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Polymorphism in the African Edible Grasshopper *Homorocoryphus nitidulus* (Tettigonoidea Conocephalidea) revisited

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Introduction

A paper by D. F. OWEN (1965) in these proceedings discussed swarming and polymorphism in *H. nitidulus* and established that the phenomenon in this orthopteran was markedly different from that which occurs in locusts. Colour polymorphism decidedly is genetically determined with little or no difference observed between swarming and non-swarming forms. OWEN recognised five distinct sympatric colour forms but since then he has added a sixth one (OWEN, 1965 b). At present the six sympatric colour forms are: (1) green, (2) brown, (3) green-with-purple stripes, (4) green-with-purple head, (5) brown-with-purple head, and (6) brown-with-purple stripes. OWEN established that the forms were cryptic and that the colour combinations and the grasses in which the insects live could be ranked with a fair chance of certainty. The association of the brown form with males and the green with females was thought peculiar and difficult to explain.

Homorocoryphus nitidulus has formed the subject of other studies in our laboratory and in the course of these studies further observations have been made which may add to the analyses of polymorphism in this insect. It is the purpose of this paper to consider these observations.

Methods

Since it had already been established that swarming is correlated with the incidence of rain, collecting was restricted to the peak months of November–December and April–May but was carried on for two consecutive years, 1967 and 1968; all data in this paper are thus of swarming *H. nitidulus* only.

In an attempt to resolve the apparent mystery of differences in sex ratios between swarms, the data collected in 1967 was recorded first as population samples and then resolved into swarms. Collecting in 1968 was confined to population sampling in specified areas of Kampala and the populations were at least 1.5 km from each other. For comparative purposes the data discussed here refer to the swarming period November–December only.

Sex Ratio

In Tables 1 and 2 are the summarized data. Sex ratio computations were done in three directions. Comparisons between populations in Table 1 indicate no significant differences between the numbers of males and females for all populations except in samples 6 and 7 both of which have significantly more females than male. Since these two samples are part of the three populations which form the second swarm, it should not be surprising to find a significant difference between the swarms. The overall sex ratio in 3014 specimens collected is one male to 1.62 females, slightly higher but not significantly different from that recorded by OWEN. Comparisons in Table 2 indicate equal numbers of females and males in populations 1, 3 and 6. Population 2 has significantly more males than females

Table 1. Frequencies of colour forms in populations and swarms of *H. nitidulus* in 1967

Colour forms	Males							Females						
	Swarm 1, Nov 26—29				Swarm 2, Dec 3—6			Swarm 1, Nov 26—29				Swarm 2, Dec 3—6		
	Populations				Populations			Populations				Populations		
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
1	23	29	20	3	75	471	20	49	59	36	10	127	1,086	75
2	26	38	18	3	90	296	18	8	9	3	1	35	291	40
3	1	1	2	—	5	14	2	1	2	—	—	8	17	2
4	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Population totals	50	68	40	6	170	781	40	58	70	39	11	170	1,394	117
Swarm totals	164				991			178				1,681		

Table 2. Frequencies of colour forms in populations samples in swarms of *H. nitidulus* in 1968

Colour forms	Males							Females						
	Populations							Populations						
	1	2	3	4	5	6	Totals	1	2	3	4	5	6	Totals
1	106	241	27	124	11	5	514	177	272	78	286	6	10	829
2	145	365	74	140	31	13	768	60	98	35	100	2	3	298
3	8	13	2	11	1	0	35	8	12	3	17	1	—	41
4	—	0	—	0	—	1	1	—	—	—	—	—	—	0
5	—	4	—	1	—	—	5	—	2	—	3	—	—	5
6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Population totals	259	623	103	276	43	19	1,323	245	384	116	406	9	13	1,173

but the opposite is true for population 4. Population 5 has not been analysed as the numbers are small. The place is a top of a hill with poorer lighting than the surrounding areas; this might explain why the sample was so small, but the data of the previous year (population 7) showed definitely more females than males. The overall ratio of females to males does not deviate significantly from 1:1 in a collection of 2496 specimens. Thus it would be clear that whilst sex

ratios are normal in some populations in some of them one of the sexes predominates. Without knowledge of the genetic and ecological characteristics of the native populations of *H. nitidulus*, and without adequate understanding of the mechanisms prompting swarming, explanations for these differences in sex ratios will be still incomplete.

Colour Forms and Mating

Another puzzling observation has been the association of the two predominant colour forms green and brown with females and males, respectively. The greens constitute about 63 and the browns 34% of the population, leaving barely 3% to made up for the remaining four colour forms. Among the males there are, on the average 1.4 brown to one green but among the females there are 3.8 greens to one brown. These observations were noted with interest and aroused our curiosity about the possible role of colour polymorphism in mating. We therefore set out to observe as many copulating pairs as we could and Table 3 indicates that although this process is tedious and difficult, we collected and analyzed 117 mating pairs. As expected and because of the rarity of the colour forms 4, 5 and 6, these data covered only three forms.

Table 3. Mating frequencies by colour forms of *H. nitidulus*

♀ Colour forms	♂ Colour forms			Totals of mating pairs
	1	2	3	
1	24	44	1	69 (58.98)
2	16	26	1	43 (36.75)
3	1	4	—	5 (4.28)
Totals of mating pairs	41 (35.04)	74 (63.25)	2 (1.71)	117

A number of important points emerge from these data. Numbers in brackets are those of percentage frequency of mating types. In all the matings, a very significantly higher pairing occurs with the brown form as the male, with about 60% of the 63.25% overall frequency being a pairing of a green female and a brown male. Similarly, in all the matings with the green female as one of the partners, the greatest frequency was of the green-brown pairing. The other mating pairings expected to be frequent are green female – green male, brown female – green male and brown female – brown male matings. The data in Table 3 show these to occur in about equal frequencies. A final interesting observation concerns the appearance of green-with-purple-stripe female mating with the brown male. We recorded just over 4% of the observed pairings. If it is remembered that in more than 20,000 *H. nitidulus* observed no more than 3% represented colour forms 3, 4, 5 and 6, this figure of 4% is highly significant.

There are strong suggestions, that mating in *H. nitidulus* is not at all a hap-hazard, random occurrence but that the polymorphism which is present in the insect is made use of in the selection of mates. This should not at all be unexpected. If the occurrence of polymorphism is genetically determined it must be

genetically preserved. Repeated reference has been made of the association of the two predominant colours one with the female and the other with the male. That this situation can be taken advantage of ensures that heterogeneity is preserved.

H. nitidulus is difficult to study in the laboratory and no reports have yet appeared discussing laboratory breeding, although concerted efforts are being made. When data are forthcoming, a more definite statement about the maintenance of polymorphism would emerge. However, on the strength of these data it would appear that multiple alleles with varying degrees of dominance maintain the polymorphism.

General Observation

Whilst collecting from street lights, we were struck by one observation. A length of a street is normally supplied with a number of lights. It would therefore not be unreasonable to expect that on the days of the swarming, numbers would be randomly distributed on the lamp posts. What we saw was quite different; there were obvious concentrations at some lamp posts whilst others remained free of circling *H. nitidulus*. Moreover, in cases where it was possible to observe *H. nitidulus* forming around a lamp post, it appeared that a lamp post that had already attracted some of the insects tended to attract more and more until, during peak swarming, a swarm was so dense around a lamp post that motorists found difficulty in crossing the street.

We have also looked for *H. nitidulus* in Kenya, and whilst successful collections have been made of the non-swarming forms in grasses and shrubs, no swarming around city lights has been observed. It would appear that there are genetic differences between the low altitude and the high altitude forms of *H. nitidulus*.

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