

OBSERVATIONS ON THE HOST PLANT ADAPTATION OF *BUSSEOLA FUSCA* (LEPIDOPTERA: NOCTUIDAE) IN NIGERIA¹

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Abstract. — The change of diets in the northern and the southwestern populations of *Busseola fusca* (Fuller) in Nigeria produced high mortality, unbalanced sex ratio, and sterility. When the two populations were crossed, the hybrid adults did not mate with each other, although the gonads of both sexes were mature. These observations seem to indicate that adaptation to different diets is leading to genetic differences in this species.

In May 1980, while investigating the food plants of *Busseola fusca* (Fuller) in Nigeria, I tried to rear this insect on the stems of *Sorghum bicolor* brought to Ibadan (southwest) from Zaria (north). This rearing produced unexpected results; not only was the larval mortality very high, but also the adults were sterile. In my subsequent visit to Zaria, I learned that northern *B. fusca* developed perfectly normally on the diet of sorghum stems, which later proved to be the case in my own laboratory in Ibadan. These findings made me wonder if the northern and southwestern populations actually belonged to the same species. It seemed to me that they represented at least two different races or subspecies. Not only have the investigators of this insect in Nigeria (Harris, 1962; Usua, 1970; Adesiyun, personal communication) treated it as a single species, but they have not even suggested the possible existence of geographical races. Moreover, *B. fusca* has been described as a major pest of both maize and sorghum (Swaine, 1957; Hill, 1975).

This paper presents the results of a preliminary study on the adaptation of *B. fusca* to its major host plants in the two geographical areas of Nigeria mentioned above.

GEOGRAPHICAL DISTRIBUTION

Busseola fusca is said to occur throughout Africa, south of the Sahara (Swaine, 1957; Hill, 1975). In Nigeria, it is found abundantly in and around the northern towns of Kano, Zaria, and Kaduna where the climate is semi-arid, and, for the last few thousand years, the major crop has been *Sorghum bicolor* which thrives in that environment. *Zea mays*, introduced in the 15th century, is occasionally planted, but the practice is limited due to irrigation difficulties and the preference

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of sorghum to maize as food by the local inhabitants. *Busseola fusca* is the major pest of sorghum throughout the north.

Busseola fusca populations become more infrequent toward the south so that in the neighborhood of Ibadan, some 360 miles to the southwest from Zaria, it occupies at most 9% of the total maize stemborer populations. In the humid southwest, where *Z. mays* is the main crop and where sorghum is seldom cultivated, the major pests consist of *Eldana saccharina* (Walker) (Pyralidae) (51%) followed by *Sesamia calamistis* (Hamps) (Noctuidae) (30%); the rest are composed of four minor species including *B. fusca* (Kaufman, unpublished data). Maize is also the major crop in the southeast where the climate is even more humid; the occurrence of *B. fusca* in this area is infrequent, as 92% of the maize stemborers are *S. calamistis*.

MATERIALS AND METHODS

About 50 prepupae and pupae of *Busseola fusca* were extracted from the stems of sorghum planted at Amado Bello University's experimental farm in Zaria and were brought to Ibadan. Adults that emerged from the pupae were put into wooden-frame, wire-gauze cages ($30 \times 30 \times 30$ cm), each provided with several stems of rice placed in a jar of water for oviposition. Eggs were isolated in petri dishes until they were about to hatch, then half of them were wrapped in soft terminal leaves of young sorghum (planted in the experimental plots of IITA from the seeds brought back from the north), while the rest were enveloped in those of young maize. Both groups were left in this state with no further handling for a week; after one week the hatchlings had grown to 6–7 mm long. Subsequently, 200 of a few thousand larvae were randomly taken from each group and reared separately in two groups of Kilner jars (diam.: 8 cm; height: 15 cm) containing stems of sorghum and maize, respectively. Since *B. fusca* attacks normally young plants, only the stems of preflower food plants, cut into 3 cm long pieces were used for convenience.

In Ibadan, the larvae of *B. fusca* were obtained from the stems of maize planted at the IITA experimental farm. They were fed with young maize stems until pupation and the eggs from the emerged adults were processed in the same way as F1 eggs of Zaria *B. fusca* mentioned above. Initially, therefore, there were four groups of F1 larvae, each consisting of 200 individuals; of these, two groups belonged to the northern and two groups to the southwestern *B. fusca*. Each of the geographical groups was further divided into two dietary units, one with sorghum, and the other with maize (Table 1). The food plants were changed every three days and the body length of the larvae and the number of deaths were recorded at each time. When the larvae stopped feeding, they were removed to other Kilner jars with layers of paper towel for pupation. Pupae were individually weighed using a Roller-Smith precision balance.

For cross breeding, four identical wire-gauze cages described above were set up. Into each of these, ten newly emerged southwestern females and the same number of newly emerged northern males were released simultaneously. Eggs were collected daily from the rice stalks placed in the cages, counted, and put into petri dishes until they were close to hatching. Then, as in the dietary experiments already explained, half of the eggs were wrapped in maize leaves and the other half in sorghum leaves for one week, followed by the rearing of 200 randomly taken larvae from each group on two dietary units of sorghum and maize. Hybrid

adults were housed in the cages mentioned, and the dead adults of both sexes were dissected within a few hours of death for spermatozoa and spermatophores.

The experiments described above were first conducted in 1980 and were repeated in 1981. The total number of *B. fusca* larvae subjected to the dietary analysis was 2000, while the number of adults used for the cross breeding experiments totaled 160.

Three generations descended from the F1 hybrids of 1980, and these were reared under similar conditions as to the number of larvae in the beginning; the dietary units and breeding methods were also the same. No backcross could be attempted until May, 1981, since the three generations were bred in the dry season (November to April) during which southwestern *B. fusca* was in diapause. In this backcross, 20 F4 males and 20 southwestern females that developed from diapaused larvae were divided equally in two cages for mating and oviposition. The larvae obtained from this cross were reared on maize only, since sorghum was not yet available in Ibadan. The experiment had to be terminated at the end of June, 1981.

RESULTS

When the young larvae of northern *B. fusca* were offered maize stems, they accepted the food plant without hesitation, developed faster, and the pupae were heavier than those reared simultaneously on the stems of sorghum. However, while the sex ratio of the sorghum-fed group was about equal, that of the maize-fed group consisted predominantly of males. Nonetheless, the F1 adults that developed from the maize diet mated and produced viable eggs. The F2 generation from these eggs yielded an identical or similar sex ratio as in the F1 (Table 1), but the adults were sterile; no mating flight (Kaufmann, unpublished data) took place, sexes were not attracted to each other, and the dissection of the females after death showed that their ovaries were very small with no developed eggs and their bursa copulatrix was empty of spermatophores. Likewise, there were no free spermatozoa in males.

Conversely, when the young larvae of southwestern *B. fusca* were given sorghum stems, the larvae did not begin feeding until starved; development was markedly slow; mortality was high (the great majority of the larvae died during their early instars); their sex ratio was unbalanced; and the gonads of both sexes were immature with the same sexual indifference described above on the northern *B. fusca* (Table 1). Those fed with maize, on the other hand, grew twice as fast; were much heavier in pupal weight; produced an equal sex ratio; adults mated normally, each with 1–5 spermatophores; and females laid viable eggs (Table 1).

The mating between southwestern females and northern males took place readily, and the resulting eggs gave rise to the F1 hybrid larvae. These larvae fed willingly on sorghum as well as on maize. Forty-three (1980) and 40% (1981) of the sorghum group and 50% (1980) and 55% (1981) of the maize group developed into the last-instar larvae which were as large and as vigorous as their southwestern parent, the more vigorous of the two parents. However, these seemingly healthy larvae died shortly before pupation so that only 17% (1980) and 14% (1981) of the original number of the first group and 22% (1980) and 20% (1981) of that of the second group actually pupated (Table 1). The emerged adults of both groups did not mate with each other, although dissection showed that their ovaries were large with mature eggs and vesicula seminales contained free spermatozoa.

Table 1. Effects of sorghum (S) and maize (M) on the development of the northern and southwestern populations of *Busseola fusca* and their F1 hybrids (avg. temp.: 23°C; R.H.: 76%).

	Northern <i>B. fusca</i>						Southwestern <i>B. fusca</i>						N-SW cross					
	S			M			S			M			S			F1		
	F1			F1			F1			F1			F1			F1		
	1980	1981		1980	1981		1980	1981		1980	1981		1980	1981		1980	1981	
Incubation period (days)	8	8		8	8		8	8		8	8		8	8		8	8	
Larval period (days)	37	35		25	23		25	24		28	25		35	37		33	31	
Larval mortality (%)	58	61		60	55		87	73		85	51		83	88		78	80	
Pupal period (days)	14	14		14	13		12	14		13	14		15	14		14	14	
Pupal mortality (%)	8	10		3	5		25	6		23	4		10	9		8	10	
Pupal weight (mg)	126	131		195	190		128	195		124	200		149	143		193	195	
Sex ratio (% ♀)	52	31		17	18		33	15		30	53		40	38		30	32	
Fecundity (no. fertilized eggs/♀)	108	127		281	296		0	0		0	396		0	0		0	0	
Adult life span (days)	3	4		5	5		3	5		3	7		5	5		6	6	

Table 2. Effects of sorghum (S) and maize (M) on the descendants of F1 hybrids and the result of backcross of *Busseola fusca* (avg. temp.: 23°C; R.H.: 76%).

	F2 (Parthenogenetic)		F3 (Sexual)		F4 (Sexual)		Backcross (F4 ♂ × SW ♀)	
	S	M	S	M	S	M	S	M
Incubation period (days)	8	8	7	7	7	7	—	7
Larval period (days)	36	33	33	33	23	21	—	21
Larval mortality (%)	99.5	86.0	99.5	93.5	100	82	—	36
Pupal period (days)	14	12	14	14	—	13	—	13
Pupal mortality (%)	0	13	0	7	—	2	—	8
Pupal weight (mg)	113	190	188	196	—	203	—	225
Sex ratio (% ♀)	1 ♀	30	1 ♂	38	—	39	—	63
Fecundity (no. eggs/♀)	0	456	—	392	—	134	—	396
Egg viability (%)	—	60	—	26	—	30	—	14
No. eclosed larvae	—	1970	—	469	—	563	—	4102
Adult life span (days)	7	7	7	6	—	6	—	6

The F1 hybrid females, however, laid unfertilized eggs (221/♀) 30% of which hatched, giving rise to a parthenogenetic F2 generation (Table 2). At this point, mention should be made on parthenogenesis in this species, since this phenomenon in Noctuidae has never been reported. In absence of males, *B. fusca* often produced unfertilized eggs in captivity. The number of these eggs per female was much smaller ($\frac{1}{2}$ – $\frac{1}{3}$) than that of bisexual eggs and only about 30% hatched. The parthenogenetic eggs have the following main characteristics: (1) They do not change color shortly before hatching, when they become dark, while bisexual eggs turn from pale yellow to pink after two days, then become dark at the final stage; (2) very high larval mortality (avg. 90%) occurs shortly before pupation, instead of during the first two instars as in bisexually produced larvae; and (3) both sexes are produced. Parthenogenesis in *B. fusca* was first observed in 1979; of 283 unisexual eggs, 85 hatched and only four larvae survived to pupate, giving rise to two males and two females.

The parthenogenetic F2 generation resulted in a F3 bisexual generation and since parthenogenesis in this species yields both sexes as just mentioned, the individuals of this group mated with each other and created another bisexual generation of F4 (Table 2). Two features characterized these abnormal generations, an extremely high level of larval mortality, especially in sorghum-fed groups, and an unbalanced sex ratio.

The F4 males were backcrossed to southwestern females that had emerged in May, 1981 after diapause. As shown in Table 2, larval mortality was significantly less than the previous generations (F2–F4) and the ratio of females rose to 63%. All these females mated, each harboring 1–5 (avg. 2) spermatophores; similarly, all the males contained free spermatozoa. Although only 14% of the fertilized eggs hatched, this backcross showed sufficient “recovery” as to the size of larval population (Table 2).

DISCUSSION

The change in food plants between the northern and the southwestern populations of *B. fusca* resulting in uneven sex ratio and sterility suggests that genetic

differences may be developing as a result of evolutionary adaptation to different diets: northern population to sorghum and southwestern population to maize.

Morphologically, the northern type is a little smaller in size and has paler forewings than the southwestern type. Otherwise, the two are indistinguishable, since no differences were found in copulatory apparatus. Moreover, the size difference seems to depend on the nutritional value of sorghum and maize, for when northerners were fed with maize, the resulting adults were as large as southwesterners. Paler wing color may be an adaptation to the arid environment of northern Nigeria. Physiologically, however, the southwestern type is more active, lays a larger number of eggs, and lives longer than the northern type (Table 1). Especially interesting is the fact that the diapause in the southwestern population seems obligatory (Kaufmann, unpublished data), while that in the northern population is facultative, as non-diapausing larvae could be bred merely by providing them with fresh, green food during the dry season. Similar observations on dry period feeding have been reported by Swaine (1957) and Smithers (1960) in Tanzania and Rhodesia, respectively.

That mating between the two populations took place readily and that many hybrids not only survived, but also were as vigorous as the parental stocks until pupation, indicate that the process of genetic differences may have begun rather recently, say, during the past few hundred years after maize was introduced into West Africa from the Americas around the 15th century. I believe that the original host of *B. fusca* was sorghum, indigenous to West Africa, and that some have migrated to the southwest after the introduction of maize, eventually becoming established in the new host plant to the point of no return. However, the restoration of vigor and size of larval population as the result of backcross is suggestive of an existence of a genetically intermediate form somewhere between Zaria and Ibadan where both sorghum and maize may be available. Also, the experimented crosses were exclusively between northern males and southwestern females; limited time did not allow work on the reciprocal crosses, namely between northern females and southwestern males. Therefore, until further investigations of this sort are completed, final conclusions as to the suggested genetic differences derived from host plant adaptations remain unanswered.

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