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EFFECTS OF LONG AND SHORT DAY PHOTOPERIODS ON THE SEASONAL DIMORPHISM OF *ANAEA ANDRIA* (NYMPHALIDAE) FROM CENTRAL MISSOURI[1]

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ABSTRACT. Larvae of the goatweed butterfly, *Anaea andria* Scudder, when reared at 27°C produce summer form adults under a long day (16L:8D) photoperiod, and winter form adults under a short day (12L:12D) photoperiod. Adults from the progeny of both the summer and winter forms exhibit this response and evidence is given to support the premise that the fifth instar larva is the stage in which adult form is determined.

The length of the daily photoperiod has been shown to be an important factor in regulating the appearance of several butterfly species. Müller (1955, 1956), Müller & Reinhardt (1969) and Reinhardt (1969, 1971) have shown that in *Arashnia levana* L. (Nymphalidae) the seasonal dimorphism is primarily controlled by photoperiodic exposure during the larval stage, with temperature modifying this effect under certain conditions. Hidaka & Aida (1963) and Hidaka & Takahashi (1967) have shown that larvae of *Polygonia c-aureum* L. (a Japanese nymphalid) reared at 20°–26°C under 14 or more hours of light produced characteristic "summer form" adults, while a photoperiod of 12 or less hours produced "winter forms," and a 13 h light period produced adults of both forms with no intermediates. They also demonstrated that extreme temperatures could override the photoperiod induced effects. Additional studies by Ae (1957), Shapiro (1968), Oliver (1970) and Shapiro (1973) using the respective pierid butterflies, *Colias eurytheme* Boisduval, *Pieris protodice* Boisduval and LeConte, *P. napi oleracea* Harris and *P. occidentalis* Reakirt, and Sakai & Masake (1965) using the lycaenid, *Lycaena phlaeas daimio* Seitz, have also shown that the photoperiodic exposure of the immature stages is a major factor in the regulation of seasonal dimorphism in these species. Dimorphism is expressed principally as differences in color in the pierids, and as differences in color as well as in wing shape in *L. p. daimio*.

The goatweed butterfly, *Anaea andria* Scudder, exhibits pronounced seasonal dimorphism in the wing shape of both sexes. Individuals of the summer brood (summer forms) are characterized by

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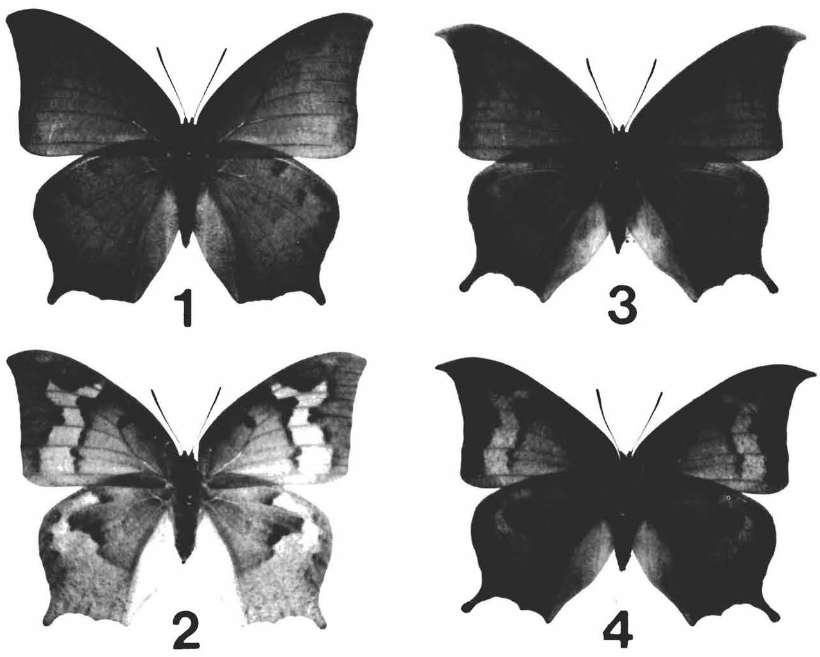

FIGS. 1–4. *Anaea andria* Scudder. **1**, ♂ summer form; **2**, ♀ summer form; **3**, ♂ winter form; **4**, ♀ winter form.

a blunt forewing apex, short, stubby tails and a reduced anal projection on the hind wing (Figs. 1 & 2). Adults emerging in the fall (winter forms) are characterized by having forewing apices developed into a slightly recurved, falcate projection, tails with a slightly expanded tip and a well-developed projection at the anal angle of the hind wings (Figs. 3 & 4). The color of adult *A. andria* males is red-orange above with a dark brown margin to the wings. Winter form males typically have a wider marginal band. In most summer form males, the dark scaling of the forewing margin is reduced and appears completely absent in some specimens. On the hind wings of both forms the dark margin originates at the anterior of the outer wing margin and continues to the anal angle. The winter forms typically exhibit a broader, darker continuous hindwing band, while in summer forms the band is narrow and penetrated by the red-orange color along the veins. In females the color of the wings above is tan to orange and paler than in the males. The dark marginal band is present to approximately the same degree on both wings in both forms, as are several dark markings in the submarginal area of the wings. The under side of each sex of both forms is cryptically colored in gray-brown. Winter forms are usually darker and mostly brown in color, while summer forms are lighter with a predominance of gray colored scales. Fresh examples of both forms exhibit a slight silvery sheen. Generally, the winter form butterflies are darker and richer in color than the summer forms, with males possessing a wider dark marginal band on the upper side of the forewings. Variation is found in both forms and a large series of each will show a range in the intensity of the red-orange color as well as in the width of the marginal band.

Winter form individuals are so designated because they emerge in the fall and overwinter as adults. In central Missouri they can be collected from late August throughout the winter months on warm days, until May or early June the following year. Successful mating of these overwintering individuals occurs in the spring. Summer form butterflies are the progeny of the overwintered adults and in central Missouri they are present from late June through August, with stragglers present on into September. These individuals mate and oviposit within a short time of emergence, and their offspring then become winter form individuals. There are, then, in central Missouri two broods of *A. andria*: one in which the adults live for as many as 9 or 10 months (winter forms); and one in which the adults survive for only 1 or 2 months (summer forms). The winter form is the form described and figured by Edwards (1868) as *Paphia glycerium*, and the summer form was formally described by Johnson & Comstock (1941).

The host plants for *A. andria* in central Missouri are *Croton capitatus* Michx. (goatweed or woolly croton) and *Croton monanthogynus* Michx.

The experiments reported here were designed to determine the effect rearing larvae of *A. andria* under a short day (12L:12D) or long day (16L:8D) photoperiod at 27°C on the seasonal form of the adults; to examine whether photoperiodically induced effects were produced in adults reared from larvae of both summer and winter form adults; and to elucidate when during development the adult form is determined.

METHODS AND MATERIALS

Eggs and larvae were collected in the field on their host plants and brought into the laboratory for rearing. Eggs were first observed on 29 May 1978; at this time the *Croton* plants were at the two leaf stage and 5.0–7.5 cm tall. The last collection of larvae was made on 12 Sept.

1978, when first through fifth instars were collected. Immatures were collected in early and late summer to obtain progeny of both the overwintered winter forms and their summer form offspring. Two pupae (collected 17 and 24 Aug. 1978), were also kept under a 16L:8D photoperiod until emergence of the adult.

Eggs and larvae were placed in clear plastic boxes measuring 30 × 15 × 9 cm for rearing. The boxes contained a raised 3 mm mesh grid platform on which fresh leaves, eggs and larvae were placed. A paper towel covered the bottom of the box and facilitated cleaning of the containers. The boxes were covered with unvented clear plastic tops (to keep moisture relatively high and constant). They were placed in one of two environmental growth chambers, both chambers kept at 27°C, one with a 12L:12D (short day) regime and the other with a 16L:8D (long day) regime.

The length of the photoperiods was chosen to represent the shortest and the longest daylengths to which larvae would be exposed in central Missouri. The shortest daily photoperiod would be 11 h 58 min on 1 October, from sunrise to sunset with no dawn or dusk twilight period. The longest daily photoperiod would be 15 h 55 min on 18 June including a 30 min civil twilight period at dawn and dusk. These data were obtained from the Department of Meteorology at the University of Missouri-Columbia, and from Beck (1968).

Two groups of larvae were also kept in clear plastic containers near windows where they were exposed to the natural daylength. The first group consisted of 16 eggs and first instars collected 19 June 1978. The second group contained 18 fourth and fifth instars and 6 chrysalids collected 31 Aug. 1978 and 7 fifth instars collected 12 Sept. 1978.

Larvae were fed fresh leaves of *Croton monoanthogynus* daily. This plant was chosen as food because it was the most common local species of *Croton*. Prior studies with *A. andria* have shown that larvae feed readily on either *C. monanthogynus* or *C. capitatus* no matter which plant they were feeding on when collected.

RESULTS AND DISCUSSION

Tables 1 and 2 summarize the results obtained by rearing larvae of *A. andria* under a short day photoperiod or under a long day photoperiod. The adults obtained from the eggs and larvae collected 19 June and reared under natural light as controls were all summer forms with blunt wing apices; those obtained from the larvae collected 31 August and 12 September and reared under natural light as controls were all winter forms with falcate wing apices. The adults obtained from the two chrysalids collected 17 and 24 August and kept under long day photoperiod were both winter form individuals.

TABLE 1. Summary of adult forms of *Anaea andria* obtained from immatures reared at 27°C under long and short day photoperiods.

Date collected and immature stage	12L:12D Summer	12L:12D Winter	Date collected and immature stage	16L:8D Summer	16L:8D Winter
May 30 egg	0	4	May 30 egg	3	0
May 30 1st instar	0	4	June 19 egg	7	0
June 4 egg	0	7	June 19 2nd instar	1	0
June 19 egg	0	9	Aug. 6 egg	18	0
June 19 2nd instar	0	12	Aug. 6 1st instar	7	0
Aug. 6 egg	0	11	Aug. 6 2nd instar	9	0
Aug. 6 1st instar	0	7	Aug. 6 3rd instar	8	0
Aug. 6 2nd instar	0	15	Aug. 6 4th instar	7	0
Aug. 6 3rd instar	0	2	Aug. 6 5th instar	5	0
Aug. 6 4th instar	0	7	Aug. 17 5th instar[1]	32	9
Aug. 6 5th instar	0	4	Aug. 27 5th instar[1]	0	6
Aug. 27 5th instar	0	6	Aug. 31 5th instar[1]	6	3
			Sept. 12 1st–4th instars	33	0
Total	0	88		129	18
Percent	0.0	100		87.8	12.2

[1] See Table 2.

Tables 1 and 2 show that at 27°C the length of the photophase to which larvae of *A. andria* are exposed affects the adult form. Eggs collected 30 May, 4 June and 19 June 1978 were assumed to have been deposited by females of the overwintering population, since in 1978 winter form individuals were quite common at this time of year and the two species of host plants had just begun to sprout during the last week of May. In nature, these eggs and larvae would have developed into summer form individuals with blunt wing apices, as did the 16 larvae reared under natural light as controls. If photoperiod had no effect, this result would be expected in laboratory reared individuals. Table 1 shows that, when reared under a short day photoperiod, all of the adults from these eggs were of the winter form with falcate wing tips. Adults obtained from larvae collected as eggs on 30 May and reared under a long day photoperiod were of the expected summer form with blunt wing apices.

The eggs and larvae collected in August and September were presumed to be from summer form adults as blunt winged specimens were then on the wing and had been for some time. In the natural environment these immatures would be expected to develop into winter form individuals with falcate wing apices, as did the larvae collected 31 August and 12 September and reared as controls under natural light. If photoperiod were not influential, they would be expected to develop into winter form adults under laboratory conditions

TABLE 2. Percentage of winter form *Anaea andria* and time between pupation and collection as 5th instar larvae (when reared under long day photoperiod at 27°C).[1]

Days between collection and pupation	Larvae pupated	% Winter form adults
2	6	100.0
3	9	100.0
4	9	11.1
5	19	10.5
6	6	0.0
7	2	0.0
8	3	0.0
9	1	0.0
10	0	0.0
11	2	0.0
12	0	0.0
13	0	0.0
14	1	0.0

[1] Larvae collected on 17, 27, and 31 August.

as well. However, when reared under long day photoperiod, 87.8% of the adults obtained were of summer form; 12.2% were winter form. No intermediate forms were obtained.

An explanation for the 12.2% winter form individuals is suggested by comparing the time between collection as fifth instar larvae and pupation for winter form butterflies with the same time span for the resulting summer form individuals (Table 2). All the larvae that became winter form adults pupated within 5 days of the date on which they were collected. This suggests that the factor(s) determining the form of the adults had already been programmed, and that the insects could no longer be influenced (as fifth instar larvae or as pupae), by daylength when subjected to a long day photoperiod in the laboratory. That the other fifth instar larvae developed into summer form adults when subjected to long day photoperiod suggests that the length of the photoperiod determines the form of the adult in the fifth instar up to approximately five days prior to pupation.

The two pupae kept under long day photoperiod both produced winter form individuals. One of these required 11 days from the time of collection to the emergence of the adult; the other required 10 days. The time between pupation and emergence of 50 *A. andria* reared under a long day photoperiod was 7 to 11 days, so it can be assumed that these two pupae were collected soon after they pupated in the field and were therefore exposed to the long day photoperiod throughout almost the entire pupal stadium. If photoperiod had an effect on these insects in the pupal stage, one would expect these to produce summer form individuals, although the natural photoperiod could have had an effect on the first days after pupation. Two specimens is too small a sample to draw conclusions. However, in the group of fifth instar larvae discussed above (those taken from the natural, short day conditions of late August and mid-September and placed in a long day photoperiod), the first larvae to pupate produced adults of the winter form one would expect under natural conditions, despite being exposed to the long day photoperiod during the first days after pupation. Those pupating later produced summer forms. These data indicate that the fifth instar larva and not the pupa is the stage in which adult form is determined.

The time required for development (from egg collection to adult emergence, at 27°C) was 4–5 weeks. For the summer forms, developmental time was 25–42 days (mean = 32.2 days). For the winter forms, developmental time was 27–50 days (mean = 37.3 days). Larvae from the summer form adults therefore would be expected to reach the fifth instar in central Missouri from mid-August until the first hard frosts of fall. The length of the natural photoperiod (from sunrise to sunset) from 15 August to 1 October in Columbia is 13 h 43 min, decreasing to 11 h 58 min, corresponding roughly to the short day (12L:12D) photoperiod. The larvae from the overwintering winter form adults would be expected to reach the fifth instar from mid- or late June through late July. The hours of natural daylight from sunrise to sunset for 1 June to 31 July in Columbia range from 14 h 43 min to 13 h 47 min, with maximum at 18 June (14 h 55 min); or if 30 min dawn and dusk twilight periods are included, 15 h 55 min. Larvae developing during these months would then be doing so under the longest days of the year, corresponding roughly to the long day (16L:8D) photoperiod.

I tentatively conclude that in central Missouri it is the length of photoperiod to which fifth instar larvae are exposed, until approximately 4–5 days prior to pupation, that is a major factor determining the seasonal form of adult *A. andria*. That seasonal wing dimorphism occurs in other species of *Anaea* is well documented by Comstock (1961). When discussing *A. aidea*, Comstock (1961) refers to the blunt winged form as the summer or dry season form; and in their discussion of *A. aidea aidea* and *A. aidea floridalis*, Johnson & Comstock (1941) also refer to the summer forms as dry season forms and to the winter forms as wet season forms. These references to wet and dry seasonal forms suggest that wing shape in these species is influenced by the seasonal moisture of their native habitat. No experimental evidence substantiates this idea in *Anaea* and no mention is made of the possible role of photoperiod. The data presented in this paper suggest that photoperiod exerts influence on determination of seasonal forms in species of *Anaea* in addition to *A. andria*.

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