

Mixed Oviposition in Individual Females of *Gryllus firmus*: Graded Proportions of Fast-Developing and Diapause Eggs

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Summary. Eggs of field crickets (*Gryllus* spp.) held at $25 \pm 1^\circ \text{C}$ hatch in 2–4 weeks (“fast-developing” eggs) or 5–28 weeks (diapause eggs). Most species lay but one type: at least 10 species lay only fast-developing eggs, and *pennsylvanicus* and *ovisopsis* lay only diapause eggs. *Gryllus firmus* from Gainesville, Florida, lays both types, and individual females do so for as long as 8 weeks. The proportion of diapause eggs laid weekly by captive females exposed to outdoor photoperiods and temperatures varies seasonally from <5% (March–June) to ca. 50% (November–December). At outdoor temperatures in late fall some eggs that are presumptively fast-developing (at 25°C) enter diapause.

Some *firmus* from Carolina Beach, North Carolina, lay both diapause and fast-developing eggs. Outdoor rearing experiments established that spring adults could result from fast-developing eggs of fall adults, refuting the hypothesis that spring and fall adults at that locality represent temporally isolated demes.

High variance in hatching times for eggs laid by one female is appropriate to the unpredictable extremes of moisture and temperature that occur in the open, sandy habitats of *G. firmus*. Physiological mechanisms of the mixed oviposition and specific environmental determinants of the varying proportions are unknown.

Introduction

In most species of insects, all eggs have approximately the same developmental competence – so long as the eggs are exposed to the same circumstances, they hatch after approximately the same lapse of time. For example, all spruce budworm eggs (*Choristoneura fumiferana*) hatch within two weeks under normal field conditions (Morris 1963), and all eastern tent caterpillar eggs (*Malacosoma americanum*) hatch after nine months of summer, fall, and winter weather (Anderson 1960). Eggs of eastern tent caterpillar are classified as diapause eggs because they have a developmental delay that continues, for a time, in the absence of environmental restraints (Lees 1965); eggs of spruce budworm have no such delay and may be termed non-diapause eggs.

In some species of insects, both diapause and non-diapause eggs are produced. For example, the bivoltine strain of the silkworm (*Bombyx mori*) lays nondiapause eggs in the summer and diapause eggs in the fall. The type of eggs produced depends on what photoperiods and temperatures the female experienced as an embryo and early larva. Under natural conditions females of the summer generation lay only non-diapause eggs, and those

of the fall generation lay only diapause eggs. Even under experimental conditions, individual females generally lay batches containing eggs of only one kind (Lees 1955).

Continued laying of mixtures of diapause and non-diapause eggs by individual females under natural conditions has seldom been demonstrated. The only established cases are for several grasshoppers (reviewed by Uvarov 1966). For example, *Locustana pardalina* lays pods of eggs containing 0–100% diapause eggs and a single female, caged outdoors, will produce as many as four consecutive pods with mixtures of diapause and non-diapause eggs (Matthée 1951). The mosquito *Aedes caspius dorsalis* may be another case (Khelevin 1958). First generation females (June–July) lay only non-diapause eggs but second and third generation females (late July–September) lay eggs that at temperatures $>18^\circ \text{C}$ become varying proportions of diapause and non-diapause eggs. Under laboratory conditions, individual females produce batches of eggs that show two modes of development. Similar eggs occur in the field, though it was not proved that females under field conditions lay mixed batches. Some species of walkingsticks (Phasmodidae) lay two types of eggs – those that hatch the first year and those that hatch the second. However, it is uncertain whether an individual female continually lays mixtures of the two types. Voy (1952, 1954) recognized the two types of eggs from batches produced by groups of females of *Clonopsis gallica*. Korboot (1961) collected eggs from single females of *Acrophylla tessellata* and *Extatosoma tiaratum* but did not segregate eggs laid at different times; though she demonstrated both types of eggs from one female, she did not eliminate the possibility that early eggs were one type and late eggs were the other (Matheson and Hurlbut, 1937, showed this to be the case for a female mosquito, *Anopheles walkeri*). Readshaw (1965) reported both type eggs for *Didymuria violescens* but gave no data on eggs laid at one time by single females. The eggs of katydids (Tettigoniidae) sometimes exhibit dichotomous hatching times but the causes are unknown. Hartley and Warne (1972) studied egg development of 46 species of tettigoniids under laboratory conditions. They suspected “maternal factors” sometimes influenced whether eggs skipped an initial diapause, but did not prove that individual females produced mixtures of diapausing and non-diapausing eggs. The same deficiency occurs in Browning’s (1952) and in Bigelow’s (1962) reports of mixtures of diapause and non-diapause eggs from caged groups of females of Australian field crickets (*Teleogryllus commodus*). Bigelow determined that a strain derived from fast-hatching eggs and a strain derived from slow-hatching eggs each produced eggs with both modes of hatching but gave no evidence that a single female produced both types of eggs.

Bigelow (1962) also studied egg development in field crickets

of the genus *Gryllus*. For ten species he reported no egg diapause: *assimilis*, *bermudiensis*, *bimaculatus*, *fultoni*, *rubens*, *veletis*, *vernalis*, and three undescribed species from western North America. In each of the ten, hatching was unimodal with most eggs hatching after 11 to 15 days at 28° C. For *G. pennsylvanicus*, Bigelow reported only diapause eggs, hatching mostly between 30 and 95 days at 28° C. For the remaining species studied, *G. firmus*, he reported that "most of the eggs hatch after 16 to 25 days (some five to ten days later than in species without egg diapause)", and gave no further data.

As part of a long-term study of life cycles of *Gryllus* spp. in southeastern United States, I discovered that individual *Gryllus firmus* females produce mixtures of fast-developing and diapause eggs with the proportions changing with the season, and that some of the presumptive fast-developing eggs become diapause eggs upon exposure to late fall conditions.

Methods

Field-collected females were held individually in screen-capped 4-l jars with substrate for oviposition (800 ml moistened, sterilized fine sand), food (Purina Dog Chow in an inverted plastic vial cap), and water (15-dram vial with a rubber stopper penetrated by a dental cotton wick). The jars were kept on the ground in a wooded area near Gainesville, Fla. A sheet of plywood supported by four posts protected the jars from rain and direct sunlight but allowed natural photoperiod and near-natural temperatures. Each week each female was transferred to a new jar. Nearly all females had mated prior to capture and remained fertile during the remainder of their egg-laying lives: up to 10 weeks and 2,576 eggs.

For each female, successive jars with 1-week's oviposition were alternately either left outdoors under the open shelter or held in a rearing room at 25 ± 1° C and 16L:8D photoperiod. All jars were tended weekly. Fresh food was added and soil moisture replenished; any hatchlings were removed with an aspirator and counted. Females from areas distant from Gainesville were sometimes held in the rearing room, rather than outdoors, for oviposition.

Results and Discussion

Eggs Held at 25° C

Eggs of *G. assimilis*, *rubens*, and *fultoni* hatched within 28 days of being brought to the 25° C rearing room (Fig. 1A–C). Eggs of *G. pennsylvanicus* and *ovisopis* did not begin their hatch for 5–13 weeks and hatch lasted as long as 13 weeks (Fig. 1D–E and unpublished). In most cases eggs of *G. firmus* from females collected at Gainesville had two modes of hatching at 25° C, one that matched the mode of *assimilis*, *rubens*, and *fultoni* and one that matched the mode of *pennsylvanicus* and *ovisopis* (Fig. 1F–I). In other words, during each week of oviposition individual *firmus* females usually laid both non-diapause and diapause eggs. The proportions of non-diapause and diapause eggs laid by a female did not change in a predictable manner with age (Fig. 2, connected points). Two examples are detailed in Fig. 1 (F–I): the first and third weeks of oviposition are graphed for two females. In some instances hatching occurred during every week between the two modes (e.g. Fig. 1G), and some eggs could not be assigned with certainty to either the diapause or non-diapause mode. Since non-diapause eggs in other *Gryllus* spp. generally hatch within 28 days at 25° C, *firmus* eggs that hatched within 28 days of the last date of oviposition were termed *fast developing* (i.e. non-diapause,

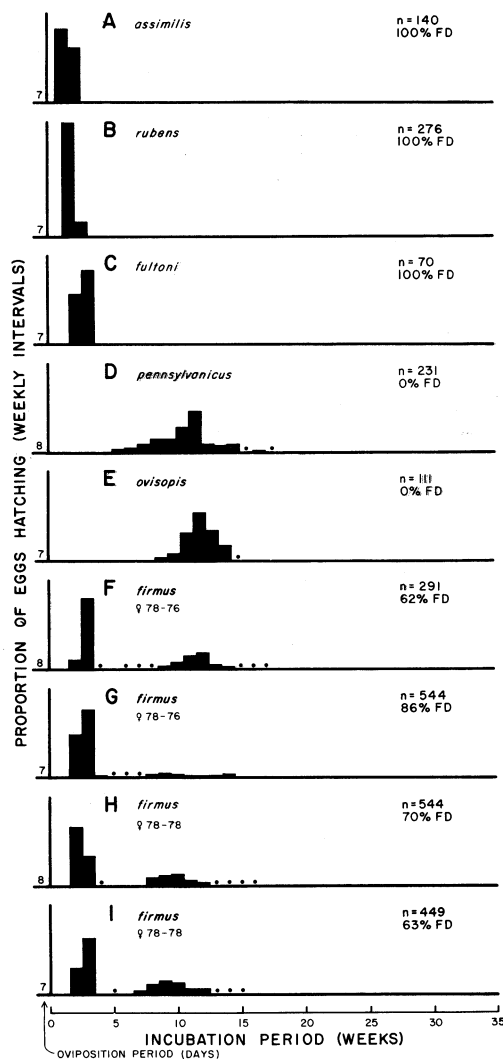


Fig. 1A–I. Representative hatching patterns for *Gryllus* eggs at 25° C. Each graph shows the hatching of eggs laid by one female during 7 or 8 days. Vertical bars indicate proportion of total hatch recorded at each weekly census. Dots represent weeks having hatch less than 1% of total. A–C All eggs fast-developing (FD) type. A *G. assimilis*, Homestead, Fla.; no diapause in any stage. B *G. rubens*, Gainesville, Fla.; juvenile diapause. C *G. fultoni*, Gainesville, Fla.; juvenile diapause. D–E All eggs diapause type. D *G. pennsylvanicus*, nr. Blowing Rock, N. Car. E *G. ovisopis*, Gainesville, Fla. F–I *G. firmus*, Gainesville, Fla., some fast-developing and some diapause eggs. F–G Same female. F Eggs laid 22–30 October G Eggs laid 6–13 November H–I Another female. H Eggs laid 22–30 October I Eggs laid 6–13 November

or diapause so weak that development is as rapid as for some non-diapause eggs of other species).

Females of *G. firmus* collected at Gainesville in the spring and early summer usually produced a smaller proportion of diapause eggs than females collected in the fall (Fig. 2). Females collected at the same time were often significantly different in the proportions of fast-developing and diapause eggs they laid, and the same female sometimes changed proportions substantially from one lab-assayed egg batch to the next (Fig. 2). In the spring the greatest proportion of diapause eggs in a batch was 9%, whereas the average for November–December was ca. 50%.

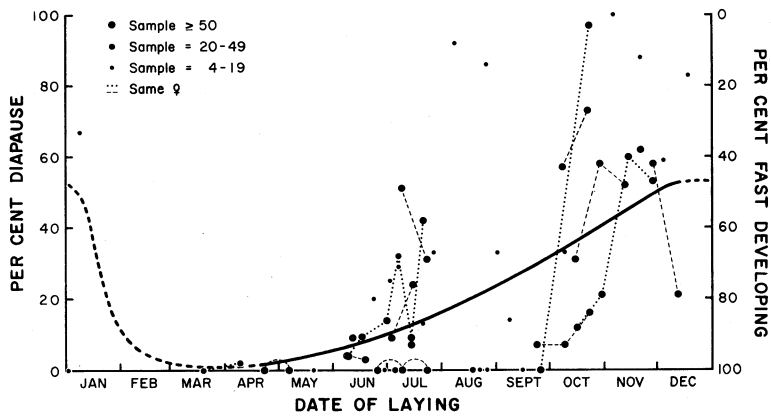


Fig. 2. Per cent diapause and fast-developing eggs laid by *Gryllus firmus* females, Gainesville, Fla., as a function of date of oviposition. Each point represents eggs laid outdoors during one week by a single female and incubated at $25 \pm 1^\circ \text{C}$. Points connected by dotted or dashed lines are for batches of eggs laid during different weeks by the same female. Heavy line shows trend of monthly means; dashed portion is largely an interpolation

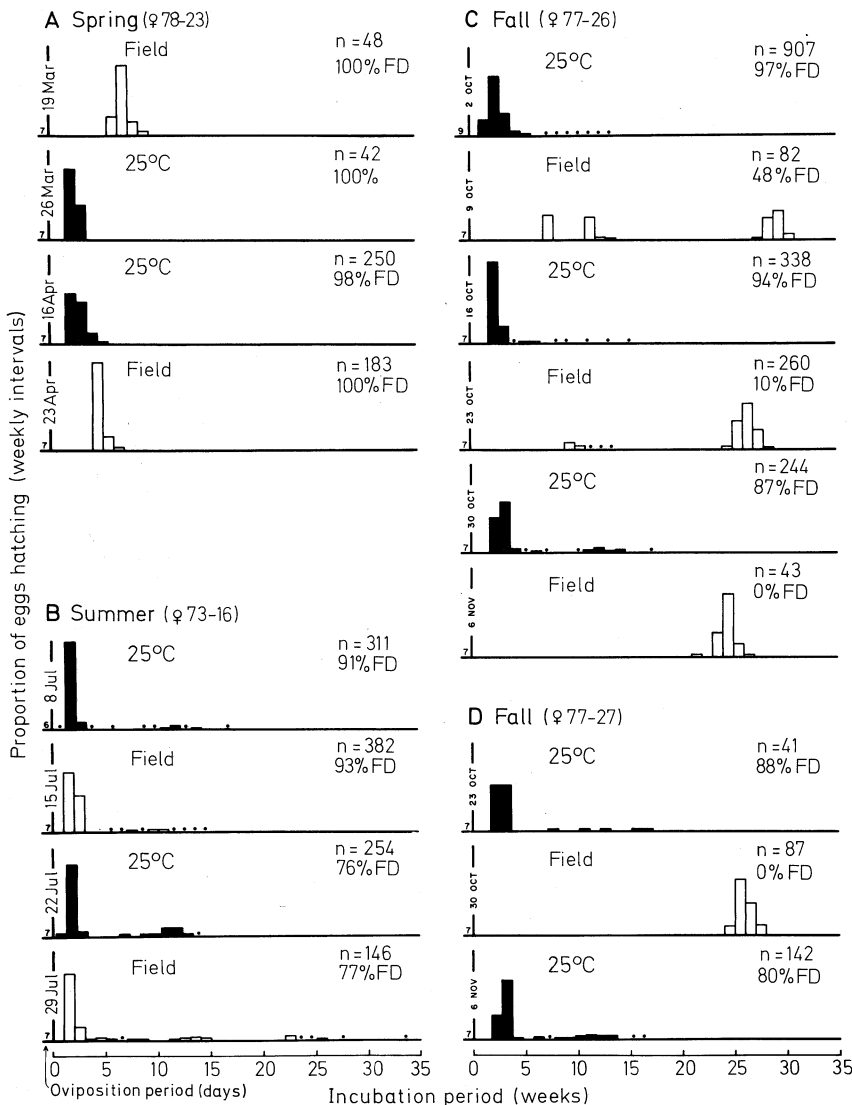


Fig. 3A-D. Representative hatching patterns for eggs of *Gryllus firmus*, Gainesville, Fla. Eggs laid outdoors by caged wild-caught females; each week's eggs segregated and incubated either outdoors (*open bars*) or at $25 \pm 1^\circ \text{C}$ (*black bars*). Dots indicate weeks having hatch less than 1% of total. End of oviposition period designated by vertical line and date at left of each graph. **A Spring.** Hatch was unimodal and most eggs were fast developing; hatching pattern of field-incubated eggs was similar to that of eggs incubated at 25°C , later hatching in the field being attributable to lower temperatures. **B Summer.** The fast-developing eggs (76–93% of total) hatched after similar intervals whether left outdoors or incubated at 25°C . Diapause eggs incubated at 25°C required no more than 18 weeks to hatch. Diapause eggs laid 8–15 July and left outdoors hatched in fall (within 15 weeks); those laid 22–29 July and left outdoors hatched in fall (65%; within 15 weeks), winter (32%; 23–28 weeks), and spring (3%; $n=1$; 34 weeks). **C Fall (Female 77-26).** Eggs incubated at 25°C proved to be 87–97% fast developing – i.e. fewer than 15% were diapause eggs. Most eggs laid during the alternate weeks and left outdoors were therefore presumptively fast developing; however, most (52–100%) hatched at the same time as diapause eggs. **D. Fall (Female 77-27).** Eggs incubated at 25°C were 80–88% fast developing. Eggs laid 23–30 October and left outdoors hatched as though all had been diapause eggs

Eggs Held Outdoors

Hatching patterns of eggs of Gainesville *firmus* held under outdoor temperatures and photoperiods were interpreted in comparison with eggs from alternate weeks held at 25°C (Fig. 3).

Eggs laid in spring (Fig. 3A) had a single mode of hatching

in the field and in the laboratory. A few eggs required more than 28 days to hatch at 25°C (Fig. 3A, 16 April), but no diapause mode was evident. Field temperatures (Fig. 4) averaged substantially lower than 25°C , and the mode of hatch outdoors was 2–4 weeks later than in the laboratory (Fig. 3A).

Eggs laid during the summer months had more than one mode

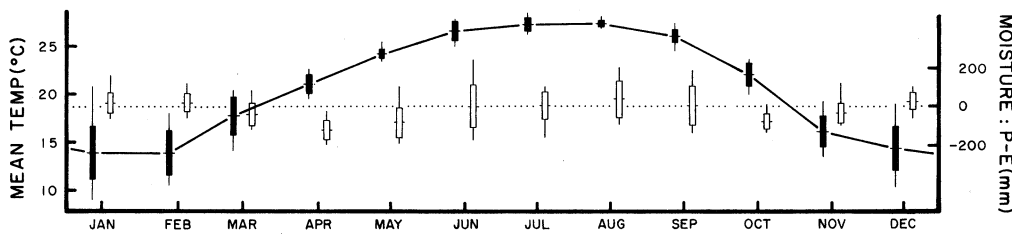


Fig. 4. Gainesville, Fla., weather. Heavy line connects 17-year means of mean monthly temperatures (1962–1978, Gainesville 3WSW, NOAA). Solid vertical symbols depict range and one standard deviation on either side of the mean. Open vertical symbols denote monthly moisture expressed as precipitation less evaporation. Horizontal line in each symbol is mean value ($n=17$); vertical box is one standard deviation on either side of the mean; vertical line is range. Dotted line across graph indicates precipitation equalling evaporation

of hatching in the field (Fig. 3B). The first mode corresponded to the fast-developing mode at 25° C, and the time preceding hatch was similar in field and laboratory – as would be predicted from the similar temperatures (Fig. 4). Diapause eggs in the field hatched at the same time as in the laboratory until field temperatures dropped; then their hatch was delayed, sometimes until spring (Fig. 3B, 29 July).

Field hatching of fall-laid eggs (Fig. 3C, D) was puzzling. Whereas eggs classed as fast-developing and diapause types by laboratory assay had easily detectable field counterparts in spring and summer, such was not always the case in the fall. Fall eggs assayed at 25° C were often more than 80% fast developing type (Fig. 3C, D). Yet when left under field conditions, few eggs hatched in 5–10 weeks – the expected hatching time for fast developing eggs under moderate to cool fall temperatures (note spring hatch in Fig. 3A, 19 March). Instead, all or most of the hatch was late the following spring – 20 to 30 weeks later and centering around 1 May. The eggs that overwintered and hatched the following spring surely included any eggs that would have been classed as diapause eggs at 25° C: similar late-spring hatching occurs for eggs of *G. oviposis*, which lays only diapause eggs (Walker 1974). The small or missing modes of earlier hatch for fast-developing eggs could be attributed to differential mortality (all or most fast-developing eggs perish whereas diapause eggs survive) except that numbers of “diapause” eggs hatching the following spring were far greater than expected from the numbers of diapause eggs hatched at 25° C from batches laid the preceding and following weeks (Fig. 3C, 23 October; Fig. 3D, 30 October). Eggs laid by five other females in October–November, during 3 years, hatched in patterns similar to eggs of the two females selected for Fig. 3C, D. The simplest hypothesis that fits the available evidence is that some fall-laid eggs that are presumptively fast-developing type (at 25° C) initiate diapause under fall temperatures and become developmentally equivalent to eggs that are presumptively diapause eggs (at 25° C).

An annual cycle of egg development in the field can be postulated on the basis of 54 batches of eggs held outdoors during 5 years (Fig. 5). Eggs that were presumptively fast-developing hatched in minimum time during summer months and after longer intervals in spring and fall. In fall a portion of these eggs entered diapause and hatched with the presumptively diapause eggs late the following spring. Diapause eggs laid during the summer were highly variable in their hatching times with the variance increasing rapidly from June through August. In the fall the variance rapidly diminished, and December-laid eggs, whether presumptively diapause or fast-developing, hatched nearly synchronously the follow-

ing spring. Annual differences in spring temperatures account for some of the variation in median date of hatch for spring hatching eggs (Fig. 4 and 5).

Voltinism in Gainesville firmus

The most frequent life cycle for *firmus* in North Florida seems to be two generations a year. Though adults occur at all seasons, the proportional frequencies of life stages (Walker, unpublished), and the numbers of adults caught in pitfalls (Veazy et al. 1976) and of males heard calling (Walker 1980) show annual patterns suggesting that a majority of the population overwinters in the egg stage and matures in late June and July, that these adults beget late-September and October adults, and that these lay eggs that overwinter. Complicating this basic, bivoltine, egg-overwintering cycle is the fact that eggs laid in July and August contribute both to the late fall peak of adults and, via overwintering juveniles, to a small contingent of adults in April, May, and early June. Furthermore some eggs laid in August and early September don't hatch until the following spring; others produce overwintering juveniles that become adults as their egg-overwintering sibs are hatching; and still others produce late fall adults that lay eggs that overwinter and hatch in synchrony with some of their aunts and uncles!

Variable nymphal development (Walker unpublished) contributes importantly to the overlapping of generations. For example, progeny that hatched during two weeks in late August from fast-developing eggs laid one week by one female and that were reared outdoors with ample food and moisture matured as early as November, as late as the following June, and in all but one month in between.

Thus even without probable (though unproved) starvation-caused developmental delays in nymphs and drought-caused developmental delays in eggs, the mix of life stages of *firmus* changes seasonally in an exceedingly complex pattern: univoltine, bivoltine, and perhaps trivoltine life cycles coexist and intertwine, and eggs, mid-to-late juveniles, and adults occur at all times of year.

The short, moderate winters at Gainesville accommodate the varied seasonal life cycles of *firmus*. The annual freeze-free period averages 295 days (Dohrenwend 1978), and the lowest winter temperatures, ca. –7° C at 1.5 m, are apparently not lethal to any stage – in five winters of outdoor rearing of *firmus*, severe cold and high mortality were not correlated. Furthermore, free crickets have access to warmer winter microclimates than do crickets on bare sand in glass jars under an open shelter.

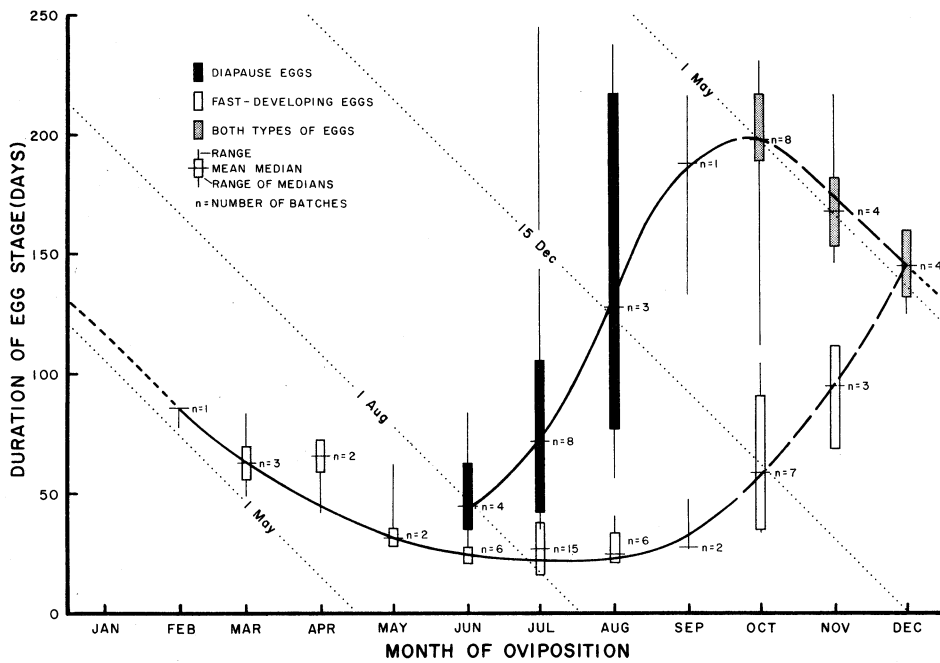


Fig. 5. Duration of egg stage for *Gryllus firmus* as a function of month of oviposition: (field temperatures and adequate moisture; Gainesville, Florida, 1971–1978). Weekly batches of eggs laid by captured females caged singly outdoors were held outdoors and monitored weekly for hatch. These eggs were classified as fast developing or diapause by their hatching times and by the hatching times at 25° C for eggs laid by the same female during alternate weeks. Some eggs laid in October–December were fast-developing at 25° C but required as long to hatch in the field as did diapause eggs laid by the same female at the same time (see Fig. 3C and D). For each egg batch laid during a particular month (regardless of year) the range and median of hatching times were noted. Vertical lines on graph are total range; vertical bars are ranges of median durations; horizontal lines are mean median durations. Solid lines and long dashes show apparent trends; short dashes are an interpolation. Dotted lines show dates of hatch – e.g. some eggs laid in October, November and all eggs laid in December, February, March had peak hatch ca. 1 May

Voltinism in Northern *firmus*

G. firmus occurs along the Atlantic Coast at least as far north as Maryland (Alexander 1968) and perhaps as far as Connecticut (R.G. Harrison, personal communication); its distribution in the Piedmont Region of Alabama, Georgia, and the Carolinas is poorly defined and includes apparently disjunct populations (Fulton 1952; Alexander 1968). Life cycles of *firmus* north of Florida are of above-average interest because they are candidates for illustrating initial and intermediate stages of speciation through temporal isolation. Alexander and Bigelow (1960) and Alexander (1968) proposed that increasingly severe winters (as for *firmus* northward) could divide a *Gryllus* population into two temporally isolated demes – an egg-overwintering, fall-adult deme and a juvenile-overwintering, spring-adult deme. Given enough time and the fact of different stage-specific selective regimes, such demes could become specifically distinct.

Sympatric, temporally isolated demes of *firmus* could occur from the northern limit of spring adult *firmus* southward to Florida. I investigated the life cycles of northern demes by assaying eggs of fall adults from two sites: Atlanta, Georgia, where spring adults are not known (but have not been looked for) and Carolina Beach, North Carolina, where spring adults occur each year.

Eggs of two females from Atlanta were held at 25° C. All eggs of one were in deep diapause (Fig. 6A); eggs of the other had a modal incubation time 4 weeks shorter (13 vs. 17), and 2 of 2,115 eggs (0.1%) hatched 3 weeks prior to any others but not early enough to be classified as fast-developing.

Observations by Fulton and Alexander of spring- and fall-adult *firmus* at Carolina Beach are compatible with the existence of two temporally isolated demes having independent univoltine life cycles similar to those of *G. veletis* and *G. pennsylvanicus* farther north (Alexander 1968). However, the hatching patterns of eggs of five *firmus* females I collected at Carolina Beach, 14 September 1977, indicated that some (perhaps all) spring adults come from late-summer eggs. One of the fall-adult females laid 40% fast-developing eggs and another laid 4% (Fig. 6B). The other three laid only diapause eggs, which curiously showed two peaks of hatching (e.g. females 77-17 and 77-19 of Fig. 6B).

The data in Fig. 6 do not prove that any eggs of fall-adult *firmus* hatch in the fall at Carolina Beach – eggs that are fast-developing at 25° C may outdoors under fall conditions become diapause eggs (Fig. 3C, D). However, on 7 August 1978, I collected more *firmus* at Carolina Beach and held two females outdoors at Gainesville. Their eggs hatched outdoors during September and the following April; some of the September hatchlings successfully overwintered outdoors as medium nymphs, and one matured at the end of May. Temperatures in Gainesville during the winter of 1978–1979 were colder than the average for Wilmington, North Carolina – just inland from Carolina Beach (USDA, 1941). These data refute the hypothesis that spring and fall adults of *firmus* represent separate demes at Carolina Beach. On the other hand, they neither disprove nor support a hypothesis of partial isolation – i.e. that spring adults produce some progeny that bypass the fall-adult generation, overwinter as juveniles, and become adult the following spring. Since Carolina Beach is the northernmost

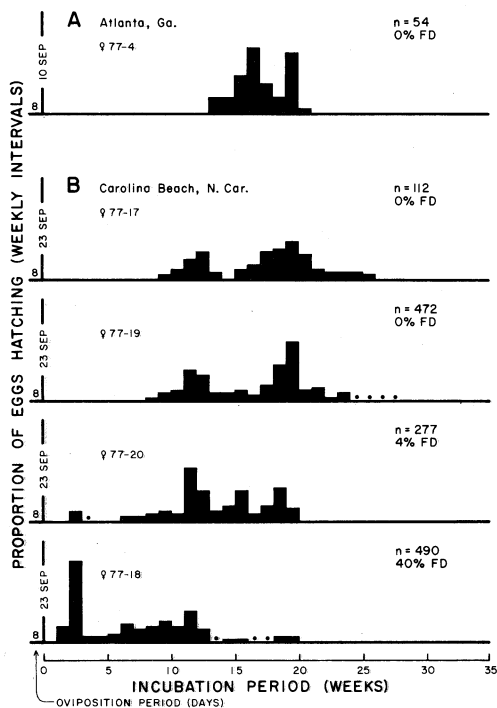


Fig. 6 A and B. Hatching patterns for eggs of *Gryllus firmus*, northern populations. Females brought to laboratory ($25 \pm 1^\circ \text{C}$, 16L:8D) and allowed to oviposit. Eggs incubated under same conditions. **A** Atlanta, Georgia; female collected as juvenile 23 August; mature 29 August; mated with male collected at same site. **B** Carolina Beach, North Carolina; four females (77-17, 19, 20, 18) collected 14 September 1977 at same site, put in separate oviposition jars in the lab 15 September, and removed 23 September

locality for spring adults of *firmus*, no other locality would be expected to foster greater isolation between spring and fall adults.

Ecological Implications

The closest North American relatives of *firmus* are *G. pennsylvanicus* and *G. ovisopis* (Harrison 1979), both of which overwinter only as eggs and are rigidly univoltine. *G. pennsylvanicus* occurs far to the north, where *firmus* has the same unvaried life cycle, but *G. ovisopis* occurs at Gainesville (Walker 1974), where the life cycle of *firmus* is notably protean. The local habitats of *ovisopis* and *firmus* are indicative of their life cycle differences. *G. ovisopis* occurs in mesic woods having thick leaf litter and usually a closed canopy. *G. firmus* occurs in sandy, open areas. *Gryllus* microclimates in the former habitat are maximally even and predictable; in the latter, they are maximally fluctuating and capricious.

A few weeks without rain in the open sandy habitats of *firmus*, especially when temperatures are high, cause severe drought at the surface and to the depth that *firmus* can burrow or place its eggs. Droughts are especially likely and severe in the spring (April–June) and fall (September–November) (Fig. 4). Juvenile-overwintering cycles should be favored in years having severe drought after spring hatch; egg-overwintering cycles should be favored in years having severe droughts in fall (assuming that adults and diapausing eggs are more drought resistant than developing juveniles).

The wide range of temperatures in October–December (Fig. 4)

may explain the facultative diapause of fall-laid fast-developing eggs. In years having cool falls, eggs that diapause may be more likely to survive the winter than the hatchlings they would otherwise produce.

With both moisture and temperature less predictable in *firmus* habitats than in other *Gryllus* habitats, the optimal strategy for a *firmus* female is to produce progeny with a frequency distribution of developmental programs reflecting the probabilities of failure and success. No single program is always a winner, and the payoffs for winning programs vary within a year and from year to year. Females that spread their risks avoid genetic catastrophe; those that do not may experience increased reproduction in the short term and genetic extinction in the intermediate term.

Other species living in habitats of unpredictable suitability have similarly widely varied egg development times. For example, the South African grasshopper *Locustana pardalina* lives in semi-desert areas having an average annual rainfall of 28 cm but where droughts lasting several years are not uncommon. Mathé (1951) found that females of *L. pardalina* laid mixtures of diapause and nondiapause eggs with the diapause eggs stopping their development at either or both of two embryological stages depending in part on the moisture regime. Wourms (1972) studied fish that survive dry seasons as eggs. Hatching upon egg submergence is risky because future moisture may be insufficient for maturation and reproduction. However, the eggs are dimorphic in development time at three stages – making eight different developmental programs with incubation lasting, for example, as little as 40 and as long as 316 days. Stearns (1976) discussed risk spreading (sometimes called *bet hedging*) in life cycles and proposed that the extent of risk spreading should depend on the balance between the seriousness of the risk and the cost of spreading it.

Proximate Causes of Varied Development Times

When eggs laid by female *firmus* of a single deme have a wide range of incubation times, with two or more modes, the different times probably result from differences in one or more of these proximate circumstances: (1) female's environment, (2) embryo's environment, (3) female's genotype, (4) embryo's genotype. Circumstances that cannot be excluded on the basis of present evidence but which are a priori of doubtful importance are (5) male's environment and (6) male's genotype (apart from its effect on embryo's genotype). Evidence that the first four circumstances operate in determining differences in incubation periods is summarized below.

Female's Environment. The environments of ovipositing females were not experimentally varied; however, if the gene pool relative to egg development remains constant from June to November, the increase in proportion of diapause eggs laid (Fig. 2) is logically attributed to changes in the females' environment – for example, in photoperiod.

Embryo's Environment. Embryos of (some) presumptively fast-developing eggs go into diapause when the eggs are held outdoors in the fall (Fig. 3C, D).

Female's Genotype. Females collected at the same time and place often laid eggs having drastically different hatching patterns (e.g. Fig. 6B), and these differences persisted for 5 or more weeks that the females continued to lay while confined under identical circumstances. Such differences can of course be attributed to environ-

Table 1. Ecological strategies relative to egg development in insects

Female facultatively produces diapause and non-diapause eggs ^a	Female continues to mix diapause and non-diapause eggs	Embryo facultatively diapauses ^b	Examples
no	no	no	<i>G. ovisopis</i> , <i>G. rubens</i> , most insects
yes	no	no	<i>Bombyx mori</i> (bivoltine), many other insects
no	yes	—	No insect examples?, many plants (Harper, 1977)
yes	yes	no	<i>Locusta pardalina</i> , ^c other grasshoppers (Uvarov, 1966), other insects?
yes	yes	yes	<i>G. firmus</i> , <i>Aedes caspius</i> ^d ?, other insects?

^a Environmental cues can cause females to switch at least some eggs between diapause and non-diapause states

^b Environmental cues can cause at least some embryos to switch from non-diapause to diapause state

^c Diapause eggs of *L. pardalina* have varied development caused in part by facultative diapause at additional embryologic stages; however, eggs that are presumptively non-diapause at laying never diapause (Mathée 1951; Uvarov 1966)

^d Eggs of *A. caspius* facultatively entered diapause under laboratory conditions (Khelevin 1958)

mental differences prior to the time that the females were captured; however, I agree with Maynard Smith (1978, p. 150) that “it is a good common sense principle that if environmental factors can affect some characteristic, it is likely that genes will do so also.”

Embryo's Genotype. Although plausible (according to Maynard Smith's common sense principle), no direct evidence exists for differences in embryonic genotypes affecting egg development in *firmus*. Such evidence exists for *G. pennsylvanicus*: When Bigelow (1960) mated females of *pennsylvanicus* with a male of *G. assimilis*, 27 of 33 hatchlings appeared within 19 days at 28° C, an incubation period typical of *assimilis* eggs. *G. pennsylvanicus* females mated to *pennsylvanicus* males laid eggs that required at least 30 days to hatch at 28° C. Bigelow concluded that embryonic diapause in *pennsylvanicus* is determined by the genetic constitution of the embryo and not by cytoplasmic or yolk constituents.

In summary the evidence is strong that egg incubation period is a function of the ovipositing female's environment and of the embryonic environment; genetic variation probably increases variance in incubation duration, but none of the hatching modes needs be attributed to genetic polymorphism.

The physiological mechanism of mixed oviposition in *firmus* is unknown. Indeed, only in *Bombyx mori*, where the suboesophageal ganglion secretes a hormone that causes the ovary to produce diapause eggs, has maternal control of egg diapause in insects been explained (Novak 1975). *B. mori* females do not normally

produce mixtures of two types of eggs whereas *firmus* females do so week after week, as shown by the present data, and day after day, as shown by Rohani and Walker (1980).

Table 1 compares egg development options of *firmus* with those of other insects. The terms *conditional* and *mixed* applied by Dawkins (1980) to behavioral strategies, seem appropriate here. Females or embryos that adaptively switch egg-development programs in response to environmental cues are using a conditional strategy; females that generally produce both diapause and fast-developing eggs rather than laying all of one or the other under particular circumstances are using a mixed strategy. An important difference between many behavioral strategies and the egg development strategies outlined in Table 1 is that in the former, individuals are vying against one another for a limited resource (with possible payoffs for deception and other counter strategies). In the latter the physical environment is the opponent, and its changes are not in response to the strategies played against it.

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