Status of Black-Headed and Red-Headed Types of *Hyphantria*
cunea (DRURY) (Lepidoptera : Arctiidae)

III. Distribution of Various Types and the Discussion
on the Relationship Among Them

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Besides typical red-headed and black-headed types of *Hyphantria cunea*, another type which is characterized by the larval heads 'mosaic' of red and black, were found in Pacific areas of North America. Collection of the larval specimens or the larval heads in abandoned nest-webs showed that, despite the variation in color of the larval heads from blackish to uniformly red, the behavior of larvae (nocturnalism, hiding under the nest-web till the last instar, etc.) is identical with that of the red-headed type. The type reported here could be considered as a northern strain of the typical red-headed type and thus the two were joined under the name of *Malacosoma* type, resulting that there are two biologically distinct entities in the fall webworms, that is the black-headed type (*H. cunea*) and the *Malacosoma* type webworm. It was also suggested that the examination of wing-maculation of the overwintered male moths over North America is needed before the determination of the specific status of the latter.

INTRODUCTION

Since the first discovery of the coexistence of two distinct types, black-headed and red-headed, of *Hyphantria cunea* (DRURY) in the southern United States (OLIVER, 1964a, 1964b), it has been shown that these are distinct entities from the ecological point of view (MORRIS, 1963; WARREN and TADIC, 1970; ITÔ and WARREN, 1973). In the earlier paper (HATTORI and ITÔ, 1973), we reported on the slight, but overlapping, morphological differences between the two (see also WILSON and WARREN, 1973). It was also noted by HATTORI and ITÔ (1973) that the color pattern of heads of the larvae caught in Vancouver, B. C. by ITÔ was a 'mosaic' of black and red, and the behavior pattern was similar to that of the red-headed type. The fact that all the seven colonies found in Vancouver showed the same characters raised a question whether or not this population represents the third type of *H. cunea*. Thus we attempted to obtain the larval specimens or the abandoned nest-webs including the head capsules from different localities of North America. The present paper includes a descrip-

tion of the larval heads of the 'mosaic type' according to localities from which we obtained the specimens, and a general discussion on the relationship among three types.

DESCRIPTIONS

Our descriptions of larval color are based on two kinds of specimens; that is, the larvae kept in 70% alcohol and the head capsules of exuviae found in abandoned nest-webs. The color of the latter was evidently lighter than that of those alive or kept in alcohol, but, as we can see later there was no difference in the basic color pattern of geographic cline.

The followings are the descriptions of color pattern of larvae kept in alcohol. Each vial contains larval specimens taken from the same colony. Although some vials include typical black headed larvae, description was made for the 'mosaic' type only. Even the 'mosaic' type larvae with the darkest color pattern could easily be detected from the black-headed larvae, because the heads of the latter were purely black but those of the former were not.

Description of color pattern was separated into light and dark forms for those collected at some localities.

Specimens from Vancouver, B. C., Canada

Color of head and body varying light to dark. Mature larvae usually much darker than immature ones.

Light form: Head light brown, dark brown area extending anteriorly or posteriorly; vertex sometimes with black patch. Body pale greyish yellow speckled with grey; dorsal broad longitudinal band greyish black with fine creamy dorsal line; ventral area of abdominal segments greyish brown or black. Prothoracic shield and prothoracic legs dark brown entirely; prolegs dark brown externally. Dorsal tubercles brown, lateral tubercles light brown. All tubercles bearing long pale brown setae with black or white.

Dark form: Head dark brown or blackish brown, with pale post-lateral patch. Ground color of the body greyish or blackish yellow speckled with pale black or almost blackish; dorsal broad band almost black suffused with greyish black ventrally; ventral broad band blackish brown. Prothoracic shield and prothoracic legs blackish brown entirely; prolegs blackish brown externally. Dorsal tubercles blackish brown, lateral tubercles light brown or dark brown. All tubercles bearing long pale brown setae with black or white.

Specimens from Washington, U. S. A.

Light form: Head reddish brown with black anterior area including front, adfrontals and ocelli, sometimes with black area extending to vertex or to posterior margin. Body pale dull yellow speckled with grey, with greyish black dorsal band, sometimes with dark ventral band. Prothoracic shield and dorsal tubercles on the shield dark or light brown; prothoracic legs and prolegs brown. Dorsal tubercles excepting on the prothoracic shield light brown or dull yellowish brown. Each tubercle bearing long setae mixed with pale brown or black.

Dark form: Head dark brown, with pale brown patch at posterior margin or around vertex. Ground color of the body brown, speckled with black, rather deep-

ened ventrally. Prothoracic shield, and dorsal tubercles on the shield, prothoracic legs and prolegs dark brown. All dorsal tubercles except on the prothoracic shield pale orange brown or blackish brown. Lateral tubercles usually pale orange brown tinged with light brown. Each tubercle bearing setae brown mixed with black or white.

Specimens from Oregon, U. S. A.

Head reddish brown, with black anterior area including front or adfrontals; black area sometimes extending to vertex, around ocelli and posterior margin. Ground color of the body pale creamy yellow speckled with pale grey; body with greyish black broad dorsal band interrupted at anterior and posterior margins of each segment. Prothoracic shield, prothoracic legs and prolegs brown. All dorsal tubercles light orange to light brown, lateral tubercles as same as the ground color. Each tubercle bearing long white setae with mixed brown or black.

Specimens from Idaho, U. S. A.

Light form: Head reddish brown or orange red, front and adfrontal area tinged with black; head sometimes with small brown patch at ocellar area or around vertical sinus. Ground color of the body creamy yellow speckled with pale greyish brown rather darker dorsally and ventrally. Dorsal and lateral lines creamy white. Prothoracic shield pale brown or orange brown with brown posteriorly, anal plate tinted with brown. All tubercles pale brown or pale orange brown, bearing setae white mixed with black or brown. Prothoracic shield pale brown or orange brown with brown posteriorly, anal plate tinted with dark brown. All tubercles pale brown or pale orange brown, bearing white setae with black or brown. Prothoracic legs brown or blackish brown except tarsi. Prolegs brown or dark brown externally except tips pale yellow.

Dark form: Head reddish brown, with blackish brown area extending anteriorly and posteriorly onto front, adfrontals and ocellar area, sometimes reaching vertex; with pale reddish brown patch at post-lateral area or around vertical sinus. Ground color of the body pale dull yellow speckled with pale brown or pale grey; body with broad dorsal band varying pale brown to blackish brown, with fine pale yellow dorsal line interrupted at anterior and posterior margins of each segment. Ventral area suffused with broad dark brown or pale grey. Prothoracic shield blackish brown with dorsal tubercles blackish brown; anal plate blackish brown; prothoracic legs blackish brown, prolegs brown. Dorsal tubercles orange brown tinted with brown, bearing pale brown setae; lateral tubercles yellowish brown tinted with brown, bearing white setae with brown.

Specimens from Ontario, Canada

Head dark brown to blackish brown, with small pale brown patch at posterior margin. Ground color of the body dark grey to blackish grey speckled with dull dark yellow, with black broad dorsal band; body sometimes with fine dull yellow lateral and supra-spiracular lines interrupted at anterior and posterior margins of each segment. Prothoracic shield and all dorsal tubercles blackish brown, bearing long setae brown mixed with black and white, lateral tubercles orange yellow, bearing white setae with black or white. Prothoracic legs and prolegs blackish brown.

Specimens from New Hampshire

Head dark brown to blackish brown, with pale brown patch at posterior margin. Ground color of the body greyish black speckled with dark dull yellow, body with black broad dorsal band interrupted at anterior and posterior margins of each segment; ventral area suffused with black. Prothoracic shield, prothoracic legs and prolegs blackish brown. Dorsal tubercles brown or dark brown tinged with black, and lateral tubercles pale brown. All tubercles bearing long setae brown mixed with white and black.

Specimens from Connecticut, U. S. A.

Head dark brown to blackish brown, with pale brown area extending to posterior margin. Ground color of the body dull yellow speckled with dark grey or brown, body with black broad dorsal band. Prothoracic shield, prothoracic dorsal tubercles, prothoracic legs and prolegs blackish brown. Dorsal tubercles orange brown or

Table 1. COLOR TYPES OF HEADS OF THE 'MOsaIC TYPE' LARVAE COLLECTED IN DIFFERENT LOCALITIES OF NORTH AMERICA.

Locality		No. Specimens	Instar	Percentage of color types ^a					Host plants
				I	II	III	IV	V	
Vancouver, B. C.	Sept. 24, 1970	7	7	0	0	0	100.0	0	apple
	Y. ITÔ	6	6	0	0	0	100.0	0	
Vancouver, B. C.	Sept. 26, 1970	14	7	0	0	0	100.0	0	white birch
	Y. ITÔ		6	0	33.3	0	66.7	0	
Takoma, Washington	Aug. 26, 1971	81	7	0	7.4	29.6	63.0	0	apple
	D.A. BARSTROW		6	0	35.3	38.2	26.5	0	
			5	0	70.0	30.0	0	0	
Puyallup, Washington	Sept. 15, 1971	104	7	0	0	0	100.0	0	poplar apple
	D.A. BARSTROW		6	0	0	52.8	47.2	0	
			5	0	0	33.3	66.7	0	
Alderton, Washington	Sept. 12, 1971	59	7	0	0	1.9	98.1	0	copper beech
	G. TAMAKI		6	0	0	0	100.0	0	
Yakima, Washington	Sept. 13, 1971	58	7	0	12.1	72.4	15.5	0	crab apple
	G. TAMAKI								
Yakima, Washington	Sept. 13, 1971	56	7	0	17.4	52.2	30.4	0	English walnut
	G. TAMAKI		6	0	20.0	70.0	10.0	0	
Oregon	May 27, 1971	6	7	0	0	100.0	0	0	unknown
	L. O. WARREN		6	0	100.0	0	0	0	
			5	0	100.0	0	0	0	
Clearwater Riv. near Lewiston, Idaho	Aug. 14, 1972	79	7	0	80.0	0	20.0	0	<i>Alnus incana</i>
	H. L. OSBORNE		6	0	46.3	53.7	0	0	
			5	0	57.6	42.4	0	0	
Clearwater Riv. near Lewiston, Idaho	Sept. 15, 1972	155	7	0	42.0	41.0	17.0	0	<i>Prunus</i> spp.
	H. L. OSBORNE		6	0	67.3	21.1	11.6	0	
			5	0	100.0	0	0	0	
Wellsville Canyon, Utah	Aug. 16, 1972	26	6	88.2	11.8	0	0	0	choke cherry
	DAVIS		5	77.8	22.2	0	0	0	
Voluntown, Connecticut	July, 1972	115	7	0	0	4.5	95.5	0	cherry
	S. Tojo		6	0	0	0	100.0	0	
New Hampshire	Aug. 22, 1971	17	6	0	0	0	100.0	0	unknown
	S. Tojo								

^a I : purely red; II : intermediate between I and III; III : about 50% red and 50% black; IV : intermediate between III and V; V : purely black.

Fig. 1. Frequency distributions of color types of head capsules of exuviae collected in different localities of North America. True black-headed (top) and red-headed (bottom) types are presented for purpose of reference.

blackish brown tinted with black.

The foregoing descriptions suggest that the color of the larval head is darker in cooler localities and lighter in warmer localities. Table 1 shows the distribution of color types. Most of the specimens from Oregon, Idaho and Utah are classified as the lightest form among 'mosaic' type. It must be noted that colonies of the typical red-headed type were also found in Idaho and Utah (see Table 2).

Fig. 1 shows the distribution of five color types, which are parallel with those in Table 1, of the head capsules found in nest-webs collected in different localities. A geographic cline from the northern darker form to the southern lighter form is again evident.

BEHAVIOR OF 'MOSAIC' TYPE LARVAE

In Vancouver. The senior author found 7 nest-webs (5 from white birch, one each from apple and dogwood) containing the last (probably 7th) instar larvae at the campus of the University of British Columbia, Vancouver, B. C. in September, 1970. The webs remaining on the shoots suggested that the young larvae first put several leaves together with silk, but, as the larvae grew, they began to spin compact webs on the tree trunk. It was noted that the last instar larvae were still hiding under the webs during the daytime, suggesting the nocturnal feeding pattern of large larvae. All the seven colonies showed a similar pattern. The behavior of 'mosaic type' larvae found in

Vancouver are thus similar to that of the red-headed type, except in two respects; that is, the webs are not so compact as the typical red-headed type¹, and the larvae may feed on white birch and Rosaceae which are unsuitable hosts for the southern red-headed type.

Specimens from Ontario. UMEYA (unpublished) attempted to rear *H. cunea* sent from southern areas of Ontario. Among 11 egg-masses he obtained, 6 produced progeny of a distinct type. Larvae were reared on shoots of the cherry, put in a rearing cage which was kept under constant temperatures (20°C and 25°C) and fixed day-lengths from 14 hr to 15.5 hr. No remarkable difference in color or behavior of young larvae from those of the black-headed type was recognized. When the larvae had grown up to the 6th or 7th instar, however, they tended to congregate during the light phase at a corner of the cage, spinning a communal web like *Malacosoma neustria*. This behavior suggests that they spin the web on a tree trunk in the field. Two or three hours after light-off, the larvae left the web and began to feed independently on the leaves. Only a few individuals remained in the web at the middle of the dark phase. The feeding lasted to the end of dark phase, when the larvae came back to the web. Despite the fact that the heads of most larvae were apparently black, the behavior pattern was similar to that of the red-headed type.

Description of larval behavior by WELLINGTON et al. WELLINGTON et al. (1954) mentioned field behavior of 'old' larvae of their '*Hyphantria textor*' collected in Victoria, British Columbia. As their larvae are undoubtedly the same type with larvae found in Vancouver by the senior author, it is worth referring to their sentences:

"In these older instars, web formation also occurs most frequently during the night or damp days, but it also occurs during periods of direct sunlight if the larvae are driven from the web. . . . This milling results in the formation of a loosely woven network that is rapidly filled in because larvae tend to use existing threads for only short distances, and continually strike off from the original thread, putting out new silk as they move."

These characteristics are remarkably similar to the behavior pattern of typical red-headed larvae (see ITÔ and WARREN, 1973).

Circumstantial evidence. Four abandoned nest-webs of the 'mosaic type,' sent from Victoria seemed to be more compact than that of the black-headed type, and contained exuviae and carcasses of the last (7th) instar larvae and some pupae, suggesting that the last instar larvae used these webs for a hiding place. Another nest-web of the 'mosaic type' sent from the Shenandoah National Park, Virginia also showed similar characteristics. Exuviae or carcasses of the last instar larvae and pupae were found also in compact nest-webs of the red-headed type sent from Oklahoma, Idaho and Arkansas.

Although the color of head capsules of the 'mosaic type' larvae varies from almost black to almost red, all the 'mosaic type' larvae (or remains of them) conclusively showed a common behavior pattern which was basically the same as that of the red-headed larvae.

DISTRIBUTION OF THREE 'TYPES' OVER NORTH AMERICA

Although there is much classic literature concerning the fall webworm, only a few

¹ Prof. W. G. WELLINGTON (personal communication) told the senior author that this behavior pattern is a common feature of the fall webworms in British Columbia, including Vancouver Island.

papers allow us to judge the type of larvae reported. We have to examine our data first.

From Table 2, it seems that only the black-headed type is distributed in Canada east of the Rocky Mountains. Especially in Nova Scotia and New Brunswick, the senior author found many larval colonies of the black-headed type, but none of other types. According to MORRIS (1963) only two colonies among 1,300 from Nova Scotia and New Brunswick contained 'brownish headed larvae' which remained inside the webs till the last instar. The black-headed type is found in the widespread area from Manitoba (the northern limit of the distribution of *Hyphantria cunea*—see MORRIS, 1964) to Louisiana, near the southern limit of the distribution. The density seems to be especially high in the northeastern states of the United States (e. g. Maryland). On the other hand, there is no definite evidence so far of the distribution of the black-headed type in British Columbia and the Pacific states west of the Rockies (Washington, Oregon and Idaho). All the specimens (including exuviae) we obtained so far from the western states and British Columbia belonged to the 'mosaic type' or the red-headed type. The typical red-headed type, however, seems to be distributed around the southern United States. The 'mosaic type' was also obtained from several eastern areas (Ontario, New Hampshire, Connecticut and Virginia) coexisting with the black-headed type.

Now we examine classic literature. There are many papers in which neither the color of the larval head nor the larval behavior were recorded definitely. Descriptions of color types in MORRIS (1963) and OLIVER (1964a) are considered to be precise. WARREN and TADIC (1970) presented a table indicating the occurrence of the black-headed and the red-headed types in 11 states with a supplementary note. They showed that the black-headed type was found from Washington, Mississippi, Illinois, Louisiana, Kansas, Maine, Nebraska and Arkansas, while the red-headed type came from Washington, Louisiana, Missouri, Texas, Kansas, Oklahoma, Arkansas and (in the supplementary note) Colorado, Utah, Wyoming, South Dakota, Florida and Mississippi. There remains a doubt, however, how the 'mosaic type' might have been designated in their paper—either as the red-headed type or as the black-headed—because they didn't know that the third type existed. WARREN (personal communication) told us that the larvae from Washington were now considered to be the same as the larvae found by the senior author in Vancouver (He looked color photographs of these). The occurrence of the typical red-headed type in Arkansas, Louisiana and Oklahoma is sure, and, if we suppose that the color of larval heads of the 'mosaic type' becomes darker in northern parts as compared with that in southern areas (see later), the occurrence of the black-headed type in Mississippi and that of the red-headed type in Mississippi and Florida may be accepted¹. On the other hand, WARREN and TADIC's (1970) description of the black-headed type in Maine, Illinois and Nebraska was not necessarily for the true black-headed type; their collections possibly contained some 'mosaic type' larvae with the darker head. In Kansas, from where WARREN and TADIC described both the black-headed and the red-headed types, there may be three possibilities; that is, (1) coexistence of the 'mosaic type' and the red-headed type; (2) coexistence of the 'mosaic type' and the black-headed type; and (3) coexistence of the three types. The red-headed types from Colorado, Utah, Wyoming and South

¹ Prof. R. I. SAILER (personal communication) informed us that both the black-headed and the red-headed type were present in the vicinity of Gainesville, Florida.

Table 2. OCCURRENCE OF THREE 'TYPES' OF FALL WEBWORMS IN NORTH AMERICA^a

Locality	Old literature	MORRIS 1963	OLIVER 1964 a	WARREN and TADIC, 1970	Present paper
<i>Canada</i>					
Nova Scotia		B			B (Y. ITÔ, many)
New Brunswick		B ^b			B (Y. ITÔ, many)
Ontario					B & M (K. UMEYA, B-many)
Manitoba					B (H. R. WONG)
B. C. (Vancouver)					M (Y. ITÔ)
B. C. (near Victoria)					M (D. A. ROSS)
No information : New Foundland, Prince Edward Is., Quebec, Saskatchewan and Alberta.					
<i>U. S. A. East</i>					
Main				B/M	
N. Hampshire					M (S. Tojo)
Massachussetts	B (HARRIS, 1828)				B (S. Tojo)
Connecticut	B (SNODGRASS, 1923)				B & M (S. Tojo)
New Jersey	B (SMITH, 1905)				
Virginia					M (S. Tojo)
Maryland					B (Y. ITÔ, many)
Washington, D. C.					B (Y. ITÔ, many)
No information : Vermont, Rhode Island, New York, Delaware, Pennsylvania and West Virginia.					
<i>U. S. A. North and Middle</i>					
Ohio	M (BERGER, 1906)				
Indiana	M/R (SNODGRASS, 1923)				
Illinois				B/M	
South Dakota				M/R	
Montana				M/R	
Wyoming				M/R	
Nebraska				M/R	
Utah				M/R	R (DAVIS)
Colorado				M/R	
Kansas				R/M/B	
Missouri				M/R	
No information : Kentucky, Wisconsin, Iowa, and North Dakota.					
<i>U. S. A. South</i>					
Georgia		R & B			
Florida				R	R & B (R. I. SAILER)
Mississippi				R & B	
Arkansas				R & B	R & B (Y. ITÔ ; S. Tojo)
Louisiana	R (SMITH, 1937)		R & B	R & B	
Oklahoma				R	R (S. Tojo)
Texas				R	
No information : North Carolina, South Carolina, Alabama, Tennessee, New Mexico and Arizona.					
<i>U. S. A. West of Rocky</i>					
Washington				M ^c	M (G. TAMAKI, many)
Oregon					M (L. O. WARREN)
Idaho					R & M (R. W. STARK)
No information : Nevada and California.					

^a The words 'south', 'east', etc. of the United States are not necessarily identical with those in common usage. B/M etc. mean B or M etc.

^b Two colonies among several hundreds contained larvae with 'brownish heads'.

^c L. O. WARREN (personal communication). (See text).

Dakota could contain the 'mosaic type.'

HARRIS (1828) wrote that the heads of larvae were black in Massachusetts. In Ohio, BERGER (1906) observed that fall webworms made a large nest-web at the bottom of the tree trunk and moved during the night. He also noted the composition of color types of larvae as 10 black-headed and 8 brown-headed (containing 2 'dark brown', 4 'brown' and 2 'light brown'). Most probably, BERGER observed the 'mosaic type.' But there is some possibility that BERGER's observation (as well as some of UMEYA's) was made on a hybrid colony. Readers should consult the Discussion.

SMITH (1905) described the larval color and the behavior in New Jersey, suggesting his fall webworms were the black-headed type. SNODGRASS (1923) described the morphology and larval behavior in Indiana and Connecticut. According to his description, the colony observed in Indianapolis might be the 'mosaic type' or the red-headed type, as he wrote that the large larva hides in a large compact web and fed outside it at night. On the other hand, he wrote that the larvae observed in Connecticut fed inside the web and had black heads.

NEWCOMER (1933) described the fall webworm in the Pacific Northwest. His description and a photograph of the nest-web suggests that at least some of his larvae were the 'mosaic type' or the red-headed type. SMITH's (1937) description of the larvae from Louisiana is considered to be that of the red-headed type.

Although a number of authors (BETHUNE, 1870 in Ontario; McMILLAN, 1888 and BRUNER, 1893 in Nebraska; HERRICK, 1935 in New York; SANDERSON, 1902 in Delaware and RILEY, 1871 in Missouri) wrote that their fall webworms had black heads, some of these authors possibly treated the 'mosaic type.' But it must be noted

Fig. 2. Geographical distribution of three types of the fall webworm in North America. Solid circles mean certificated occurrence of the black-headed type while shaded circles the 'mosaic type' and hollow circles the red-headed type. Curves are tentative distribution range of the three types.

that no person reported the black-headed larvae from the Pacific states and British Columbia.

From the foregoing account, it can be safely said that the black-headed type is found from the eastern half of the northernmost part of the distribution range to the Mexican Gulf, the red-headed type in the southern United States (and possibly in Mexico), and the 'mosaic type' in the northern part of the distribution range of the red-headed type, including the Pacific coast. Only the 'mosaic type' is found west of the Rockies. There is no precise information on the distribution of three types in the central prairie, but the occurrence of the black-headed type in Manitoba suggests that this type is distributed from the Atlantic coast to the Rockies, irrespective of the latitude. The red-headed type may be distributed in the southern part of the prairie, as we found this type from Utah. A possible distribution map of the three types is shown in Fig. 2.

DISCUSSION

Relationships among three types

A summary of the characters of the three types mentioned in the earlier and the present paper is shown in Table 3. As has been reported by ITÔ and WARREN (1973), the black-headed type and the typical red-headed type are sympatric in the southern states, and there are definite distinctions of the color and behavior between the two. These two are distinct entities.

There may be four possible explanations of the status of the 'mosaic type.' This type can be: (1) natural hybrid between the black-headed and the red-headed type; (2) a light colored population within the range of variation of the black-headed type; (3) a dark colored population within the range of variation of the red-headed type, or (4) a third entity.

The first hypothesis is abandoned, at least for areas west of the Rockies, because all the 7 colonies from Vancouver, 4 colonies from Victoria, 6 colonies from Washington, and 1 colony from Oregon are the 'mosaic type,' and because of a complete lack of reports on the occurrence of the black-headed type in the Pacific area. If we should find the 'mosaic type' from eastern areas only we should consider that this type might

Table 3. SUMMARY OF THE CHARACTERS OF THREE TYPES OF THE FALL WEBWORM.

Color of larval head	Preferred host	Larvae hide in nest web till:	Daily rhythm of feeding	Wing maculation
Black	Rosaceae <i>Cornus</i> <i>Diospyros</i> Salicaceae Moraceae	5th instar	every time	At least some of overwintered males are maculate
'Mosaic'	Rosaceae <i>Betula</i> spp.	last instar	nocturnal	Immaculate (may be univoltine)
Red	Juglanaceae (pecans & black walnut) <i>Diospyros</i>	last instar	nocturnal	Believed to be immaculate even in overwintered generation

be a hybrid. However, absence of the black-headed type in Pacific areas is a strong circumstantial evidence that the 'mosaic type' should not be a hybrid. This does not necessarily mean that there is no chance of natural hybridization in eastern states where the black-headed type occurs. It may be considered that the black-headed type have originated in an area east of the Rockies and never crossed this barrier.

We have some larval specimens of which the heads seem to be almost completely black but their behavior is known to be similar to that of the 'mosaic type'. But there is little possibility of the second hypothesis, because of the consistent difference in the behavior pattern of the two. Also the color of heads of the dark form of 'mosaic type' was different from true black when we examine the specimens carefully (see Descriptions).

In regard to the possibility of the 3rd hypothesis, it must be noted that the larval heads of the 'mosaic type' from the cooler parts of its distribution (Ontario, New Hampshire and Massachusetts) are near black and those from the warmer parts (Oregon and Idaho) are near uniformly red. Their behavior pattern is rather homogeneous throughout their distribution (East and West), and there is no definite difference from that of the typical red-headed larvae except two points; that is, (1) the nest-webs of larvae in cooler places are somewhat rough as compared with the very compact nest in the warmer places, and (2) species range of host plants is different. The two can be connected with intermediate forms, for example specimens found in Idaho. Thus it is possible that the 'mosaic type' is a darker, northern form of the red-headed type. It may be better to call these two types by a new term, such as the '*Malacosoma* type,' in place of the 'red-headed,' 'orange,' or 'mosaic' type.

As ITÔ and WARREN (1973) stated, the larvae of the red-headed type feed at night and hide in a dark place under the compact webs during daytime. This behavior pattern reduces the attack by natural enemies such as *Polistes* wasps and raises the survival rate during the larval stage as compared with the black-headed type (OLIVER, 1964). The light color of the head capsule of the red-headed type is possibly an adaptation related to the habit of hiding under the compact web, because it makes easy for perception of the photoperiod in a dark place. In addition, hiding in the web by day may avoid excessive heating outside in the south, while in the north, darker colors if linked with day habits, may help to keep body temperature up for feeding. The nocturnalism of the *Malacosoma* type may be disadvantageous in the north, where night temperatures fall much lower than in the south. Thus the black-headed type could be distributed to the north while the density of the *Malacosoma* type is higher in southern United States where natural enemies are more numerous than in the north.

There is not enough evidence to explain the mechanism of the divergence and isolation between the two. However, as the crossing between the two gave viable progeny (ITÔ and WARREN, 1973) and there is no definite distinction in the morphology of the two (HATTORI and ITÔ, 1973), it can be assumed that the divergence of an ancient stock into two types have taken place rather recently, possibly during the glacial period. What mechanism could isolate two populations despite absence of the ocean? Among many possibilities, the discontinuity of deciduous broad leaved forests of northeastern coast of Mexican Gulf (especially Florida Peninsula) from those of western Texas, Mexico or Pacific coast during the glacial period might be most important.

Specific status

It has been suggested that the fall webworm can be divided into two distinct entities, the black-headed and the *Malacosoma* type. HATTORI and ITÔ (1973) showed that all the morphological characters of the two, except larval color, were overlapping, but the male genitalia of *Malacosoma* type had different allometric constants from the black-headed type. Modes of the distributions of some characters of genitalia are also significantly different, while the distributions are overlapping (HATTORI and ITÔ, 1973; WILSON and WARREN, 1973). Although there is no morphological key-character for the identification of individual specimens, the behavior is consistently different between the two. We can easily identify their type by observation of the larval behavior.

ITÔ and WARREN's (1973) findings of the successful hybridization does not mean that the two necessarily interbreed in the field. Difference in major hosts and in seasonal life cycles (OLIVER, 1964a; WARREN and TADIC, 1970; ITÔ and WARREN, 1973) can isolate them, though not so completely. According to HIDAHA (1972), the mating behavior of the black-headed type consists of 4-phased sequence; that is (1) random flight of males coincided with the time of sex pheromone release by females, (2) searching flight by males which enter in the 'effective sphere' of the sex pheromone, (3) male's approach to the female guided by visual stimulus ('white object with wings raised'), and (4) recognition of the female by antennae based possibly on contact-chemical stimulus. As ITÔ and WARREN's crossing experiment was made in a small ice-cream cup, only the 4th phase could be effective. Thus there may also be isolating mechanisms acting in field, such as a slight difference in sex pheromone, which could make natural interbreeding impossible. This is an attractive subject for the future study.

There have been discussions concerning the specific status of *Hyphantria cunea* (DRURY) and *H. textor* (HARRIS) (for historical accounts the readers should consult WARREN and TADIC, 1970). In the classic literature, the moths with maculate wings were designated as *H. cunea* and the immaculate ones as *H. textor*, as HARRIS (1841) described the moth having immaculate white wings. Since MORRIS (1963) demonstrated that both forms could be obtained reciprocally, and that the intensity of maculation is the subject of climatic conditions, most authors recognized *H. cunea* as the only valid name. It must be noted, however, that LYMAN (1902) wrote that the wings of *H. cunea* males vary from immaculate to heavily maculate, but those of *H. textor* are *always* immaculate.

In the black-headed type, the summer moths are, irrespective of sex, usually immaculate. In male moths from the overwintered generation there are always some individuals which have maculate wings. The wing maculation is principally determined by a cool temperature during the pupal stage (JASSIC and MACKO, 1961). The percentage of maculate individuals among males varies according to the locality. Thus about 30 percent of males from the overwintered generation in Yugoslavia had maculate wings (PETRIK, 1956), but 96.4 percent of overwintered males in Japan are maculated (HASEGAWA and ITÔ, 1967). The percentage of maculate moths is low in the Canadian black-headed type (univoltine population) but the wing maculation is consistently seen in at least a small percentage of the males (MORRIS, 1963).

All the males which are known to be from our *Malacosoma* type larvae were, interestingly, immaculate form. A male from Victoria was immaculate even those

from the overwintered generation. All 9 males from British Columbia (univoltine area), which were lent from the Museum of the Department of Agriculture, Ottawa, Canada by the courtesy of Dr. HARDWICK were also immaculate. All of more than dozens of males of the typical red-headed type of the overwintered generation collected in Arkansas and reared by the senior (1970) and the junior (1973) authors were the immaculate form. In addition, all of several males emerged from overwintered pupae remaining in the nest-web of the *Malacosoma* type are immaculate. Thus we have no record of maculation of wings of the *Malacosoma* type except some specimens obtained by UMEYA from populations of Ontario, and NEWCOMER's (1933) description on the maculate moths from the Pacific states (he didn't mention the name of the state). WARREN and TADIC (1970) examined 550 specimens of fall webworm moths in the American Museum of Natural History, New York. It is notable that specimens from Pacific states, that is, British Columbia, California, New Mexico and Utah were immaculate only. Contrary, both the maculate and immaculate moths were found in specimens from states where we know the two types occur. These are Florida, Georgia, Maine, Mississippi, New York and Pennsylvania. Although the moths examined by them do not necessarily involve overwintered males, this contrast is remarkable. Dr. J. YUKAWA kindly examined all the specimens of *H. cunea* and '*H. textor*' in the British Museum (Natural History) and wrote us that all of 4 specimens from Utah were immaculate despite these were collected in spring. (He could not find other moth from overwintered generation in Pacific States.)

Thus a question has arisen whether or not the moths of *Malacosoma* type are always immaculate as stated by LYMAN (1902) for *H. textor*.¹ It can be concluded that, before the determination of the specific status of this type, it is necessary to check the wing-maculation of a number of overwintered male moths reared from the *Malacosoma* type larvae collected in different parts of North America, as well as to make field experiments on the sexual behavior. On the other hand, the black-headed type can undoubtedly be treated under the name of *H. cunea*.

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¹ HARRIS (1941) wrote that the head of larvae of his *H. textor* was black, but this statement does not necessarily mean that his moths are black-headed type, because the larval head of northern populations of the *Malacosoma* type was sometimes nearly black.

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