Status of Black-Headed and Red-Headed Types of *Hyphantria*
cunea (DRURY) (Lepidoptera : Arctiidae)
I. Biology of Two Types and Results of Crossing Experiment

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(Received April 2, 1973)

The larvae of the red-headed type (OLIVER's orange race) of *Hyphantria cunea* in Arkansas, U. S. A., make a silken-web which is remarkably different in shape from that of the black-headed type. The former type is considered to be reproductively isolated from the black-headed type by its seasonal life cycle and host preference. Laboratory experiments revealed that (1) the duration of larval and pupal development of the red-headed type reared under constant temperature on artificial diet was longer than that of the black-headed one; (2) the critical photoperiod for the induction of diapause was between 14 and 10 hr; (3) feeding activity of the red-headed larvae was nocturnal while the black-headed larvae fed in the day-time as well as at night; (4) full grown larvae tended to hide behind something under artificial illumination; and (5) the shape of the web-nest spun by red-headed larvae was greatly different from that of black-headed larvae. Some of the black-headed type collected from the Canadian Maritime Provinces entered diapause at 18 hr photoperiod, suggesting the possible occurrence of an obligatory diapause.

The adults of red-headed and black-headed types could easily copulate with each other. Hybrids between red-headed males and black-headed females, having an intermediate larval color, grew at a developmental rate that was similar or somewhat higher than that of the black-headed type. Feeding and web-making behavior of the hybrids was of an intermediate nature between the two parental types. Inbreeding between F₁ moths and the back-cross with adults of the two types gave viable larvae.

INTRODUCTION

The fall webworm, *Hyphantria cunea* (DRURY), is an insect species about which the taxonomic status has been remarkably confused. Two species, the "spotted" fall webworm, *H. cunea*, and the "spotless" *H. textor*, were often recognized (LYMAN, 1902; ESSIG, 1949). FRENCH (1880) and MORRIS (1963) reported that the adults of both types could be obtained from the rearing of either stocks. *H. textor* was therefore considered as a synonym of *H. cunea* (see also WARREN and TADIĆ, 1970). Although

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there may be some racial differences¹, it has been determined that the temperature during the pupal stage affected the appearance of spots on wings (Itô, unpublished).

OLIVER (1963, 1964) first recognized two "races" in this species, that is, the "black race" and the "orange race". According to him, the larvae of the black race are characterized by the black color of head and tubercles while those of the orange race by orange head and tubercles.

In addition, he described a remarkable behavioral difference between the two "races". The larvae of the black race feed inside the silken web until the 5th instar and, after the 5th molt, leave the web, becoming a free-living surface feeder. On the other hand, the mature larvae of the orange race may continue to rest in the web during the daytime and feed outside the web at night. It is rather surprising that despite such remarkable differences in larval coloration and behavior, many authors who wrote on this species prior to 1963 never distinguished between the two types.²

MORRIS (1963) described larvae of this species with "brownish heads and tubercles" which showed, despite their different color pattern, a similar behavior to that of the orange race of OLIVER. MORRIS called "the light-headed larvae" for his brown-headed and OLIVER's orange-headed individuals inclusively. In this respect, MORRIS (1963) wrote; "this (the light-headed) webworm and *cunea* may prove to be sibling species, occurring sympatrically from New Brunswick to Georgia. If so, the light-headed webworm has not yet been named." There is, however, no attempt to clarify the specific status of the two forms except OLIVER's (1964) crossing experiment. OLIVER could obtain viable progeny by crossing his black and orange races and also got F₂ larvae as a result of the crossing between F₁ moths.

WARREN and TADIĆ (1970) made an extensive survey of the status of the two types. They used the name "black-headed strain" and "red-headed strain" instead of "black race" and "orange race" of OLIVER. We wish to adopt the terms "black-headed type" and "red-headed type," before the specific status of these types is determined. According to WARREN and TADIĆ, the black-headed type is distributed in the states of Maine, Illinois, Arkansas, Mississippi, Nebraska, Kansas, Louisiana and Washington. The black-headed type has also been observed in Maryland and Washington, D.C. (personal observations of Y.I.) and Georgia, (MORRIS, 1963). On the other hand, the red-headed type has been recorded from Missouri, Kansas, Colorado, Utah, Wyoming, South Dakota, Nebraska, Mississippi, Florida, Arkansas, Louisiana, Texas, Oklahoma and Washington. Only the red-headed type was collected from Missouri, Texas and Oklahoma but the absence of the black-headed type from these states is probably due to the inadequacy of sampling. MORRIS (1963) wrote that, except for two colonies, all the larvae of *H. cunea* found in the eastern part of Canada were black-headed ones. Except on the Pacific coast (HATTORI and ITÔ, 1973) and around Lake Ontario (UMEYA, pers. com.), *H. cunea* in Canada is considered to be that of the black-headed type. Thus WARREN and TADIĆ (1970) wrote that "the black-headed form is evidently predominant in the northern part of the United States and Canada," while the "red-headed form appears dominant in the southern

¹ For example, most of the adults from the Canadian Maritime populations are immaculate even from the overwintering generation as compared with the high percentage of maculate adults (82.9% for males and 33.3% for females of the overwintered generation of 1966 and 1967) of the Japanese population.

² BERGER (1906) certainly described the body color and behavior of the red-headed type. His important findings were overlooked till WARREN and TADIĆ (1970).

United States.” Only the black-headed type has become established in eastern Europe (TADIĆ, 1964) and in Japan (HASEGAWA and ITÔ, 1967).

As the color pattern and the behavior of larvae are remarkably different between the two types, a question arises: whether these two types represent two different species or not. We attempted to compare the taxonomical, behavioral and physiological characters of the two types and also conducted a crossing experiment to determine the taxonomic status of these strains. These types may be good material for the study of the genetics of behavior, because the differences in behavior patterns are, to some extent, connected with the differences in body color.

MATERIALS AND METHODS

Field survey. Field surveys have been made in the state of Arkansas from 1962 to 1970. Trees of forests, orchards and towns in many localities of Arkansas were observed from a running car for larval colonies (which were easily noted by the presence of the silken web). When a colony of *H. cunea* was found, the type judged on the basis of larval coloration was recorded with the name of the host plant. Larvae of some colonies were brought to the Virology and Bio-Control Laboratory, University of Arkansas, and reared on a modified bollworm diet (YEARIAN et al., 1966). Interestingly enough, no black-headed larvae were noted north of the Arkansas River in Arkansas.

Studies in laboratory. Larvae of two colonies of the red-headed type collected in south Arkansas were brought to the Forest Research Laboratory, Fredericton, New Brunswick by special permission of the Canada Department of Agriculture, to observe the color pattern and behavior of the progeny. In addition, some adults of the red-headed type collected in Arkansas were crossed with adults of the black-headed type collected in New Brunswick and Nova Scotia. The color pattern and the behavior of F_1 progeny were observed. Rearing was done at a constant temperature (26°C) and relative humidity (70 % RH) under different photoperiods, e.g. 18 hr, 14 hr and 10 hr illumination per day. A gypsy moth diet (ODELL and ROLLINSON, 1966) was used for larval food. In the crossing experiment, the pupae were sexed and on emergence each pair was put into a small fiber container with a piece of rough paper. Egg-masses obtained were kept in an incubator and the larvae on eclosion were transferred to the diet by a finebrush.

RESULTS

General description of the two types based on field survey

The results of our observation on the biology and behavior of the red-headed type generally supported OLIVER's (1964) earlier findings.

More than 50 colonies of the red-headed type were found in South Arkansas late in June, 1970. All of the several thousand larvae found in these colonies had red-colored heads. The heads of 1st and 2nd instar larvae, especially at the time just before the molting, seemed to be dark colored, but we could clearly distinguish these from the black-headed larvae under microscope. In addition, the ground color and the color of the setae and hair of the red-headed type were tawny or reddish. After

the 3rd instar, the distinction between the red-headed larvae from the black-headed larvae was quite clear, for the head of the former showed a uniform reddish-brown color similar to the ripened fruit of the Japanese persimmon (see Plate 1 of HATTORI and ITÔ, 1973). On the other hand, all the larvae of the black-headed type examined in Arkansas, Maryland, Washington, D. C., New Brunswick, Nova Scotia and Japan had uniformly black-colored heads. Except for 3 colonies out of several hundreds from Eastern Canada, 7 colonies from Vancouver, B. C., and some colonies from Washington State, we observed no colony with larvae of both types or of an intermediate color pattern. The red-headed and the black-headed types could, therefore, be distinguished very easily by the color of the larval head.

Differences in color pattern of the abdominal region were not clear in the early larval instars but became distinct in the later instars. The color patterns of larvae of the two types are described in a separate paper (HATTORI and ITÔ, 1973).

OLIVER's (1964) observation that the later larvae of the red-headed type fed outside the web at night and rested in the web during the daytime even in the last instar (the last instar larvae of the black-headed type leave the web and become free-living) was confirmed by our field observations. The results of our observations are summarized as follows:

- (1) The web of the red-headed type is at first similar to that of the black-headed type. The larvae feed inside the web in which several leaves are bound together.
- (2) As the red-headed larvae grow, they often spin a very tight web at the basal part of a limb, particularly on small trees, as *Malacosoma californicum pluviale* and *M. neustria testacea* do. In the daytime, the red-headed larvae in the later larval instars do not feed but rest in the web, and at night move toward branch terminals to feed. Due to the silk spun by the larvae during their movement, a greater part of the tree may become covered by a rough silken web (Fig. 1). The central part of the web

Fig. 1. Left : A silky-net spun by colonies of red-headed larvae (Photographed by L.O. Warren). Right : Injury by black-headed larvae (Photographed by Y. Itô).

Fig. 2. Schema of web-spinning behavior by black-headed and red-headed larvae.

of the red-headed type is so tight that the larvae are more effectively protected from predation by wasps and birds than the black-headed type.

The behavior of the black-headed type are similar to that described by many authors. Up to the 5th molt, the larvae feed inside the web. When leaves inside the web have been consumed, the colony moves to another part of the shoot or limb and spins a new web enclosing the foliage. The 6th and the 7th instar larvae do not spin a web and become free-living surface feeders. Mainly due to the disturbance by predators (ITÔ and MIYASHITA, 1968), the 6th and the 7th instar larvae disperse to various parts of the tree. Thus in the later larval stages, the shape of the web-nest of the red-headed type is remarkably different from that of the black-headed one (Fig. 2).

Host plants of the two types were different as OLIVER stated for the Louisiana populations. In Arkansas, Nova Scotia, New Brunswick and Japan, the black-headed type was found on a variety of species of deciduous broad-leaved trees. Of these, cherries, *Prunus* spp., mulberry, *Morus alba*, dogwoods, *Cornus* spp., sycamores, *Platanus acerifolia* and *P. occidentalis*, Japanese and American persimmons, *Diospyros kaki* and *D. virginiana*, poplar, *Populus nigra*, aspen, *P. maximowiczii*, willows, *Salix* spp., white birch, *Betula platyphylla*, apple, *Malus pumila*, and sweetgum, *Liquidambar styraciflua*, were especially preferred. On the other hand, most of the colonies of the red-headed type, we found in many localities of Arkansas in June 1970, were recorded on only 4 species of trees, e.g. pecans, *Carya* spp., black walnut, *Juglans nigra*, persimmon, *Diospyros virginiana*, and sycamore, *Platanus occidentalis*. The last host was considered to be rather an unusual host because, we found only one colony on the sycamore in our trip made in the summer of 1970. Pecans seemed to be the most favorable host, because, in many pecan orchards, we could find colonies on 25 to more than 50 per cent of the trees. The black-headed type does not prefer pecans so strongly. It can be said that the host range of the red-headed type is narrower than that of the black-headed type

and this is one of the factors which isolate these two types in nature.

As OLIVER (1964) reported, the life cycle of the two types are different. In Arkansas, the black-headed type has 2 to 4 generations a year and the colonies of the middle instar larvae are found in May, July, August, and sometimes October, but the red-headed type has 1 to 2 generations, the larval colonies being found in the late June and late August. In north Arkansas a partial second generation is rarely observed. Thus the chance of interbreeding is considered to be rather low, apart from other isolating mechanisms.

Observations made in the laboratory showed that all the egg-masses laid by the red-headed type were deposited in double or multiple layers. The egg-masses of the black-headed type were deposited in double layers only in rare cases. These facts confirmed OLIVER's (1964) field observations.

Development under constant conditions

Progress of larval and pupal development is shown by plotting the cumulative percentage of pupation and adult emergence against the cumulative heat units above 11°C from hatching (Fig. 3). Eleven degrees centigrade is used here as a theoretical threshold of development of this species based on the results of laboratory experiments

Fig. 3. Development of black-headed and red-headed types of *H. cunea* and their hybrids. Hollow circle shows the cumulative percentage of pupation and solid circle that of adult emergence. Horizontal axis indicates cumulative heat units above 11°C summed up from the egg-hatch. Vertical lines X and Y show mean cumulative heat units for larval and larval-pupal development of Japanese black-headed type, respectively.

Table 1. AVERAGE VALUES OF THERMAL CONSTANTS FOR LARVAL AND LARVAL-PUPAL DEVELOPMENT OF THE BLACK-HEADED AND RED-HEADED TYPES AND THEIR HYBRID^a

Type ^b	Thermal constants for larval development (°C-days)	Thermal constants for larval and pupal development (°C-days)
BB	527.6 (7)	638.5 (2)
RR	672.9 (9)	785.0 (7)
BR	487.5 (2)	626.5 (2)

^a Figures in parenthesis mean the number of colonies reared. Significant differences at $P < 0.01$ and $0.01 < P < 0.05$ are presented by ** and *, respectively.

^b BB, Black-headed female $\times$ Black-headed male. RR, Red-headed female $\times$ Red-headed male. BR, Black-headed female $\times$ Red-headed male.

by UMNÖV (1956), JASIC et al. (1964), ITÔ et al. (1968), and MORRIS and FULTON (1970). The cumulative percentage of emergence was calculated for non-diapausing individuals only. Vertical lines at 460 degree-days and 630 degree-days show the thermal constants for larval and larval-pupal development of the black-headed type (UMNÖV, 1956; ITÔ, et al. 1968), respectively. As shown in Fig. 3, the progress of development of the black-headed type was, to some extent, delayed as compared with the results obtained by other authors, but a far greater delay was found in the red-headed type. As shown in Table 1, the difference between thermal constants for the red-headed type (RR) and the black-headed type (BB) was statistically significant. Whether this delay was due to a larger thermal requirement of the red-headed type than that of the black-headed one or to the stronger sensitivity of the red-headed type to the poor nutrient condition of the artificial diet is however, not clear.

From Fig. 3, it seems that the individual variation of the developmental rate was larger in the red-headed than in the black-headed type, but the comparison of individual variation by means of MORISITA's index (I_d) showed that there was no difference between the intensity of individual variation in developmental rate.¹

There was no difference in the thermal constants among larvae and pupae reared under different day-lengths.

Table 2 shows the per cent of individuals which entered diapause under different photoperiods. In Japanese and European populations (BB type), diapause was known to be induced by a short day below 14 hr during the early developmental stages (JASIC, 1962; MASAKI et al. 1968). For Canadian populations, MORRIS (1967) showed that the onset of diapause was regulated by the interactions of temperature, moisture, food quality and photoperiod. At higher humidity, diapause was induced by a day-length below 14.5 hr at the time of pupation. This value roughly corresponds to 15.5 hr photoperiod during the early larval stages when diapause is determined (JASIC and MACKO, 1961; H. ITÔ, 1968).² Contrary to these results, some of

¹ The coefficient of variation has often been used for the purpose of the comparison of individual variation. As this coefficient is affected by the value of the mean, however, this method is not so suitable for comparing the values for which means are greatly different.

² MORRIS (1967) suggested that the day-length at the later instars could modify the previous effect on diapause during the early instars. He wrote that 14.5 or 14.3 hr photoperiod at later larval stages might be the critical photoperiod. H. ITO's (1968) experiments showed, however, that the onset of diapause in this species was principally determined by the photoperiod from the 1st to the 3rd larval instars and the effect of photoperiod during the later larval stages was negligible.

the progeny of the black-headed type from the Canadian Maritime Provinces entered diapause even at an 18 hr photoperiod (Table 2). Most of the black-headed individuals entered diapause at 14 hr and all of them at 10 hr photoperiods. Thus, at least a part of the black-headed type from the Canadian Maritime Provinces is considered to have an obligatory diapause or a remarkably long critical photoperiod not normally experienced in nature.

On the other hand, most of the pupae of the red-headed type reared at 18 hr and 14 hr photoperiods and some of those reared at 10 hr photoperiod did not enter diapause. The critical photoperiod may lie between 14 hr and 10 hr (probably near 10 hr).

All the larvae of the red-headed type passed through 7 larval instars. Although MORRIS and FULTON (1970) reported that many of the black-headed individuals of the Canadian Maritime Provinces has 6 larval instars, most of the black-headed larvae we used for these experiments had 7 larval instars.

Diurnal behavior in the laboratory

Quantitative observation was made on the diurnal behavior pattern of the black-headed and the red-headed larvae by two methods, that is, (1) frass counts, and (2) recording the number of larvae found on the diet-dish.

Five larvae of each type were caged in a fiber carton (c.a. 7 cm in diameter and 6 cm in depth) with a small plastic petri dish (3.5 cm in diameter and 1 cm in depth) in which the gypsy moth diet was poured. The top of the carton was covered with transparent cellophane paper. The diet-dish was leant against the wall of the carton with a piece of scotch tape, so that the larvae could hide behind the dish. The cartons were kept in an environmental chamber regulated at 26°C, 70% RH and a 14 hr photoperiod. The dark phase of the photocycle started at 21 : 00 everyday. The feeding activity

Table 2. THE PHOTOPERIODIC RESPONSES OF THE BLACK-HEADED AND RED-HEADED TYPES AND THEIR HYBRID^a

Photoperiod (hr)	Stock	Diapause (%)		
		BB	RR	BR
18	1	83	0	0
	2	27	0	0
	3	—	12	—
	4	75	20	—
	Mean	62	8	0
14	1	100	0	—
	2	—	5	—
	3	62	10	—
	4	96	—	—
	Mean	86	5	—
10	1	100	100	—
	2	—	88	—
	3	—	—	—
	4	—	89	—
	Mean	100	92	—

^a For symbols BB, RR and BR, see Table 1.

was measured by the number of frass-pellets produced during 3 hr periods. Seventh instar black-headed and red-headed larvae were used for this experiment. As the rate of feeding is closely related to the rate of frass production (MORRIS and FULTON, 1970), the fluctuation of frass-production is considered to represent the diel rhythm of the feeding activity. In some cases, frass-pellets were counted at 6- or 9-hour intervals, and the counts were divided by 2 or 3, respectively, to obtain the average for each 3 hr unit (dotted lines of Figs. 3 and 4). Counting of the pellets was done as quick as possible under artificial light, and then all pellets were removed.

The results of frass-pellet counts are shown in Figs. 4. From this figure, it is clear that the red-headed larvae showed remarkable nocturnal feeding activity while the black-headed larvae did not. The number of frass-pellets produced by a red-headed larva per hour during the dark phase was 4 to 10 times as large as that produced during the light phase (Table 3). On the other hand, the number of frass-pellets produced by a black-headed larva decreased at the beginning of light-phase but increased again to a level similar to that during the dark phase. Thus the feeding activity of the black-headed larvae during the dark phase is slightly higher than that during the light phase. These results from the black-headed type are similar to those obtained by MORRIS and FULTON (1970).

In order to check the difference in the reaction of red-headed and black-headed larvae to light the number of larvae found on the diet-dish at the time of the frass-count was recorded. As shown in Table 4, the results showed that the per cent of black-

Fig. 4. Fluctuation of the frass-pellet production in relation to the light condition. Striped area shows dark-phase.

headed larvae found on the diet-dish during the dark phase was not significantly different from that during the light phase. On the other hand, a few red-headed larvae could be seen on the diet-dish during the light phase. The remaining larvae were seen hiding behind the dish. Thus it was suggested that the red-headed larvae, at least in the later larval instars, tend to avoid light. It was also noted that, during the dark phase, a greater per cent of the red-headed larvae were observed feeding. Thus the percentage of red-headed larvae found on the dish in the dark phase was significantly higher than that in the light phase.

Spinning

The spinning behavior of the red-headed larvae was different from that of the black-headed larvae not only in nature but also in the laboratory. As shown in Fig. 5, red-headed larvae spun a tight web between diet-dishes while the black-headed larvae spun a rough one. The web of the red-headed larvae was so tight that it was necessary to scissor the web in order to examine the larvae in it. As the last instar larvae of the red-headed type has been known to hide in the web during daytime, it has been questioned whether the last instar larvae spin the web or not (The 6th and the 7th instar larvae of the black-headed type do not spin web except indistinct trails). By an experiment where five or ten 6th or 7th instar larvae of the red-headed type were caged in a fiber carton with two diet-dishes, it was shown that the 6th instar larvae

Table 3. NUMBER OF FRASS-PELLETS PRODUCED DURING DARK AND LIGHT PHASES^a

	1st experiment			2nd experiment		
	BB	RR	BR	BB	RR	BR
No. frass-pellets/hr/ individual in light phase	3.12	0.87	1.16	3.25	0.45	2.10
No. frass-pellets/hr/ individual in dark phase	3.67	3.47	3.13	3.85	4.65	4.62
Ratio (light phase=1.0)	1.18	4.43	3.00	1.15	10.90	2.35
	*		*	**		**

^a For abbreviation BB, RR and BR, see Table 1.

Table 4. PER CENT OF THE NUMBER OF LARVAE FOUND ON DIET-DISH TO TOTAL NUMBER OF LARVAE DURING DARK AND LIGHT PHASES^a

	1st experiment			2nd experiment		
	BB	RR	BR	BB	RR	BR
During dark phase	70.00	87.50	85.71	36.25	91.13	73.46
During light phase	49.15	4.87	26.04	44.37	13.33	18.56
Ratio (light phase=1.0)	1.40	17.97	4.19	0.89	9.45	4.64
	**		**	*		*

^a For the abbreviations BB, RR and BR, see Table 1.

^b Statistical test was conducted after the *arc sin* transformation of the data.

Fig. 5. Nest-webs formed in cartons by RR(right top), BB(left two) and hybrid (right bottom) larvae.

spun the web but the 7th instar larvae did not. The last instar red-headed larvae continued to hide in their old web during daytime.

Results of crossing experiments

As a result of the crossing experiment between males of the red-headed type from Arkansas and females of the black-headed one from the Canadian Maritime Provinces, two viable egg-masses were obtained (abbreviated as BR hereafter). Females of the red-headed type could copulate with males of the black-headed type but no viable eggs were obtained. Emergence of red-headed adults took place several days earlier than that of black-headed adults, and, therefore, the adults of the former type were kept in a cold room. Thus it is not known whether the cause of this unsuccessful interbreeding between the red-headed females and black-headed males is attributed to a genetic barrier or to the effects of cold storage.

On hatching, BR larvae were transferred to the artificial diet and reared in an environmental cabinet at 26°C, 70% RH and 18 hr photoperiod. The results of this experiment are as follows:

Color pattern. The color pattern of the head of the hybrid lay between those of the parents. That is, the color of the larval head was a mosaic of black and reddish-yellow or reddish-brown. A detailed description of the shape and color of the hybrid will be made in a separate paper (HATTORI and ITÔ, 1973).

Larval and pupal development. As shown in the top of Fig. 3, the BR larvae grew faster than their parents and the mean cumulative heat units above 11°C for the mean duration of the larval and larval-pupal development were 487.5 and 626.5 degree-days, respectively (Table 1). (The cumulative heat units for 50% pupation and 50% emergence were somewhat smaller than these values, 432.5 and 622.5 degree-days, respectively.) Thus the developmental rate of the hybrid was similar to that of the black-headed strain reported so far (460 degree-days for larval and 630 degree-days for larval and pupal development). In this experiment, however, the developmental rate of BR was faster than either parent.

This might be a heterosis-like phenomenon, which was also suggested by the lower mortality of the hybrid larvae than that of the parent stock, especially in the male. No quantitative data, are available, however.

Diapause. As shown in Table 2, all the BR pupae did not enter diapause under an 18 hr photoperiod. No definite conclusion can be drawn on the nature of inheritance of diapause until further rearing experiments under shorter photoperiods, are accomplished.

Behavior. The diurnal behavior of BR larvae was observed in the laboratory using 6th (1st experiment) and 7th (2nd experiment) instar larvae. Fig. 4 and Tables 3 and 4 show that the diel rhythm in feeding activity of the BR larvae was intermediate between the parental stocks. As seen in Fig. 5, the structure of the silken web spun by the BR larvae was also intermediate between the webs spun by the parental stock. There is a possibility that the genetic mechanism of color pattern in this species seems to be connected with that of behavior.

Table 5. PER CENT HATCH OF EGG-MASSSES OBTAINED BY F_1 CROSSES (BR $\times$ BR) AND BACK-CROSSES

Combination	BR $\times$ BR	B $\times$ BR	BR $\times$ B	R $\times$ BR	BR $\times$ R
No. egg-masses obtained	20	4	6	3	5
% egg-masses hatched	35	50 ^a	50	67	0

^a Two egg-masses hatched but one gave only a few larvae.

F_2 hybrid Adults of the hybrid were crossed each other or backcrossed to the parent stocks. The number of egg-masses laid and the per cent of egg-masses of which all or some of the eggs hatched are shown in Table 5. The larvae obtained were reared on artificial diet till September 20 when the senior author left Fredericton. Larvae from all of the egg-masses obtained from inbreeding of F_1 and the backcrosses established and developed to the 4th instar.

DISCUSSION

It is clear from the foregoing accounts that the black-headed and the red-headed types are not extremes of a continuous variation but belong to two distinct entities. Observations on the hybrid and parent stocks suggest that significant differences in the color pattern and behavior of larvae between the two are genetically determined.

Although these two strains are sympatric in southern United States, they are effectively isolated by their different seasonal life cycles and ranges of host plants.

The pupal diapause of the black-headed type had been reported to be induced by a short day below 14 hr during the early larval instars (JASIC, 1962; MASAKI et al. 1968). Contrary to this, some of the black-headed individuals collected from the Canadian Maritime Provinces entered diapause even at an 18 hr photoperiod. In the black-headed type collected near Kingston, Ontario, the critical photoperiod lies between 16 and 15 hr (UMEYA, unpublished). This critical photoperiod is remarkably longer than those reported so far for Japanese and European populations, but may be expected since the day-length near the northern border of distribution of *H. cunea* in July (early larval stage) is longer than 15 hr. In the northern part of the range of many species of insects, the critical photoperiod tends to elongate to adjust to the longer day-length, or to evolve the trait of obligatory diapause (DANILEVSKII, 1965). There is a possibility that some populations of *H. cunea* in the Canadian Maritime Provinces enter diapause regardless of the day-length.

Most of the red-headed individuals from Arkansas did not enter diapause at 14 hr photoperiod, but most did at a 10 hr photoperiod. It was noted that 10 per cent of the red-headed individuals emerged less than 1 month after pupation even at a 10 hr photoperiods. These facts suggest that the critical photoperiod for this strain lies between 14 hr and 10 hr, probably near 10 hr. In this respect, it is noted that the critical photoperiod of the black-headed type in Arkansas is considered to be near 12 hr (WARREN, unpublished), adjusting probably to short day-length in summer of the southern United States. It was also observed that some of the red-headed type entered diapause at 18 hr photoperiod. This fact suggests that the red-headed type from Arkansas is more physiologically heterogeneous than the black-headed type or more strongly influenced by nutritional factors.

The limited host range of the red-headed type as compared with that of the black-headed type suggests the lower limit of tolerance of nutrient conditions of the former. This may be a reason for the higher mortality and slower development of the red-headed larvae on artificial diet as compared with the black-headed type.

The results of observations on the diel rhythm in larval feeding in the laboratory showed the nocturnal habit of the feeding of the late instar larvae of the red-headed type. This behavior pattern may, in combination with the habit to hide in web in the daytime, have a survival value for this type against predation by birds and wasps which are effective predators of *H. cunea* in the warm temperate region (OLIVER, 1964; ITÔ and MIYASHITA, 1968; WARREN and TADIĆ, 1970), and this may be the reason the red-headed type is more abundant than the black-headed one in the southern United States.

On the other hand, the nocturnal habit may be unsuitable for the propagation of the red-headed type in the northern area where the night temperature falls to a low level. Feeding of the mature larvae may be suppressed by the low temperature at night, but the respiratory energy loss in the daytime may not be very different from that in the southern areas. Thus one of the possible causes of the limited range of this type in the southern area may be the energy problem. Future study is, of course, needed to prove this assumption.

Adults of both types could easily copulate each other in the laboratory. The crossing between the black-headed and red-headed types gave viable F_2 larvae. The

back-crosses of F_1 with either of its parents also gave viable larvae.

The color pattern, the diel rhythm in the feeding and the spinning behavior of F_1 larvae were intermediate between the parental types. Such an intermediate type was also found in F_2 larvae, among which no clear separation was found. These facts suggest that the inheritance of the color of head and the behavior of larvae may be determined not by a simple allele but by multiple alleles or polygene systems. As suggested in p. 168, if the inheritance of behavior in this species connected with that of color pattern, these two strains of *H. cunea* will afford good resource material for future study of the genetics of behavior.

ACKNOWLEDGEMENTS

The authors express their sincere thanks to Dr. I. C. M. PLACE, Forest Research Laboratory, Fredericton, N. B. for providing facilities during the course of our study. Thanks are also due to the Department of Agriculture, Canada, for allowing the importation of specimens for study from Arkansas to Fredericton, and to Dr. R. F. MORRIS for reading the manuscript.

Laboratory assistance by personnel of the Virology and Bio-control Laboratory, University of Arkansas and Mr. C. BENNETT, Forest Research Laboratory, Fredericton, is also appreciated.

Partial support from NSF Grant GB-3941, to the University of Arkansas, is acknowledged.

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