis (Fig. 2) Movement away from the posterior end of the egg. Movement is slight relative to other Orthoptera (Warne 1972) and may be neglected altogether (Ingrisch 1984). Anatrepsis is a brief phase in the Tettigoniinae (Warne 1972).

Stages 7 to 8: By the end of Stage 7, segmentation of the thoracic region is complete. The head of the embryo is at the posterior end of yolk, bending slightly backwards. As the segmentation proceeds into the abdomen, the embryo is moving from Stage 7 into Stage 8. The protocorm has elongated, while the protocephalon is somewhat broadened. Limb buds are not visible.

Stage 9: Abdominal segmentation is proceeding. At Stage 9, the abdomen is more than half segmented. The abdomen is noticeably longer now but not yet full length. The thoracic and gnathal limb buds (i.e, rudimentary legs and mouth parts, respectively) now protrude (Suppl. material 2: fig. S3). The thoracic appendages become larger than the gnathal appendages but difficult to

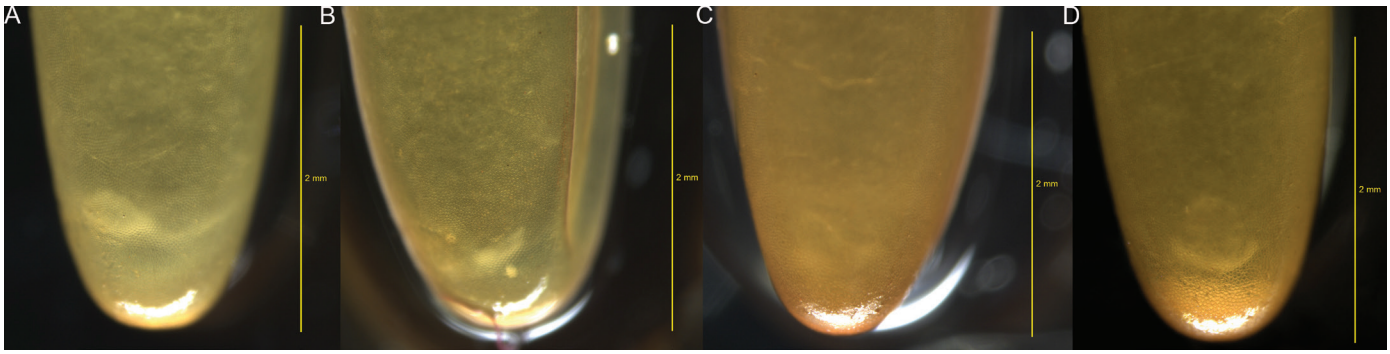

Fig. 1. Phase I: Formation and differentiation of the embryonic primordium. Images show the posterior end of the egg only: **A.** Stage 4; **B.** Stage 5; **C.** Stage 6; and **D.** Stage 6 transitioning to Stage 7. Scale bars: 2 mm.

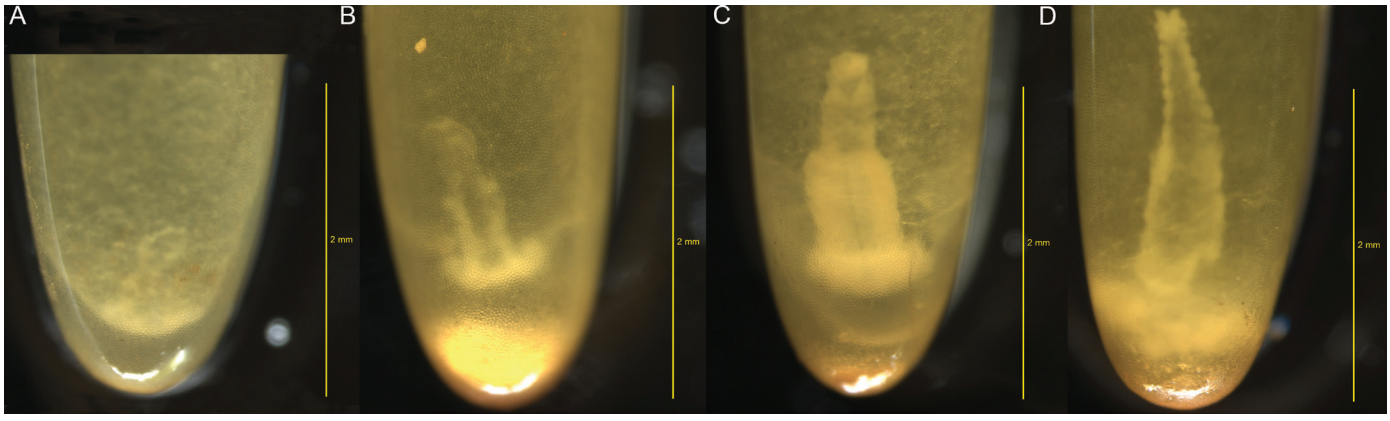

Fig. 2. Phase II: Anatrepsis. Images show the posterior end of the egg: **A.** Stage 7 to 8; **B.** Stage 9; **C.** Stage 10; **D.** Stage 11 with micropyles clearly visible. Scale bars: 2 mm.

see through the chorion. The anterior end of the embryo remains at the posterior end of yolk, bending slightly backwards.

Stages 10: At Stage 10, the proctodeum (i.e., rudimentary anus) is just visible and the abdomen has become completely segmented. Thoracic appendages oriented approximately parallel to the body (Ingrisch 1984) or outwards (Warne 1972) (Suppl. material 2: fig. S4).

Stage 11: Abdomen completely segmented and full length (Suppl. material 2: fig. S5). The proctodeum is clearly visible. The legs point outwards at right angles to the body. The appendages begin segmentation at this stage; however, this aspect of development is not visible in these images. The tip of abdomen curls forward. The head of the embryo remains at posterior end of yolk, bending backwards. Anatomic details are more visible in the specimen with chorion removed (Suppl. material 2: fig. S6).

Phase III: Mesentrepsis (Fig. 3) Embryo is stationary (Warne 1972).

Stage 12: The tip of the abdomen bends over the ventral side of the embryo (Suppl. material 2: fig. S7). The thoracic appendages are now directed toward the midline of the body, rather than extending outward as they were previously. The caput is broad and remains bent back slightly. The embryo has not yet begun to broaden (also see dissected specimen, Suppl. material 2: fig. S8).

Stage 13: The embryo has begun to broaden conspicuously. The tip of the abdomen, also now noticeably widened, is curled under towards the ventral side (Suppl. material 2: fig. S9).

Stage 14: The entire embryo has further broadened with respect to the previous stage (Suppl. material 2: fig. S10). The tip of the abdomen still bends over the ventral side. The antennae reach well past the palpus maxillaris, which is the length of the antennae in Stage 13. In the dissected specimen (Suppl. material 2: fig. S11), the antennae extend to the second pair of developing pedes (thoracic limbs).

Phase IV: Katatrepsis (Fig. 4) Remaining on the surface of the yolk, the embryo moves around the yolk's posterior end, reversing the embryo's orientation and positioning the head towards the anterior end of the egg.

Stage 15: The head bends back over the end of the yolk, being at approximately right angles to the body. The embryo is beginning to move around the pole of the yolk, initiating the reversal of its antero-posterior orientation (Suppl. material 2: fig. S12).

Stage 16: The embryo curves around the end of the yolk, with the head and thorax arching as the embryo undergoes katatrepsis. At the posterior end of the yolk, a clear fluid filled space has formed from the uptake of water, which occurs before katatrepsis (Warne 1972). The eyespots are visible, although faint (Suppl. material 2: fig. S13).

Stage 17: Only the very tip of the abdomen remains bent back under the yolk as the head is now oriented toward the anterior end of the egg. The ventral side of the embryo is apparent along what is now the opposite side of the egg from where it was situated before katatrepsis. The eyes are reddish pigmented and visible (Suppl. material 2: fig. S14).

Stage 18: Katatrepsis is complete, as the embryo has finished rounding the posterior pole. The tip of the abdomen has

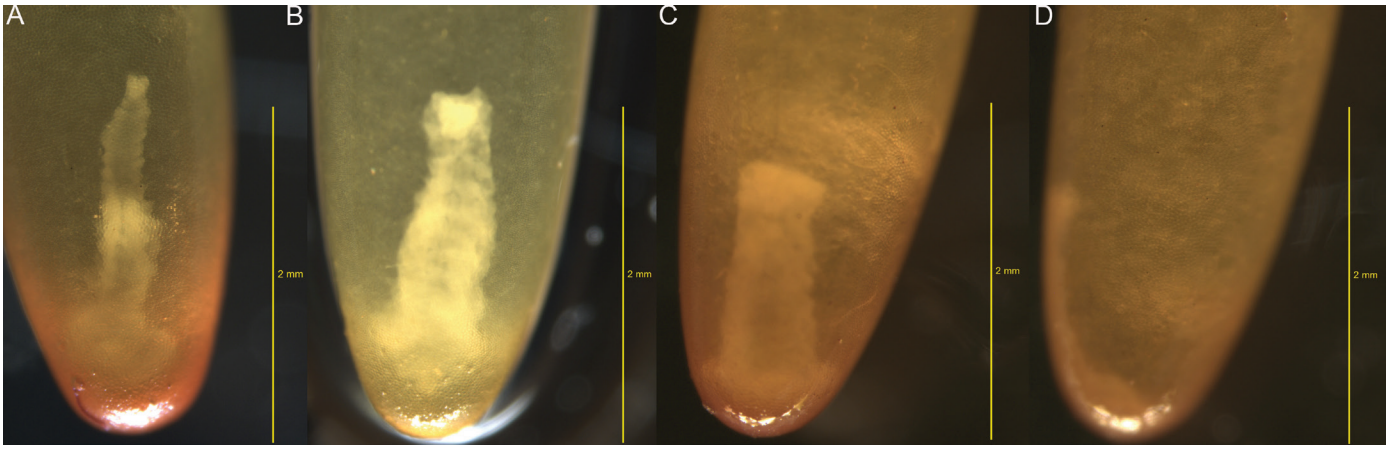

Fig. 3. Phase III: Mesentrepsis. Images left to right showing the posterior end of the egg: **A.** Stage 12; **B.** Stage 13; **C.** Stage 14; **D.** Lateral view of same stage 14 embryo. Scale bars: 2 mm.

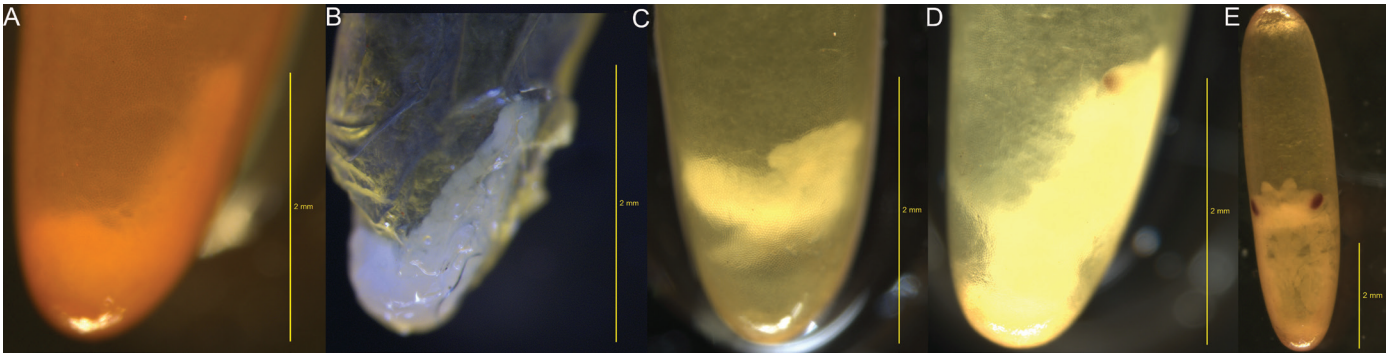

Fig. 4. Phase IV: Katatrepsis. **A.** Stage 15, lateral view with anterior end of embryo to the left; **B.** Stage 15, dorso-lateral view with chorion removed; **C.** Stage 16, lateral view with anterior end of embryo to the right; **D.** Stage 17, lateral view; **E.** Stage 18, ventral view showing its length relative to the whole egg. Scale bars: 2 mm.

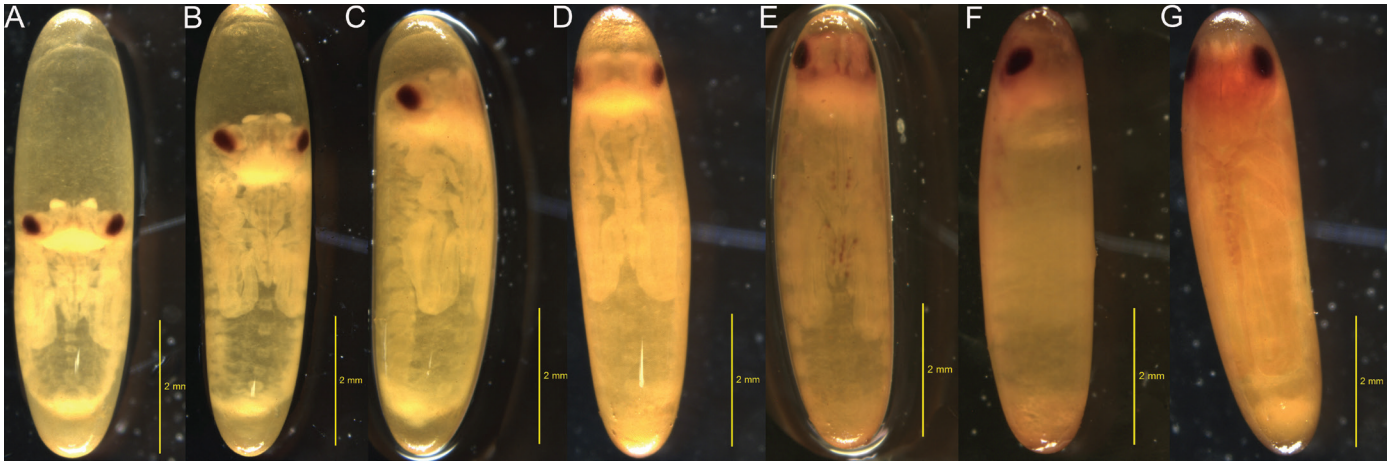

Fig. 5. Phase V: Dorsal closure **A.** Stage 19, ventral view; **B.** Stage 20, ventral view; **C.** Stage 21, lateral view; **D.** Stage 21 to 22, ventral view; Phase VI: Completion **E.** Stage 23, ventral view; **F.** Stage 23, lateral view; **G.** Stage 24, ventral view. Scale bars: 2 mm.

straightened out. The developing legs, antennae, and mouthparts are more conspicuous. The darkened eyespots are readily visible, having a reddish pigmentation and an angled ovoid appearance (Suppl. material 2: fig. S15). The top of the head is shaped like two blunt prongs. The embryo is less than half the length of the yolk.

Phase V: Dorsal closure (Fig. 5) The body grows dorsally around the yolk to envelop it.

Stage 19: The embryo is half the length of the yolk (Suppl. material 2: fig. S16). The eyespots are larger, more rounded, and generally darker than previously. The top of the head retains the blunt two-pronged form. The posterior femurs are fairly short, as approximately half of the abdomen extends beyond the joint between the tibia and femur of the hindmost legs. In Stage 19, dorsal closure begins, although this aspect of development is not visible in the image. At mean temperatures greater than 26°C, Mormon crickets arrest development at Stage 19 and apparently aestivate (Srygley 2022).

Stage 20: The embryo is three-quarters the length of the yolk (Suppl. material 2: fig. S17). While the embryo has elongated, the relative length of the legs has not changed much compared to Stage 19, with approximately half the length of the abdomen projecting beyond the tips of the folded hindmost appendages. The shape of the head has rounded out somewhat, with the two-pronged shape becoming less pronounced. The reddish-brown eyespots are conspicuous.

Stage 21: With only a small plug of yolk protruding beyond the head (Suppl. material 2: fig. S18), the embryo almost completely fills the egg. The legs remain somewhat short, covering approximately half the length of the abdomen and having not elongated much compared to Stage 20.

Stages 21 to 22: Only a small plug of yolk protruding beyond the head is still visible, and the legs are shorter than in Stage 23. While dorsal closure completes in Stage 22, this is not readily visible from the ventral view. The Stage 21 to 22 embryo has not yet shown any pigmentation of the appendages or head.

Phase VI: Completion. Stage 23: The embryo is the full length of the egg. The posterior femurs have become longer, are of medium length, and cover more than half of the abdomen (Suppl. material 2: fig. S19). The eyes are larger and dark. There is some pigmentation in the caput and in the pedes.

Stage 24: The embryo is the full length of the egg, and the hindmost femurs are long, extending most of the way but not completely to the tip of the abdomen (Fig. 7). The pigmentation of the legs and tarsal spines and head is much advanced. As with *Decticus verrucivorus* (Ingrisch 1984), the obligate diapause over winter, which is known as embryonic diapause, tends to occur in Stage 23 or 24 for Mormon crickets.

Stage 25: Final developmental stage that occurs after embryonic diapause and prior to hatching (Fig. 7).

Timing of the embryonic stages.—The developmental stages are in successive order, and so for an individual embryo, the minimum time to reach Stage n+1 cannot be less than the time to reach Stage n. However, this is not necessarily true for the different embryos portrayed (Figs 1–5). To obtain a rough estimate of the time to reach each stage, the embryos in the photographic images were graphed with their age from oviposition (Fig. 6). The initial stages can develop very quickly. For example, an embryo developed to

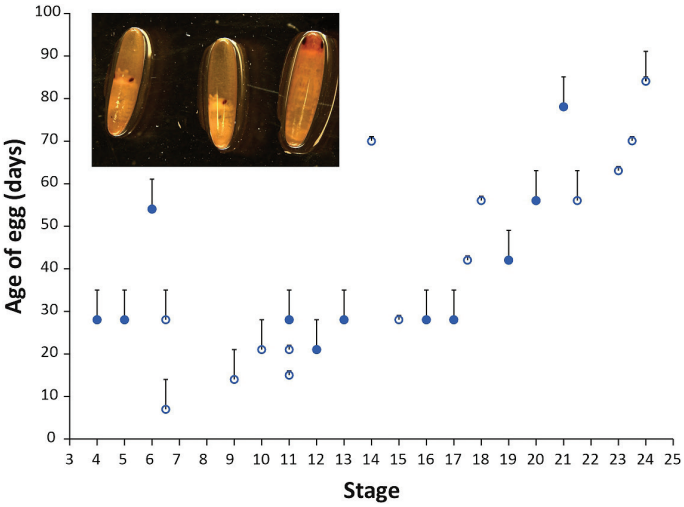

Fig. 6. The minimum age of each embryo from day of oviposition (maximum age indicated by error bar). Embryos that were between two stages (e.g., Stage 6 to 7) were given a value half-way between the two stages (e.g., 6.5). Closed circles: embryos incubated at a daily 12:12 h cycle of 30:15°C; open circles: embryos incubated at 30:15°C for the initial 35 days and then the daily maximum and minimum temperatures were varied each week thereafter. Inset: embryos in various stages of development in week 8.

Fig. 7. Phase VI: Completion. Ventral view of stage 25 embryo with chorion and membrane removed.

Stage 6 within a week or two after oviposition. Other embryos took longer to reach earlier stages, such as two embryos that reached Stage 4 and Stage 5 within 28–35 days and an embryo that reached Stage 6 in 54 days. As in other Orthoptera (Van Horn 1966, Ingrisch 1984, Donoughe and Extavour 2016), developmental timing can be highly variable. Two weeks after oviposition, an embryo had reached Stage 11. The later stages took longer to complete. For examples, it took four weeks for an embryo to reach Stage 17 and six weeks for a specimen to reach Stage 19. Stage 23, the beginning of the Completion phase, was reached in nine weeks, and Stage 24 in about 12 weeks.

Cowan and Shipman (1940) are credited with the first photographic series of katydid embryology, which they organized so that they could more precisely characterize the development of Mormon crickets in nature. To make it easier to draw comparisons with the literature that came later, we have attempted to reflect their series considering the stages of morphological embryogenesis that Warne (1972) and Ingrisch described (Suppl. material 1). For embryos in the stages before katatrepsis, it is difficult to see details necessary to separate them. Many more photographs are made of stages during katatrepsis and later, which suggests that Cowan and Shipman may have organized their photographs on a temporal scale in addition to a scale of external morphology. Organization by a temporal series is also evident in the occasional appearance of a figure that appears to be out of order when organized by morphogenesis (e.g., C&S 12b is Stage 19, but C&S 13a is Stage 18 in Suppl. material 1).

To summarize, we have organized a series of photographs of Mormon cricket embryos by their external morphology in accordance with Ingrisch (1984). This photographic series will prove valuable for understanding the proximate conditions by which development is arrested at different embryonic stages. The ability to predict outbreaks of Mormon crickets depends in part on our understanding the proximate and ultimate causes of their embryonic development.

Acknowledgments

We thank April Aamodt for collecting Mormon crickets in Oregon, D. Branson for lending the dissecting scope used to photograph the embryos, and F. Vencl for comments on a draft of the manuscript.

References

Buhl J, Sumpter DJT, Couzin ID, Hale JJ, Despland E, Miller ER, Simpson SJ (2006) From disorder to order in marching locusts. Science 312: 1402–1406. https://doi.org/10.1126/science.1125142

Chapman RF, Whitham F (1968) The external morphogenesis of grasshopper embryos. Proceedings Royal Entomological Society London A 43: 161–169. https://doi.org/10.1111/j.1365-3032.1968.tb01020.x

Cowan FT, Shipman HJ (1940) The effects of soil moisture and temperature on the development of Mormon cricket embryos. First quarterly report, U.S. Bureau of Entomology and Plant Quarantine.

Cowan FT, Shipman HJ (1947) Quantity of food consumed by Mormon crickets. Journal of Economic Entomology 40: 825–828. https://doi.org/10.1093/jee/40.6.825

De Geer C (1773) Mémoires Pour Servir à l'Histoire des Insectes. Tome troisième. Stockholm. (Hesselberg).

Donoughe S, Extavour CG (2016) Embryonic development of the cricket *Gryllus bimaculatus*. Developmental Biology 411: 140–156. https://doi.org/10.1016/j.ydbio.2015.04.009

Haldeman SB (1852) Appendix C. Insects. In: Stansbury H, Exploration and Survey of the Valley of the Great Salt Lake of Utah, Including a Reconnoisance of a New Route Through the Rocky Mountains. Washington, 366–379.

Hartley JC, Warne AC (1972) The developmental biology of the egg stage of Western European Tettigoniidae (Orthoptera). Journal of Zoology 168: 267–298. https://doi.org/10.1111/j.1469-7998.1972.tb01349.x

Hogan TW (1959) A rapid method for examining diapause embryos of *Acheta commodus*. Nature 183: 269. https://doi.org/10.1038/183269a0

Ingrisch S (1984) Embryonic development of *Decticus verrucivorus* (Orthoptera: Tettigoniidae). Entomologia Generalis 10: 1–9. https://doi.org/10.1127/entom.gen/10/1984/1

Linnaeus C (1758) Systema Naturæ per Regna Tria Naturæ, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio decima, reformata, [1–4], 1–824. Holmiæ. (Salvius). https://doi.org/10.5962/bhl.title.542

Mviha, PJZ, Holt J, Green SV (2022) Armoured bush cricket, *Acanthoplus discoidalis* (Walker) (Orthoptera: Tettigoniidae) outbreak prediction using rainfall patterns in three zones of Botswana. International Journal of Tropical Insect Science 42: 1113–1121. https://doi.org/10.1007/s42690-021-00627-z

Petrunkevitch A (1933) An inquiry into the natural classification of spiders, based on a study of their internal anatomy. Transaction Connecticut Academy of Arts and Sciences 31.

Pfadt RE (2002) Field Guide to Common Western Grasshoppers. University of Wyoming, Laramie.

Simpson SJ, Sword GA, Lorch PD, Couzin ID (2006) Cannibal crickets on a forced march for protein and salt. Proceedings of the National Academy of Sciences 103: 4152–4156. https://doi.org/10.1073/pnas.0508915103

Srygley RB (2016) Diet drives the collective migrations and affects the immunity of Mormon crickets and locusts: A comparison of these potential superspreaders of disease. Integrative and Comparative Biology 56: 268–277. https://doi.org/10.1093/icb/icw035

Srygley RB (2020a) Parental photoperiod affects egg diapause in a montane population of Mormon crickets *Anabrus simplex* (Orthoptera: Tettigoniidae). Environmental Entomology 49: 895–901. https://doi.org/10.1093/ee/nvaa062

Srygley RB (2020b) Coping with drought: Diapause plasticity in katydid eggs at high, mid-, and low elevations. Ecological Entomology 45: 485–492. https://doi.org/10.1111/een.12820

Srygley RB (2022) Temperature effects on Mormon cricket *Anabrus simplex* embryo development, hatching and nymphal growth: Thermal performance curves change with ontogeny. Journal of Thermal Biology 110: 103356. https://doi.org/10.1016/j.jtherbio.2022.103356

Srygley RB, Senior LB (2018) A laboratory curse: variation in temperature stimulates embryonic development and shortens diapause. Environmental Entomology 47: 725–733. https://doi.org/10.1093/ee/nvy024

Srygley RB, Jaronski ST (2019) Mormon cricket, *Anabrus simplex* Haldeman, 1852 (Tettigoniidae). In: Lecoq M, Zhang LSc (Eds) Encyclopedia of Pest Orthoptera of the World, China Agricultural University Press, Beijing, 219–223.

Van Horn SN (1966) Studies on the embryogenesis of *Aulocara elliotti* (Thomas) (Orthoptera, Acrididae), I. External morphogenesis. Journal of Morphology 120: 83–114. https://doi.org/10.1002/jmor.1051200105

Walker F (1869) Catalogue of the Specimens of Dermaptera Saltatoria in the Collection of the British Museum 2: 230.

Warne AC (1972) Embryonic development and the systematics of the Tettigoniidae (Orthoptera: Saltatoria). International Journal of Insect Morphology and Embryology 1: 267–287. https://doi.org/10.1016/0020-7322(72)90034-7

Wakeland C (1959) Mormon crickets in North America. Technical Bull. 1202, U.S. Department of Agriculture, Washington, D.C.

Supplementary material 1

Author: Robert B. Srygley, Laura B. Senior
Data type: pdf
Explanation note: Comparison of developmental stages of Ingrisch (1984) and Warne (1972) and the approximate equivalent of the stages illustrated in Cowan and Shipman (1940).

Link: https://doi.org/10.3897/jor.33.98763.suppl1

Supplementary material 2

Author: Robert B. Srygley, Laura B. Senior
Data type: pdf
Explanation note: **fig. S1.** Stage 4 circular disc of cells. **fig. S2.** Stage 6–7 with key characters labeled. **fig. S3.** Stage 9 with key characters labeled. **fig. S4.** Stage 10 with key characters labeled. **fig. S5.** Stage 11 with key characters labeled. The micropyles, clearly visible in this photo, are also indicated. **fig. S6.** Stage 11 with chorion removed. **fig. S7.** Stage 12 with key characters labeled. **fig. S8.** Stage 12 with chorion removed. **fig. S9.** Stage 13 with key characters labeled. **fig. S10.** Stage 14 with key characters labeled. **fig. S11.** Stage 14 with chorion removed and key characters labeled. **fig. S12.** Stage 15 with key characters labeled. **fig. S13.** Stage 16 with key characters labeled. **fig. S14.** Stage 17 with lateral (left) and frontal (right) views of the same embryo. **fig. S15.** Stage 18 with key characters labeled. **fig. S16.** Stage 19 with key characters labeled. **fig. S17.** Stage 20 with key characters labeled. **fig. S18.** Stage 21 with key characters labeled. **fig. S19.** Stage 23 with key characters labeled. **fig. S20.** Stage 24 with key characters labeled.

Link: https://doi.org/10.3897/jor.33.98763.suppl2