

THE COURTSHIP OF PHYCIODES, AND THE RELATIONSHIP BETWEEN PHYCIODES THAROS THAROS AND PHYCIODES THAROS MORPHEUS (=PASCOENSIS) IN COLORADO

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Abstract. The courtship of Phyciodes tharos/morpheus and P. campestris is described, and is very similar between species. Reared released female morpheus courted and mated readily with wild male tharos in Colorado. Together with the viability and fertility of the hybrids and the breakdown of the antennal and larval characters that distinguish them in W.Va.-Va. (where they behave as separate species), this evidence indicates that tharos/morpheus are not reproductively isolated in Colorado, where they seem to be a bit more than subspecies, but are not completely distinct species. Phyciodes have an interesting outcrossing mechanism involving timing of adult emergence, which ensures rapid spread of genes between parent forms after natural hybridization.

Introduction

The relationship between Phyciodes tharos (Dru.) and P. morpheus (Fab.) (= pascoensis Wrt.) is controversial. They had been considered ssp., but Opler & Krizek 1984 treat them as species. Oliver (1978-1983) obtained lab hybrids between various Phyciodes spp., so the ability to produce lab hybrids is characteristic of the genus, and study of courtship and mating in nature are critical in defining species within the genus. To study courtship isolating mechanisms I reared both species, and the present paper reports experiments in which I reared females of morpheus and released them near males of tharos in nature. Details of courtship of these entities and P. campestris (Behr) are given, and then the relationship between them is discussed. I thank Charles G. Oliver and Paul A. Opler for reviewing the paper.

P. morpheus (Fabricius) 1775, type locality "America Boreali", is the oldest name that could be applied to the "species" now called pascoensis Wright 1905 or selenis (Kirby) 1837. Fabricius mentioned orange antennae, but because morpheus could be applied to either morpheus or tharos, I restrict morpheus type locality to Nova Scotia (where only morpheus occurs), making selenis & pascoensis synonyms.

Methods

Ssp. morpheus adults were reared from Golden Gate Can., 6700', Jefferson Co. Colo. in the mountain foothills, and reared on the natural host Aster laevis. (Only morpheus is known from this area, based on many years collecting and three years of finding the larvae; the nearest tharos population is about 10 miles away on the plains in Wheat Ridge, a Denver suburb.) The morpheus developed without diapause in the unnatural 24-hr.-light lab conditions and emerged when tharos was flying on the plains in late August, providing an opportunity to release virgins in a plains tharos population to study prezygotic reproductive isolation. Virgin female morpheus 1-4 days old were taken to a creek near Bijou Creek, 6000', Elbert Co. Colo., a creek on the unforested plains (where larvae and pupae of tharos were also reared), on Aug. 22 and 24, 1984. Aug. 22 was mostly cloudy and the tharos males did not patrol much, but it was found that a wild tharos male and a virgin morpheus female could be placed under a net until the male noticed the female, and then the net slowly removed, and the female could then fly and normal courtship would then ensue. Aug. 24 was sunny, and by finding the spot where males were most frequent in their patrols, it was found that a female

could be released there and watched, and would be discovered by a tharos male after a few minutes (though some females flew and were lost).

Results

Courtship and mating occurred readily between the species. The male tharos were active and persistent, and the female morpheus accepted the males, so that nine matings were obtained. Nothing that could be considered a barrier to courtship was observed. The mated pairs were collected (slowly so that they would not be disturbed and mating could continue), and 7-8 females laid several hundred eggs which produced 129 male and 120 female offspring (Fig. 1). First instars of several abnormally small egg clusters died, and a few older hybrid larvae died, as well as 36 pupae (some pupal deaths were probably due to inadvertent dropping the box containing them), but some deaths have always occurred during my rearings of immature lepidoptera, so it cannot be concluded that this mortality is of any significance; 249 live adults were reared, with a sex ratio not significantly different from equality. Females seemed to emerge slightly before males on the average, however (Fig. 1), which occurs in about a third of the tharos X morpheus hybrid broods (Oliver 1980, 1983) evidently because of some type of maternal inheritance of diapause and male-female emergence lag. In most butterflies males emerge prior to females by 1-2 days on the average (Scott 1977) so that males can fly when virgin females emerge, and females can emerge when males are most common to minimize time required to find a male. Mountain morpheus have only one flight versus 3-4 in plains tharos, and evidently the genes regulating the lag in development between males and females are influenced by or linked to maternally inherited diapause (female hybrids develop fast when the female parent was morpheus, slow when the female parent was tharos, Oliver 1983), so that hybrids between populations with differing number of generations are not well adjusted in male-female lag.

Courtship behavior. Males patrol to seek females, all day, especially in low spots of wet meadows or low spots along creeks. They fly about 1/4 to 1/3 m above vegetation and often alter their course to investigate flowers for nectar-feeding females. The male finds a female most often while she rests on a leaf or flower, sometimes while she is flying. If she was resting, the male lands nearby, or if she was flying, he pursues her and she soon lands and the male lands behind. The male rarely hovers over the landed female for a second before landing (and very rarely the male may hover over the female after she moves during courtship). Then courtship commences.

The following ritualized elements of courtship occur (the male may also hover above the female for a few seconds before landing, but this behavior does not appear to be ritualized):

1) Male wing display. While resting beside the female, his wings are opened, each about 50 degrees from the vertical, and are motionless, or are imperceptibly vibrated 1 mm, and frequently the forewings are drawn forward during the display, which lasts one to several seconds or more. Males often face the female in this display. The male wing display occurs after the female flutters or moves while on a plant or after she flies and lands again.

2) Male wing fluttering. While resting by the female, instead of displaying his wings the male spreads them and flutters them either at small or large amplitude, for a few seconds. His fluttering also occurs after the female flutters or moves, and there is every type of intermediate between the male wing display and full wing fluttering. Male fluttering is less common than the display.

3) Male bending. After displaying or fluttering, to attempt to couple the male holds his wings slightly apart (each wing about 10 degrees from vertical), crawls under her spread left or right wings slightly, and bends his abdomen 180 degrees laterally (left or right) and about 45 degrees vertically to attempt to join. The male may crawl after the female in this position if she rotates or crawls slowly.

4) Female mating posture. To accept the male, she holds her wings spread (during courtship the female nearly always keeps her wings spread, each wing about 50-60 degrees from vertical) and raises her abdomen about 20 degrees above horizontal.

5) Female fluttering. She often flutters at small amplitude (5 mm), and occasionally flutters at wider amplitude, when the male approaches near or attempts to mate. This seems to be a rejection dance to try to discourage the male (mated females of tharos and morpheus always flutter strongly when a male approaches, and the male sooner or later flies away).

Other rejection behaviors of females include these: she turns away (and may rotate in a circle with the male behind) or crawls away, drops down into the vegetation, or flies a short distance. The male usually pursues close behind these maneuvers, unless she drops, in which case his search for her is often unsuccessful. One virgin female flew vertically 3 m, then quickly downward, and succeeded in eluding the male (mated females were more often seen to do this). Or, she quickly moves her abdomen up if the male touches it, or she keeps it raised about 45 degrees so the male cannot join. If she is resting on a flower or plant, she may close her wings when a male passes overhead, to avoid detection.

These elements are often repeated. For instance if the female flutters or flies or moves, the male will again display (or flutter) and then bend. As is usual in butterflies, variation occurred in successful and unsuccessful courtship due to the degree of receptivity of the female. In the simplest courtship (about 10-20 sec.) the female flew 10 m with the male behind, she landed and kept her wings spread and motionless, he landed behind and (without fluttering or displaying) bent his abdomen to couple. In another quick courtship (5 sec.), after recognition the female fluttered very weakly at small amplitude, raised her abdomen the proper 20 degrees, the male made a brief wing display beside her then curved his abdomen and coupled. In the longest successful courtship (8 min.), the female fluttered and flew and turned away often, while the male fluttered, displayed, and bent his abdomen often before finally joining. Most courtships lasted about a minute or two. In butterflies the receptivity of a female depends mostly on her mating status (whether virgin or mated, and how long since the last mating), on her feeding state (if dehydrated, a female will try to feed on flower nectar rather than mate), and on her age.

After joining, the female closes her wings, and after a few seconds the male faces opposite her and closes his wings. The female often (the male seldom) basks during mating, which lasts 28 to 158 min. (mean 72 min., N=9; the mated pairs were stored in the dark which possibly lengthened mating somewhat). If a mating pair is disturbed, the female flies, with the male dangling beneath.

Some courtships were unsuccessful, because the female flew horizontally and the male lost track of her (3X), she flew vertically and the male lost her (1X), she dropped into vegetation and the male lost her (1X), the male lost track of her (1X), wind blew them apart (1X), another male chased the courting male and the males left together (1X), or the male flew away (1X).

Courtship of P. morpheus male and female. A natural successful courtship was observed at Tinytown, Jefferson Co. Colo. 20-21 July 1984, which serves as a comparison. A male pursued a female, she landed and he landed behind, the male fluttered briefly and the female may have fluttered very briefly also, then after only a few seconds the male bent his abdomen and joined. This pair was pulled apart to study courtship again, and owing to clouds which appeared, the female was fed and released the next day, when three unsuccessful courtships with her involved male wing fluttering, male bending, female fluttering, and female flight, until the male departed. The fourth courtship an hour later, after constant flower feeding, was successful, in which she was on a flower and fluttered when the male landed, he fluttered and bent his abdomen, and after she flew and these events were repeated four times, he finally succeeded in coupling.

Failure of hybridization of P. morpheus with P. campestris, and courtship of campestris. In contrast to the ease of mating P.

morpheus and P. tharos, it was not possible to mate P. morpheus with P. campestris. Four virgin female morpheus reared from Golden Gate Can. were released at a spot on Green Mtn., Jeff. Co. Colo., 29 Aug. 1984. Some male campestris did court the morpheus females, and often positioned the male abdomen tip at the proper spot for joining beneath the female abdomen tip and then waited patiently, but the female refused to extrude her genitalia, or she moved her abdomen upward, and thus mating could not occur.

A few courtships of campestris were observed in 1984-85. Courtship behavior rituals of P. campestris seem very similar to those of P. tharos and morpheus, pointing to odor differences (at least odor of males) as the probable isolating mechanism. Male campestris often hover for a second near the female or circle briefly before landing (perhaps not a distinct ritual in either species, but at least 3 male campestris did seem to circle in more-or-less vertical loops over the female, as is usual in the courtship of Chlosyne gorgone (Hub.), so the propensity for flying loops possibly is greater in campestris), they perform the male wing display the same way (forewings often jerked forward), and wing fluttering and male bending are the same. If the female drops down into vegetation the male circles about to relocate her. Female campestris also flutter when unreceptive to reject males, and they also sometimes fly vertically 3 m then downward to get away from pursuing males.

A completed campestris courtship was seen on Green Mtn., Jefferson Co. Colo. 7 June 1985. When first seen, the female was flying with the male behind, she landed and closed her wings (slowly opening and closing them a few times), the male landed behind her and vibrated his nearly-closed wings slightly and approached her and curved his abdomen to attempt joining. She flew and the above behavior was repeated roughly similarly 3 times, she flew again and after landing the male fluttered while on the plant behind her, she flew and landed again and closed her wings, and the male had his wings nearly closed behind her and curved his abdomen toward her for 15 sec. until coupling; when disturbed, the female flew toting the male below. Total courtship time was about 1.5 min. (the first meeting of the two, and perhaps some subsequent actions, was missed).

Relationship Between tharos and morpheus

In W.Va., Va., and apparently SW Penn. at least, Phyciodes tharos and P. morpheus are separate species according to most criteria (Opler & Krizek 1984). P. tharos has three (and a partial fourth) flights, is smaller, usually has white-and-black antenna clubs, has black lines breaking through the orange upf patch of males, and supposedly has more chocolate-colored larval tubercles, whereas P. morpheus has one flight, is slightly larger, usually has orange-and-black clubs, has a large unbroken orange upf patch on males, and supposedly has more pinkish-gray larval tubercles. In addition, both species are sympatric at several sites there with little or no interbreeding.

Oliver (1980, 1983) states that evidence from lab hybrids proves that they are different species, but his results show that F1 and backcross hybrids are perfectly viable and fertile. Oliver (1980) made 82 F1 and backcross matings between tharos and morpheus, and 31 matings within species, and the least fertile of them was in fact a within-species mating of morpheus male and female (.826 hatched/fertile). Oliver found no significant departures from normal in sex ratios. The only departures from normality found by Oliver were, first, that the probability of larval diapause of an individual is similar to the probability of diapause of the mother's population (demonstrating maternal inheritance of diapause threshold). Second, (Oliver 1980, 1983), male hybrids emerge after females on the average if the mother was morpheus and the father tharos (male butterflies normally emerge prior to females by a day or two, Scott 1977, but in this case the heterogametic females develop faster than normal), but males emerge much prior to females (the females very often develop slower than normal) if the mother was tharos and the father morpheus. Third, larvae of both sexes of some of the hybrid broods were speeded up or slowed down in development (male hybrids are usually faster

than their fathers). Disturbance of diapause and development are perhaps to be expected when one hybridizes a one-generation population to a multi-generation population. Thus Langston & Watson (1975) found that after 4-5 generations of selecting for "early diapause termination" and "late diapause termination" strains of a moth, crosses between strains had early-emerging females.

The selective value of these three effects are uncertain. On the one hand, the speedup of development of some hybrids would allow them to produce more generations of offspring; but the slowdown of some would allow only one generation per year. P. morpheus flies for about two months of the year in Colo., P. tharos about six months, so slight differences in emergence are relatively unimportant for the latter, but might be important in morpheus. Thus if the single-generation morpheus is harmed by hybridization with tharos (because some hybrids might emerge at the wrong time when no mates were flying), female morpheus should show reproductive isolation from male tharos (which does not occur in Colo.).

The earlier or much later emergence of females than males in some hybrid broods of tharos X morpheus (Fig. 1) actually is an effective outcrossing mechanism, which ensures that genes of an immigrant of one of them will rapidly flow into the other's gene pool, as follows: an immigrant female (or her offspring) will mate with native males, and her female offspring will emerge slightly earlier or much later than most sibling males, and thus will mate more often with native males (rapidly transferring genes); likewise, her male offspring will emerge earlier than most sibling females (Oliver 1983), and thus will have to mate with native females (rapidly transferring genes).

P. tharos and morpheus will hybridize in small laboratory cages (Oliver 1980), which demonstrates their close genetic relationship. Other Phyciodes are reproductively isolated from tharos/morpheus, because Oliver found hand pairing required to obtain interspecies hybrids: Oliver (1978) obtained some hybrid P. campestris X tharos by hand pairing (my attempts to mate campestris males X morpheus females in nature were unsuccessful), and Oliver (1979) obtained hybrid P. batesii X P. tharos/morpheus (especially using female batesii) by hand pairing.

The situation in Colo. is similar in some ways to W.Va.-Va.: Colo. tharos has 3-4 flights, is smaller, and has broken up orange patches, whereas morpheus has one flight, is larger, and has a larger orange upf patch.

However, in Colo. two of the characters that distinguish morpheus and tharos in W.Va.-Va. break down. First, both usually have orange-and-black antenna clubs in Colo., whereas in W.Va.-Va. clubs are mostly black-and-white in tharos, orange-and-black in morpheus. (Populations with mostly orange-and-black clubs occur northward to Mont. and Sask., east to S Minn. and S N.Y.; black-and-white clubs occur southward and west to Ariz. where distincta Bauer is a synonym of tharos).

Second, Colo. larvae and pupae often cannot be distinguished. Colo. tharos and morpheus were reared in 1983 and 1984, and tharos was reared in 1985. Some variation in larvae and pupae was found, but no constant differences occur between the "species." Scott (1986) describes and compares in detail the larvae and pupae of both from Colo. Reddish-brown larvae are frequent in morpheus but are absent in tharos. A few grayer larvae were noted in tharos. Pupae vary from cream to yellow-brown in different individuals; morpheus pupae are more often cream and are seldom yellow-tan, whereas tharos pupae are most often creamy-tan, usually slightly oranger (yellow-tan) than morpheus. These differences are the kind often seen between ssp., but hinder rather than promote the idea of separate species. (It should be noted here that the larva of Phyciodes "mylitta" in Pyle 1981, photo 17, actually is tharos; mylitta larvae are almost completely maroon-black.)

Considering that Colorado tharos and morpheus readily court and mate in nature, and hybrids and backcrosses are known to be fully viable and fertile, and there are no constant antennal and larval differences, from this information alone Colo. tharos and morpheus fit the concept of subspecies, P. tharos tharos and P. tharos

morpheus. And reared Colo. tharos and morpheus seem not as different in appearance as wild ones.

Whereas in W.Va.-Va.-Penn. they are sometimes sympatric, in Colorado they are basically allopatric: tharos occurs on the eastern plains (and in the hot lower Colorado and Gunnison River valleys of western Colo.), whereas morpheus occurs only in the mountains (from the foothills upward). I found no sympatric populations in Colo., though half a dozen individuals from the foothills, generally in spring, resemble tharos (these are probably morpheus variants whose late larvae experienced short photoperiod the previous fall, resulting in the marcia phenotype which C. Oliver sometimes rears in morpheus). However, Paul Opler (pers. comm.) recently found that both fly together near Horsetooth Reservoir near Fort Collins, Larimer Co. Colo. There, the broods are asynchronous, reducing contact and possibly allowing overlap of the plains tharos and mountain morpheus; but occasional interbreeding is certainly possible there, and the fact that they are sympatric would suggest to most biologists that they are separate species.

Historically, P. tharos tharos no doubt continuously occupied the Great Plains for at least the last 6000 years, but may not have occupied W.Va.-Va. when it was covered with virgin forest and contained morpheus. But when the eastern forests were mostly cut 100-300 years ago, P. tharos may have invaded W.Va.-Va.-Penn., and somehow the sudden interbreeding of populations of greatly different geographical origin may have selected for reproductive isolation (presumably the one-generation genes of morpheus are superior in the Appalachians, the multi-generation genes of tharos in the lowlands). (Appalachian populations of P. batesii (Reak.) have become extinct also, due to unknown causes, perhaps including interference with a huge invasion of tharos.)

In Colo., both are relatively unaffected in distribution, although irrigation possibly increased the range of tharos. The hosts of morpheus and tharos are natural, and have not been affected much by man. P. tharos and P. campestris eat Aster ericoides on the plains, but campestris occurs on dry prairie as well as moister areas so has not changed its distribution since human cultivation, whereas P. tharos (and morpheus) occur only along watercourses or in moist meadows, so that irrigated pastures may have increased the range of tharos on the plains including Larimer County (human influence has been to devastate the major rivers such as the South Platte, and to irrigate the flats near the rivers).

Are they really separate species? Because they will mate readily in nature and produce F1 and backcross hybrids, it seems difficult to believe that the disturbance of eclosion sequence (Fig. 1) in some hybrid offspring is enough to maintain reproductive isolation between them, because this disturbance acts as an outcrossing mechanism. But it seems clear that the two are a bit more distinct than mere subspecies, and yet are not completely distinct species. The Phyciodes have no problem with how humans classify them, because Colo. adults cannot telephone their W.Va. relatives to ask with whom to mate, and it must take hundreds of years for genes to work their way through mating and dispersal between these areas. The problem concerns people's names for them.

Other cases are known which confound one-word "species" or "subspecies" names. Based on morphology, hosts, and intergradation or sympatry without intergradation (Scott 1978, Ehrlich & Murphy 1983), Euphydryas chalcedona chalcedona (Dbl.) and E. c. colon (Edw.) are the same species, and E. c. chalcedona and E. c. anicia (Dbl. & Hew.) are the same species, but E. c. colon and E. c. anicia are distinct species. These Euphydryas names are justifiable because they are only one-third wrong (E. c. colon and E. c. anicia are wrongly implied to be the same species, whereas the other two relationships in the triad are correct); raising the three names to species rank (as E. chalcedona, E. colon, and E. anicia) is two-thirds wrong. Another absurd case challenging a one-word species name concerns Colias philodice God. and C. eurythema Bdv. (summarized by Scott 1986) in which it has been shown that nearly all the differences between the "species" reside on the X chromosome. Thus, when the two hybridize, the male hybrids have one philodice X and one

eurytheme X chromosome and can be recognized as hybrids only because the orange/yellow color and black border width are inherited with nondominance, but the female hybrids obtain their X from their father, so the female hybrids are the species of their father! Pure adults absurdly reappear out of subsequent matings of the male hybrids as well.

Because evolution has produced all living species and is occurring within them now, at the point when one species is splitting into two species it is impossible to tell whether one or two species occur. Because this is a natural biological process, it is not a "problem" at all. The only problem exists in the Linnaean two-word system for naming species, which cannot properly assign names for a dividing species; this failure of the Linnaean two-word system causes confusion in people who believe that words represent real concepts. The "superspecies" and "semispecies" concepts have been miserable unused failures as well, because one of their faults is that they are single words as is the species name.

Careful thought reveals that there is a solution to this naming problem: if a species is dividing into two species, its name should be divided as well. The two names should be divided by a slash, the older name preceding the younger, printed and italicized (including the slash) as one word without spaces. For instance, if one believes that the subspecies P. tharos tharos and P. tharos morpheus are one dividing species, and not two distinct species P. tharos and P. morpheus, then the name should be P. tharos/morpheus. This system has numerous virtues: the divided name reflects the dividing species, the system is simple, has been used by many persons already, and requires no formal changes of the ICZN rules (although the ICZN should recognize the occurrence of evolution with this system).

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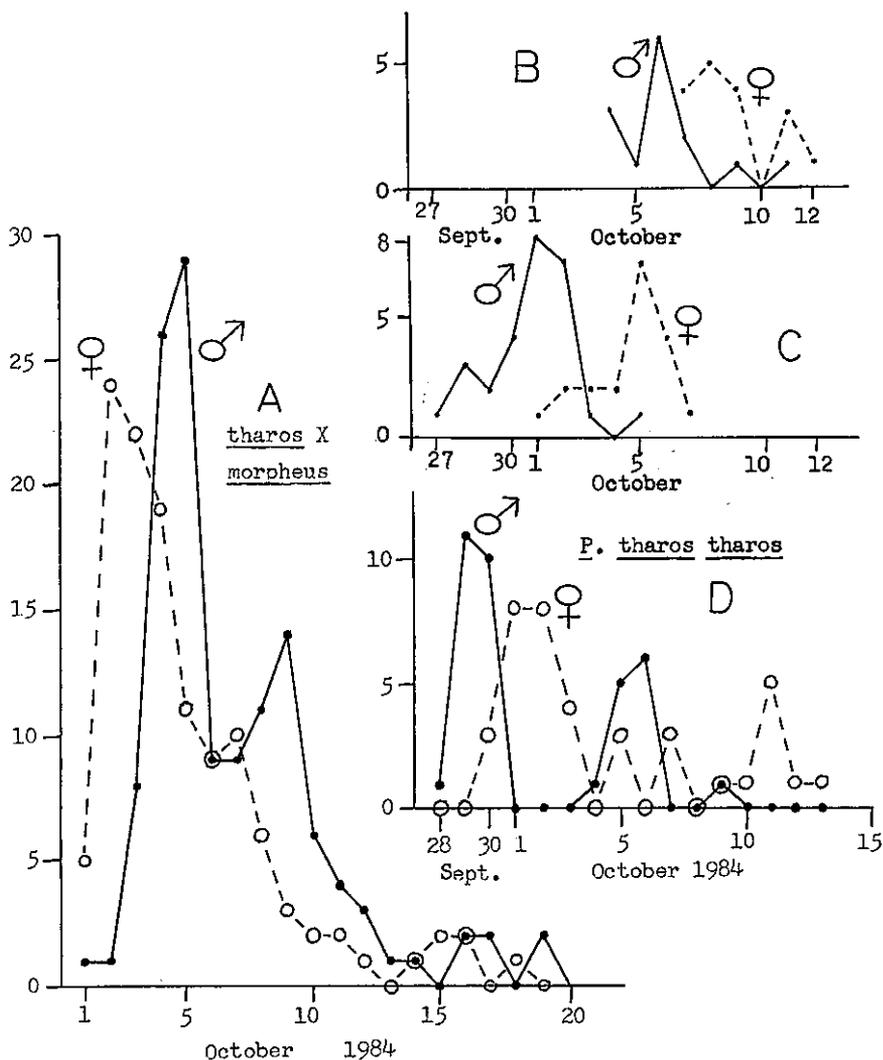


Fig. 1. Hybrid males emerged several days after hybrid females (A, eggs laid over several days by 7-8 *morpheus* females mated to *tharos* males), whereas in pure *tharos* colonies (B-C) males emerge before females: B and C show emergence of adults from single egg clusters found at Barr Lake, Adams. Co. Colo. (in B, males averaged 50.2 days from finding of cluster to emergence, females 52.8, an emergence lag of 2.6 days; in C, males averaged 44.7, females 48.5, a lag of 3.8 days); D, *tharos* from Bijou Creek, Elbert Co. Colo. (eggs laid by several females).

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