ISOLATION MECHANISMS IN POPULATIONS OF *HYALOPHORA* (SATURNIIDÆ)

by ROBERT D. WEAST

As is generally known, species comprising the large moths of the subgenus *Hyalophora* (=*Platysamia,* see MICHENER'S revision 1952), freely attract and interbreed when they come into contact with one another. The several species that I have worked with are *H. euryalus* Bdv. of the West Coast, *H. gloveri* Strecker of the Rocky Mountains, *H. cecropia* Linné east of the Great Plains, and local colonies of *H. columbia* J. B. Smith in Wisconsin, Michigan, and Maine.

In certain areas where two of the species make contact several things can happen: 1. the species intergrade, forming a fertile, self perpetuating race, *e.g., kasloensis* Cockerell occuring in parts of Idaho and Montana where *H. gloveri* and *euryalus* merge; 2. the two species remain pure, with occasional hybrids appearing, but having no noticeable effect on either species, *e.g., H. columbia* and *cecropia* in local areas; 3. one species replaces the other, *e.g., H. cecropia* replaces *gloveri* in certain areas where they make contact. In the early thirties W. R. SWEADNER did extensive work with this genus which culminated with his treatise "Hybridization and the phylogeny of the genus *Platysamia*" (1937). This intensive study revealed a good deal of information on the relationship of the several species and races plus their habitats, points of contact, and their hybridization.

To investigate the reasons for the above occuring as they do, I have for the past ten years been engaged in rearing the hybrids, backcrosses, and the pure species. The crosses have been made in the field by tieing females of one species in the territory of another, or by securing cocoons from various parts of the country and having the adults cage mate. The fact that all species of this subgenus fly during the same hours and that they easily mate and oviposit in captivity greatly facilitates their study.

I have noticed no significant differences in the hardiness of hybrid larvæ from that of the pure species. When highly selective feeders like *columbia, euryalus* or *gloveri* are crossed with *cecropia,* their range of acceptable foods is increased, but never to the wide selection of pure *cecropia.* When two restricted feeders like *euryalus* and *gloveri* are crossed, their food acceptance remains restricted to the acceptable foods of either pure species. The triple cross *gloveri* ♂ × *euryalus* ♀ × *cecropia* ♀ has a very limited food acceptance, even less than the *euryalus* × *cecropia.*

F_1 hybrid males are normally fertile and can be backcrossed to a pure parent species. F_2 backcrossed males are equally fertile. Surprisingly, the crossing of the three species just mentioned was fertile. Five such matings were secured in 1959 and thirty four large cocoons were reared. In 1960 I shall cross these males back to pure *gloveri, euryalus,* and *cecropia* females. If I am for-

tunate in collecting female Columbia cocoons in Wisconsin this winter they shall also be mated to the 3× males, attempting a four-species hybrid. It will be interesting to determine what amount of backcrossing will finally produce viable females, as they are normally barren.

A great deal of variability exists regarding the four species to hybridize. These are fertility and physiological differences, depending on the populations involved, for it is clearly one or the other, and sometimes it appears to be both. Here are a few examples as they occur, or could occur in nature. *H. cecropia* females mated to Arizona *gloveri* (Madera Canyon, Pima Co.) behave as if they weren't mated. They lay few eggs and continue to "send" during subsequent flight periods. Nevertheless, the few eggs laid by the five females in the experiment produced hybrid larvæ. In Helena, Montana, the same cross produces very low fertility, but the females will oviposit completely. *H. gloveri* from the Salt Lake City, Utah, area is more fertile with *cecropia* but still less than 50%. By contrast, *gloveri* from Wyoming are highly fertile with *cecropia*. The reverse pairing is equally fertile. *H. euryalus* females are highly fertile with *cecropia* males, but for some unknown reason they often die during or shortly after copulation. The reverse pairing is usually sterile, but I have had two such matings with high fertility. California *euryalus* females mated to northern *gloveri* produce good fertility, but like other hybrids only males are fertile. The fertile, self-reproducing form *kaslœnsis* occuring where the two species naturally meet in the north is the result of many years of contact, unlike the sudden meeting of two pure species. *Columbia* and *cecropia* occupy the same areas in United States where *columbia* occurs. Fertility is high when the two interbreed. The hybrid cocoons and adults are not exceptionally rare.

I believe several factors take place, singly or in combination, when two species occur in the same habitat. These reasons explain, in part, the extent of population isolation or lack of it in this subgenus: 1) females, upon being mated to another species' male, may re-mate with additional males until one of her own species mates with her; 2) physiological differences may prevent successful copulation even though the female may completely oviposit; 3) fertility of many pairings is low or absent; 4) cross-mated females still seek out and oviposit on plants of their own preference, and thus hybrid larvæ may refuse to eat, or thrive on what is available; 5) hybrid larvæ comprise but a small percentage of the total larval population, and the odds at survival to the adult stage are low; 6) 50% of the hybrid adults are barren females, and the remaining males are very few compared to the total number of pure males; for that reason, backcrossing is a rare occurance.

I am convinced that saturniid moths cannot occur at rare levels in their habitat, due to their short adult life and specialized breeding patterns. The lethal pressures of parasites and birds require that they maintain high numbers scattered over a considerable breeding area. In the light of this, hybrid influence and the drain of population numbers due to useless crossbreeding is, under most circumstances, not a major factor in survival. If, however, one

species should be locally reduced to a low density, and should males of an adjacent species invade the territory (the wind commonly carries males well over ten miles) there might not be enough pure matings to withstand normal pressures. The less common of the two species would be replaced by the other.

Considerable evidence has been accumulated regarding the flight distance of males. Some good evidence is also available on oviposition flights of females. This information is important to a better understanding of the species' ability to invade new breeding areas.

It appears quite conclusive that males can detect females up to a distance of a half mile. Through the use of marked males returns are very high within those limits, but drop sharply at greater distances. In Texas I have seen a male *Eupackardia calleta* Westwood appear as a speck in the distance and fly directly to a female in my yard.

Although the actual detecting distance may be something like a half mile, males undoubtedly cover a much greater territory in random flights, being carried predominately over the greater distances by the wind. Here in Des Moines I can expect several hundred male *cecropia* to arrive at my breeding cage in the course of the flight season. One night alone 43 males were attracted. It can be presumed that for every male that arrived, a female emerged in the habitat, since the sex ratio is about 50-50. Thus, if a season total of 300 males arrive, an additional 300 females are to be found throughout the area. There simply are not 600 wild cocoons to be found within a two or three mile radius of my breeding cage. Careful cocoon collecting techniques reveal the density of living cocoons to be much less. The only explanation appears to be that the males have come from distances of many miles, perhaps fifteen miles.

To further illustrate this point, a closely related species, *H.* (*Callosamia*) *promethea* Drury, maintains a large colony in Milwaukee, Wisconsin. Fourteen miles west in Waukesha the species definitely does not breed. *H. promethea* females taken to Waukesha invariably attract old, frayed males, in all probability from the Milwaukee area.

On the Arizona desert I marked twelve male *cecropia* and released them at half mile intervals from a caged female. Half of these males returned; the last to arrive came in three days late from the five-and-one-half mile distance. There were no other Saturniidæ species to interfere with this experiment on the desert.

To see that males can easily traverse many miles, one has only to observe the day-flying males of *E. calleta* and *H. promethea* in open country. Upon taking wing they often quickly disappear from sight, their course being determined to a good extent by the wind. It is not unreasonable to assume that under certain conditions they can travel great distances. Should they come somewhere within the half mile attracting distance of a female they will, under favorable atmospheric and wind conditions, locate her.

Heavily laden females cannot fly great distances, although marked females have been taken at light as far as a half mile from the point of release. They had the full complement of eggs. It is good that a female cannot leave the successful niche at first, since chances of survival of the larvæ are good

there — she made it. Females ordinarily commence laying within two city blocks from the point of emergence. After having completed most of their egg-laying they become stronger flyers and can undoubtedly travel several miles.

It appears then, that this genus of Saturniidæ has a quite plastic mobility, not being the sluggish flyers that they are commonly believed to be. They can overcome natural barriers of several miles, and two related species might make contact even though their respective habitats may be separated by many miles.

References

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In accordance with a decision of the 13th International Congress of Zoology, 1948, public notice is hereby given of the possible use by the International Commission on Zoological Nomenclature of its plenary powers in connection with the following case, full details of which will be found in *Bulletin of Zoological Nomenclature,* Vol. 17, Parts 6/8, published on 8 April 1960:

Validation of the specific name *dardanus* Brown, 1776 (*Papilio*) (Class Insecta, Order Lepidoptera). Z.N.(S)1403.

Any zoologist who wishes to comment on this case should do so in writing, and in duplicate, as soon as possible, and in any case before 8 October 1960. Each comment should bear the reference number of the case in question. Comments received early enough will be published in the *Bulletin.* Those received too late for publication will, if received before 8 October 1960, be brought to the attention of the Commission at the time of commencement of voting.

All communications on the above subject should be addressed as follows:

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