IV.2 Grasshopper Egg Development: the Role of Temperature in Predicting Egg Hatch

J. R. Fisher, W. P. Kemp, F. B. Pierson, and J. R. Wight

Hatch, the emergence of a nymph from the egg, is an important phenomenon in the life of a grasshopper. The embryo, the developmental stage that precedes the nymph, is the longest living stage, often lasting more than 10 months. The timing of hatch is important to grasshopper management because the timing of management activities is linked to nymphal emergence from eggs in the soil.

Most North American grasshoppers have one generation per year. Eggs are usually laid (oviposited) during late summer and early fall and hatch the following spring. There are usually five developmental stages (instars) that are present over a period of about 45 days during the late spring to early summer. Grasshoppers can usually be found as adults in the summer months up to late September, depending on the occurrence of the first hard frost.

Development and distribution of grasshoppers is largely governed by temperature. Each species has adapted to temperatures and other conditions of its habitat. The ancestors of modern grasshoppers were probably general feeders and lived in areas that had mild temperatures (>32 °F) all year. Over time, climate and habitat changed, as did food resources. Each species adapted, migrated, or perished.

Overwintering Adaptations

A number of adaptations have been described for insects that occur in the temperate regions. Most insects that spend the winter as a nymph or an adult have adapted by inreasing the amounts of complex sugars or glycerols (antifreeze-like compounds) in their blood. As winter approaches, these insects seek out areas such as the bases of plants, crevices on the outsides of buildings, soil cracks and crevices, nooks under rocks or tree bark, or even the insides of buildings. These insects overwinter in a dormant state (stupor) called quiescence or aestivation. They are inactive but will become active whenever the temperature in their microhabitat warms enough to support physiological processes: you may recall flies flying around on a warm day in January. However, these insects will go back to the quiescent state when the temperature cools.

Another adaptation to environmental adversity is a phenomenon called diapause. Diapause commonly occurs either in the embryonic stage, the late larval stages, or the pupal stage. Diapause is like quiescence, but instead of a stupor brought on by cold temperature, diapause is a state of suspended animation of nearly all physiological processes. That state has been genetically programmed in the insect over evolutionary time.

There are two kinds of diapause. Facultative diapause is brought on by certain environmental conditions and may only happen to individuals that are exposed to that condition or set of conditions. Obligatory diapause occurs to nearly every individual of a population at the same stage of development regardless of climatic or photoperiodic conditions. With either kind, once an insect is in the state of diapause, it stays in that state, no matter what kind of climate is encountered, until a certain event or events occur. These events can be a specific sequence of moisture regimes (such as contact moisture), temperature, photoperiod, time, or combinations thereof.

Overwintering in Grasshoppers

Grasshoppers lay eggs in the soil. In the act of laying eggs: first, a female grasshopper digs a hole in the soil with the tip of her abdomen to the depth of 0.4–1.0 inch (1–2.5 cm); second, she secretes a viscous material to line the hole (this becomes the pod); third, she places the eggs in the pod; and last, she plugs the pod with a frothy substance. Subsequently, the pod is covered with fine soil; the female places nearly each grain of soil with her hind legs. Temperature at pod depth in the soil is critical to the development of an embryo.

Most species of rangeland grasshoppers have one generation per year and have an embryonic diapause that occurs several weeks after the eggs are laid and usually lasts until the ground is frozen or freezing temperatures are common. Through diapause, these grasshoppers avoid hatching in the late summer and fall, when conditions would be unfavorable for growth and development. Diapause is the primary reason why most North American grasshoppers have only one generation per year.

For most species of the genus *Melanoplus,* embryonic diapause is facultative. With *Melanoplus sanguinipes,* a major pest grasshopper of rangeland and crops in the Western United States, diapause may last from 0 days to more than 200 days when eggs are held at room temperature. Environmental conditions, such as photoperiod length (daylight length) and temperatures experienced by the female, have been mentioned as possible factors that influence the occurrence and length of diapause in this species. However, in North America north of latitude 36° (Las Vegas, NV), *M. sanguinipes* eggs appear to require either some diapause or cold quiescence before winter because no partial or whole second generation has been reported.

Aulocara elliotti, the bigheaded grasshopper, is a grass-feeding specialist and rangeland pest that has, in the northern tier of the Western United States, an obligatory diapause. The diapause occurs when an individual *A. elliotti* embryo is about 60 percent developed; this stage is reached within 8 days after egg laying if the daily temperatures average about 86 °F (30 °C). If the temperatures average only about 68 °F (20 °C), *A. elliotti* eggs will take about 14 days to reach 60-percent development. *Ageneotettix deorum,* the whitewhiskered grasshopper, another grass-feeder on rangelands, appears to have an obligatory diapause similar to that of the bigheaded grasshopper.

Termination of Embryonic Diapause

Some persons aware of the process of embryonic diapause may think that diapause is “broken” (terminated or completed) by exposure to cold winter temperatures. This idea is partially true. With some insects, the amount of time spent in embryonic diapause has been found to be controlled by a hormone called the diapause hormone (DH). Hormones in insects are much the same as hormones in humans; each has a specific purpose and each can enhance or reduce the actions of certain other hormones. DH is initially at a high level (titer) in diapausing eggs. A high titer prevents a growth promoting hormone, esterase A (EA), from doing its job. With some insects, time decreases the activity of DH. In other insects, cool temperatures (around 37–59 °F [3–15 °C]) promote an increase in EA titers and activity and a regression of titers of DH.

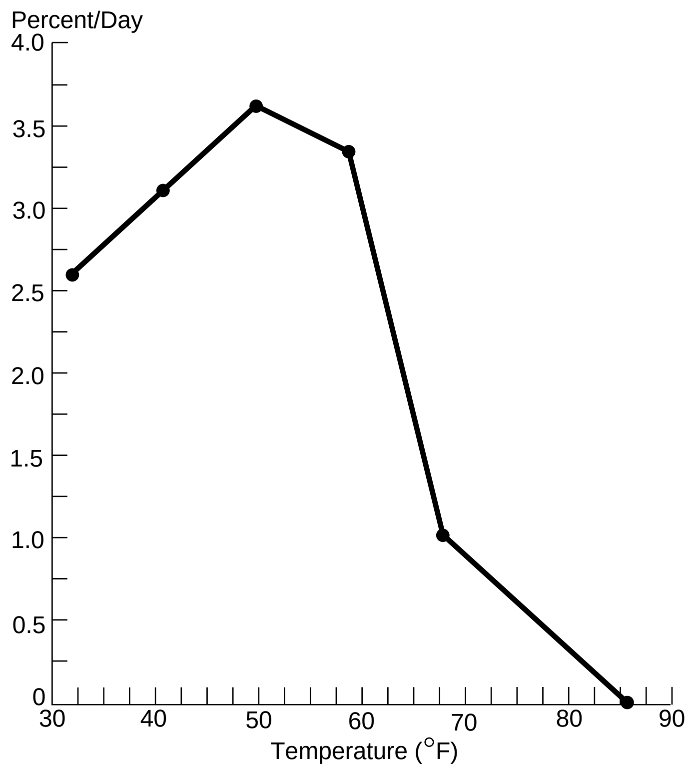

Figure IV.2–1—Generalized illustration of the percent of diapause completed per day when a diapausing embryo is exposed to certain cool temperatures.

Figure IV.2–1 illustrates, in general, the amount of diapause completed per day by a hypothetical insect that requires cool temperature to terminate diapause. This illustration was compiled by the authors after an extensive review of embryonic diapause of a number of insect species from temperate climates that spanned three orders—Lepidoptera (moths and butterflies), Coleoptera (beetles), and Orthoptera (grasshoppers, roaches, walking sticks, crickets). This illustration could represent, in a circumstantial way, the amount of DH dissipated daily at the temperatures represented.

The time between diapause initiation and termination is often called diapause development; not much is developing, but hormonal action and some metabolism are going on. Figure IV.2–1 shows that the fastest diapause development times (>3.0 percent per day) would occur near 45–54 °F (7–12 °C). This is true for the grasshoppers *Aulocara elliotti* and *Ageneotettix deorum* and possibly other rangeland grasshoppers. To put this in perspective, the following example helps explain the meaning of figure IV.2–1. If the daily temperatures averaged 50 °F, diapause development would occur in increments of about 3.5 percent per day. To determine the amount of time needed to complete diapause at 50 °F, divide 100 percent by 3.5 percent. The result—29 days—is the period of development needed to have complete diapause.

North of 40° latitude (Salt Lake City, UT), this ideal temperature range (the range of fastest diapause development, 45–54 °F) occurs in the months of September, October, and November. Of course, we are considering average temperature; most nights are colder, and many daylight hours are much warmer. Even so, for many species, diapause usually is terminated by early to mid-November (> 90 days after the end of egg laying by most grasshoppers).

Spring Egg Hatch (Postdiapause Development)

Once diapause terminates, normal embryonic development will proceed whenever temperatures exceed 50 °F (10 °C). This is called the developmental threshold (DT), the temperature below which nearly all metabolic processes cease (quiescence). At temperatures above the DT, metabolic processes proceed at increased rates with increasing temperatures (the higher the temperature, the faster the metabolism) until a lethal temperature, usually >106 °F (41 °C), is reached. The increases in metabolic processes translate into a rate of development for the embryo. Table IV.2–1 shows the postdiapause embryonic development rate in relation to soil temperatures for four pest species of grasshoppers. These development relationships were derived from several of our experiments with egg development and hatch.

Predicting *Aulocara elliotti* Hatch

To predict the hatch of an insect such as *Aulocara elliotti*, two key pieces of information are needed: when diapause terminates and the rate of embryonic development. Because these are insects that hatch at spring temperatures, grasshoppers are extremely temperature dependent. They also have an obligatory diapause that stops development until certain temperature requirements are met. Most insects take very little time to resume normal metabolism once the DT is reached. But if they are in diapause, time exposed to temperatures above the DT does not contribute to development. Thus, it is important to know when diapause terminates. Knowledge of the rate of embryonic development at various nonlethal and nonquiescent temperatures is necessary if daily or hourly temperature averages are used as drivers for a model that predicts hatch.

Table IV.2–1—Days needed for a grasshopper egg to hatch when exposed to various constant soil temperatures

Temperature		Days to hatch			
°F	°C	*Melanoplus sanguinipes*	*Melanoplus bivittatus*	*Melanoplus differentialis*	*Aulocara elliotti*
50	(10)	—	595	250	602
59	(15)	33	26	49	135
68	(20)	15	13	27	36
77	(25)	10	9	18	15
86	(30)	7	6	14	11
95	(35)	6	5	11	10
104	(40)	5	4	9	9

Aulocara elliotti Diapause Termination

We determined the time of diapause termination (completion) for *A. elliotti* by collecting egg pods from the field periodically from early October through the spring of 1990–91 and 1992–93. We subjected the egg pods to temperatures of 86 °F in the laboratory for 120 days. At that time (120 days), we determined how many had hatched, how many were dead, or how many were still alive.

In Figure IV.2–2, live eggs can be interpreted to still be in diapause. From these studies, we found that more than 70 percent of the eggs hatched and thus had completed diapause by the collection on Julian date (JD) 317 (Nov. 13) (fig. IV.2–2). However, note that more than 30 percent had hatched from collections on JD 287 (Oct. 14) in 1992 and by JD 300 (Oct. 27) in 1990. By the collection date 334 (Nov. 30), in both seasons nearly 100 percent of the eggs that survived to hatch had terminated diapause. When we considered these results and the normal variability in vital life events for most animals and, in particular, *Aulocara elliotti*, we decided to begin our hatch predictions by accumulating above-DT temperature units from JD 303 (Oct. 30).

Aulocara elliotti Rate of Embryonic Development

Table IV.2–2 shows the days needed for hatch and the rate of development of an embryo of *Aulocara elliotti* when held, after diapause, at constant temperatures from 59 °F (15 °C) to 108 °F (42 °C). The observed median is from our actual data. But, to predict hatch from an actual temperature base, we needed to create a model (equation) from our data that represented the embryo's reaction to a continuum of temperatures. For this we went to simple high school algebra and derived a rate model, an equation that fitted a sine curve because the data appeared similar to a sine curve. The rate of development per day is the reciprocal of the predicted median days to hatch.

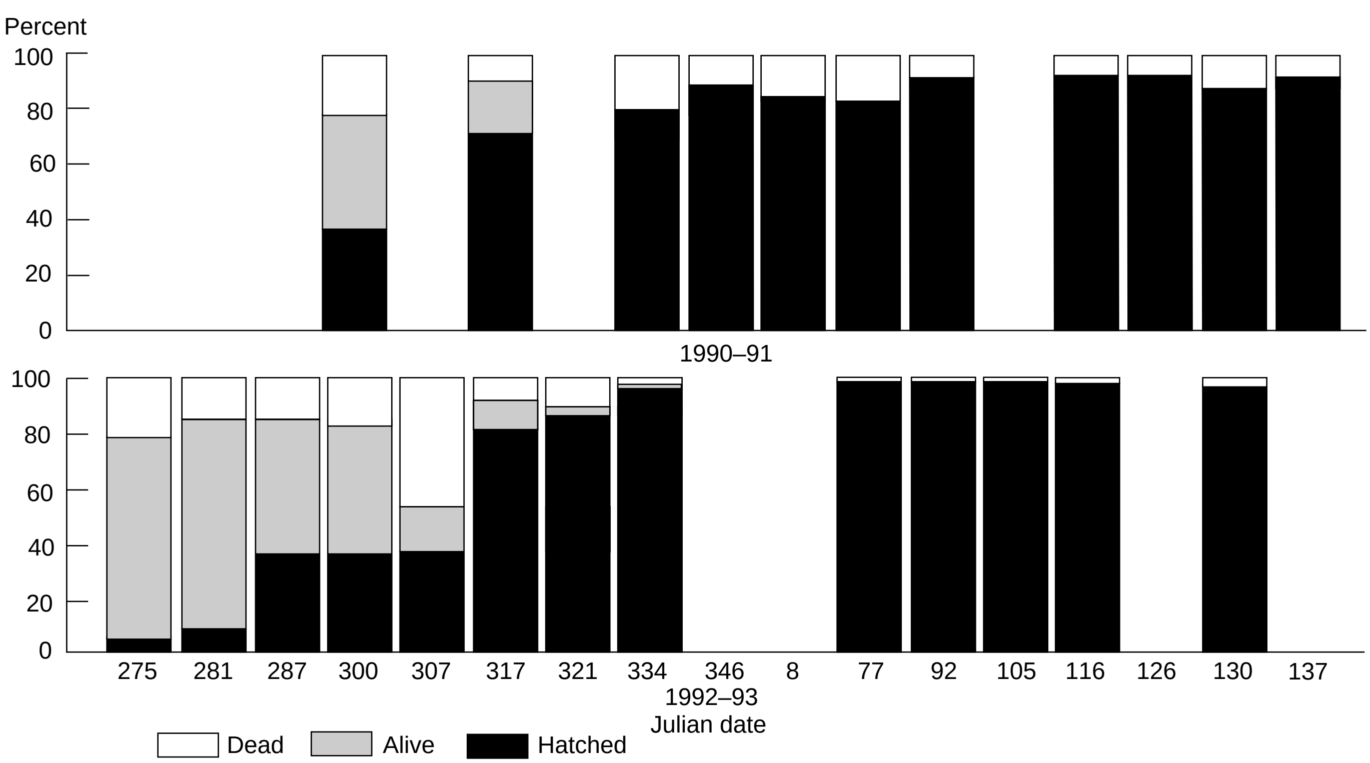

Figure IV.2–2—Proportion of hatch (alive *v.* dead eggs) of *Aulocara elliotti* collected in the field from October to the spring of 1990–91 and 1992–1993 when exposed to 86 °F (30 °C) for 120 days after collection.

Table IV.2–2—Observed median days to hatch and predicted median days to hatch and rate of embryonic development per day for *Aulocara elliotti* eggs after diapause, when held at various constant temperatures

Temperature °F	(°C)	Median (observed)	Median (predicted)	Rate of development/ day
				Percent
59	(15)	136.00	92.9	1.01
64	(18)	56.00	59.17	1.7
75	(24)	21.08	25.38	4.0
81	(27)	15.18	17.42	5.8
86	(30)	16.29	12.50	8.0
91	(33)	9.66	9.46	10.6
97	(36)	7.28	7.8	12.8
102	(39)	6.00	6.42	15.6
108	(42)	5.98	5.70	17.5

Prediction of Hatch of *Aulocara elliotti*

Most air and soil temperatures are monitored for a daily high–low record or an average hourly record. For this study we used an hourly record of soil temperature from egg-pod level, three quarters of an inch (2 cm) below the surface of the soil. A straightforward prediction of hatch could be made by taking the hourly temperature after JD 303 (Oct. 30) and placing it in the rate of development equation and tallying the amount of development for each hour over a 24-hour period and then tallying this predicted development over each day of the winter and spring. However, this calculation does not take into account the variation that is omnipresent for every metabolic process among individuals in a species. This problem was corrected by using another model that accounted for the variation in development times found for each group of eggs tested at the various constant temperatures.

Through some computer software (PMDS, Version 5) we were able to take the two models mentioned earlier and the temperature data and derive predictions for hatch for two sites in southwestern Montana over 2 years (table IV.2–3). Site MH1 is at 4,412 ft (1,345 m) above sea level, and site MH2 is at 5,075 ft (1,547 m) above sea level. The two sites are about 2 mi (3.2 km) apart. To see how accurate our predictions were, each day from late April through mid-July in each year we collected first-instar grasshoppers at each of the sites (MH1 and MH2) (table IV.2–3).

Model Efficiency

Accuracy of these models is best noted when the prediction of 50-percent hatch is indicated. If you examine table IV.2–3, you will notice that the predicted 50-percent hatch was within 1 day or less of the actual first-instar samples for three of the four comparisons. With MH1 for 1992, the 50-percent hatch was predicted to occur only 7 days beyond actual. In both years, MH2 actual hatch did not start until at least 10 days later than at MH1. Temperatures at the higher altitude were cooler; thus, hatch was later.

Utility and Implications of These Models

The sensitivity of these models is remarkable. We feel that accuracy in the predictions was obtained by (1) knowing a starting time to begin our temperature accumulation for hatch (diapause termination), (2) taking temperature at pod level (microclimate of the egg), (3) knowing an estimate of the variation in hatch of species at an array of temperatures, and (4) knowing the rate of development of the postdiapause embryo at an array of above-quiescent, below-lethal temperatures.

Our two sites had a difference of 650 ft (198 m) in altitude. At the higher altitude site, hatch was later—at least 10 days. Many areas within a management district will vary in altitude, land aspect, distance from mountains, and more. These features cause changes in microclimate. When these microclimatic differences are tallied over a 5- to 6-month period, their influence on embryonic development may be significant.

Most range managers do not have access to records of soil temperatures at 0.4 inch to assist with prediction of hatch at a site. However, air-temperature records at 1 ft (30.4 cm) or 3 ft (91.4 cm) are common, and instrumentation to assist in maintaining records is reasonably priced and readily available. We have developed a simulation model with the objective to predict soil temperature accurately at 1–2 cm by using air temperature at 3 ft

Table IV.2–3—*Aulocara elliotti* egg hatch, by percentage and Julian date, at two Montana sites (actual sampling *v.* model predictions)

Site, year	Initial	Percent of egg hatch 1	5	25	50	75	90
MH1 1991							
Sweep sample	133	144	149	153	156	159	164
Model	130	140	145	153	157	161	165
MH1 1992							
Sweep sample	111	119	122	126	128	131	134
Model	93	97	122	129	135	139	142
MH2 1991							
Sweep sample	154	154	158	163	168	171	176
Model	144	147	155	163	168	171	176
MH2 1992							
Sweep sample	120	120	128	139	143	145	149
Model	98	125	129	139	143	148	152

above the ground (see V.9). Thus, by using the soil temperature simulation model and our *A. elliotti* hatching models that are based on soil temperature at 1–2 cm, air-temperature data banks that have been kept over a number of years at any site may be able to accurately predict when hatch of this species would begin (this work is in progress). Accurate soil temperature prediction from air temperatures used with these models for hatch would assist with the timing of survey assessment of populations and with the timing for consideration of management options.

Suggested References

Danks, H. V. 1987. Insect dormancy: an ecological perspective. Biol. Surv. Canada Monogr. Ser. 1. Ottawa, ON: Biological Survey of Canada. 439 p.

Downer, R.G.H.; Laufer, H. 1983. Endocrinology of insects. New York City: Alan R. Liss, Inc. 707 p.

Fisher, J. R. 1993. Location of *Aulocara elliotti* egg pods in a crested wheatgrass field in Montana. Journal of the Kansas Entomological Society 65: 416–420.

Fisher, J. R. 1994. The effect of temperature on the post-diapause development and survival of embryos of three species of *Melanoplus* (Orthoptera: Acrididae). Annals of the Entomological Society of America 87: 604–608.

Fisher, J. R.; Kemp, W. P.; Pierson, F. B. 1996. Hatch of the bigheaded grasshopper, *Aulocara elliotti* (Thomas) (Orthoptera: Acrididae). Environmental Entomology 25: 1158–1166.

Hewitt, G. B. 1985. Review of factors affecting fecundity, oviposition and egg survival of grasshoppers in North America. Bull. ARS-36. Washington, DC: U.S. Department of Agriculture, Agricultural Research Service. 35 p.

Kemp, W. P. 1986. Thermoregulation in three rangeland grasshopper species. Canadian Entomologist 118: 335–343.

Kemp, W. P.; Sanchez, N. E. 1987. Differences in post-diapause thermal requirements for eggs of two rangeland grasshoppers. Canadian Entomologist 119: 653–661.

Logan, J. A.; Weber, L. A. 1991. Population model design system (PMDS). A user's guide. Blacksburg, VA: Virginia Polytechnic Institute and State University, Department of Entomology and Department of Forestry. 72 p.

Shotwell, R. L. 1941. Life histories and habits of some grasshoppers of economic importance of the Great Plains. Tech. Bull. 774. Washington, DC: U.S. Department of Agriculture. 47 p.

Tauber, M. J.; Tauber, C. A.; Masaki, S. 1986. Seasonal adaptations of insects. New York City: Oxford University Press. 411 p.