Zeitschrift: Acta Tropica
Herausgeber: Schweizerisches Tropeninstitut (Basel)
Band: 22 (1965)
Heft: 1

Artikel: Miscellanea : Swarming and polymorphism in the African edible grasshopper, "Homorocoryphus nitidulus" (Tettigonioidea, Conocephalidae)
Autor: Owen, D.F.
DOI: https://doi.org/10.5169/seals-311259

Miscellanea.

Swarming and polymorphism in the African edible grasshopper, *Homorocoryphus nitidulus* (Tettigonioidea, Conocephalidae).

D. F. Owen.

Department of Zoology, Makerere College, University of East Africa, Kampala, Uganda.

Introduction.

Swarming behaviour in the Orthoptera has chiefly been studied in certain pest species of Acrididae; little attention has been paid to apparently similar phenomena in other groups. Among the tropical African Tettigonioidea, one species, *Homorocoryphus nitidulus* (Scopoli) (= *H. longipennis* [Redt.]), occurs periodically in great numbers. Like many alate Tettigonioidea, *H. nitidulus* is chiefly nocturnal and were it not attracted in immense numbers to lights its swarming behaviour would probably not often be observed. *H. nitidulus* is polymorphic, existing in a variety of distinct sympatric colour forms that are evidently not determined by direct environmental stimuli.

Little is known of the breeding areas, development of swarms, migratory behaviour, or indeed any other aspect of the biology of these grasshoppers. At Kampala, Uganda, the immature stages are occasionally seen, but most of the enormous numbers of adults that appear must have originated elsewhere. *H. nitidulus* appears to feed chiefly on flowers of tall grasses. Damage to crops has been reported (Chopard and Kevan, 1954).

My aim in this paper is to describe swarming behaviour at Kampala during the year October 1962-September 1963, and to analyse the distribution and relative frequency of the colour forms. Throughout the period, a 100-watt mercury vapour lamp was operated for the first three hours of the night about two or three times a week. The lamp was switched on every night during swarms. All the specimens that came to the light were collected except during swarms when a large random sample was obtained. During the year, 6,129 specimens were collected and classified by sex and colour.

Swarming.

Table 1 shows the occurrence of swarms at Kampala during the period of observations. Each of the swarms arrived suddenly, and, for a few consecutive nights during each, there must have been millions of grasshoppers in the area. Numbers were spectacular at each peak: thousands could be seen around every street light in the City. People collected them in bag-fulls and next day they could be bought in the market and obtained cooked in some restaurants. As shown in Table 1, swarming occurred six times during the year and at two periods: November-December and April-May. The species occurred in all other months of the year, except August, but numbers were low. According to local information November-December and April-May are the usual times of the year that swarms are expected.

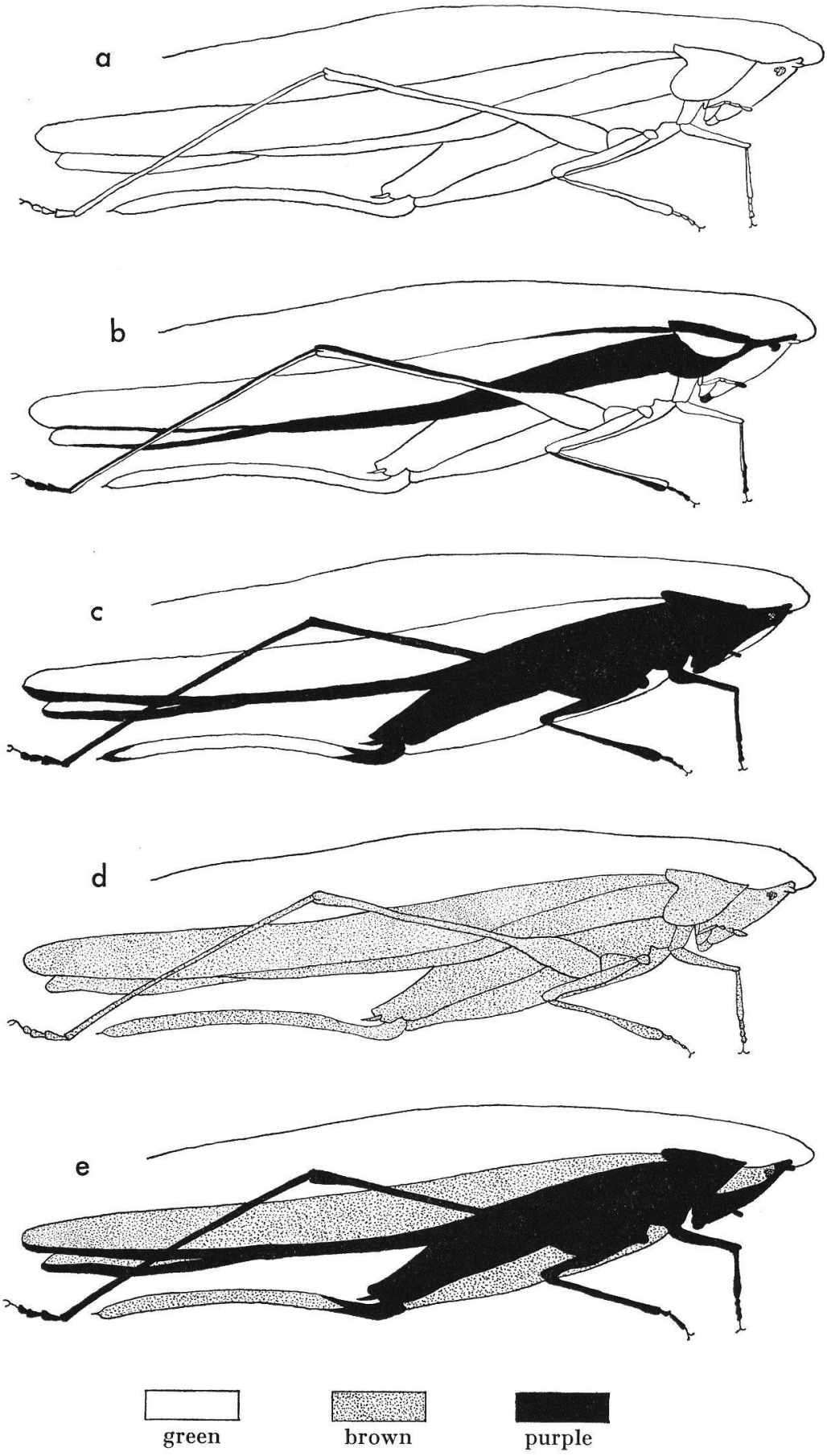

Fig. 1. Colour forms of *H. nitidulus*. a: green, b: purple-striped green, c: purple-headed green, d: brown, e: purple-headed brown.

TABLE 1.

Numbers of *H. nitidulus* at Kampala, October 1962-September 1963.

	peak number at m.v. light per three hours	number of swarms	mean rainfall 1953-62 (inches) *
October 1962	38	–	4.41
November	"thousands"	1	4.87
December	"thousands"	2	3.40
January 1963	5	–	2.28
February	2	–	2.09
March	5	–	4.34
April	"thousands"	2	6.59
May	"thousands"	1	5.57
June	14	–	2.43
July	11	–	2.21
August	–	–	4.34
September	1	–	3.90

* Data from the East African Meteorological Department.

As shown in Table 1, the occurrence of swarms is correlated with the months of higher rainfall. Local information suggests that this too is the usual pattern: swarms may be earlier or later than usual, depending upon the amount of rain that has fallen. The occurrence of swarms does not seem correlated with any other factor: at Kampala there is little seasonal change in air temperature, and at 0° 20′ N. change in daylength is small.

TABLE 2.

Sex ratio of *H. nitidulus* in six consecutive swarms at Kampala.

swarm	N	per cent male
1 (26-30 Nov. 1962)	3,097	27.4
2 (3-5 Dec. 1962)	668	49.5
3 (27-28 Dec. 1962)	1,151	49.1
4 (12-15 April 1963)	59	22.0
5 (27 April 1963)	131	32.8
6 (21-24 May 1963)	468	60.9

The overall sex ratio of 6,129 *H. nitidulus* collected at Kampala during the year is one male to 1.24 females. This may be because the females are more readily attracted to mercury vapour light than the males. There is some evidence of a change in sex ratio during a swarm. Thus, in a swarm that appeared on three consecutive nights in 1962, 57% (n = 487) were males on 3 December, 30% (n = 80) on 4 December, and 29% (n = 101) on 5 December. Much greater differences in sex ratio occurred between swarms. As shown in Table 2, differences in sex ratio between swarms ranged from 22.0 to 60.9% males, indicating real but inexplicable differences between swarms. Apart from Swarm 6, females numerically exceeded males.

When swarming, *H. nitidulus* appears at street and other lights soon after dark. Many circle the lights, while others find resting places on nearby vegetation. Males stridulate continuously and mating occasionally occurs. All the females dissected contained eggs. Both sexes were very fat, the abdomen having a slightly greasy feel. The morning after a swarm they were seen in thousands on vegetation near lights. Apart from man (see later) the following species of birds were seen feeding on them: *Bubulcus ibis* (egret), *Sphenorynchus abdimii* (stork), *Milvus migrans* (kite), *Lanius excubitorius* (shrike), *Corvus albus* (crow), *Lamprocolius* spp. (starlings), and *Passer griseus* (sparrow). Probably several species of nocturnal mammals also eat them.

Polymorphism.

Five distinct sympatric colour forms of *H. nitidulus* are shown in Fig. 1. There are two common forms: one green like a typical conocephaline grasshopper, and one brown. There is considerable continuous variation in the brown form, with rufous-brown and yellowish-brown at the two extremes and greyish-brown in between. Some brown specimens are lightly speckled with a darker brown. Then there are three rare forms: green with purple stripes; green with a purple head, thorax, legs, and upper abdomen; and brown with a purple head, thorax, legs, and upper abdomen. The intensity of the purple varies slightly in these three forms, but they are all absolutely distinct from each other and from the green and brown forms.

In Table 3, all specimens collected are classified by sex and colour. All five forms occur in each sex; in both sexes the greens and the browns predominate, comprising together 97.2% of the males and 96.5% of the females. But the relative frequency of the greens and browns differs in the two sexes:

TABLE 3.

Relative frequency of colour forms of *H. nitidulus* at Kampala.

	males	females
green	967	2,948
brown	1,265	751
purple-striped-green	57	122
purple-headed green	5	12
purple-headed brown	1	1
total	2,295	3,834

TABLE 4.

Relative frequency of colour forms in six consecutive swarms of *H. nitidulus* at Kampala.

	Swarm *.											
	males						females					
	1	2	3	4	5	6	1	2	3	4	5	6
green	522	141	149	6	15	71	1745	289	420	40	66	137
brown	305	198	398	7	27	217	423	68	141	4	20	33
purple-striped green	20	10	15	–	1	7	75	9	23	1	2	3
purple-headed green	2	–	2	–	–	–	5	3	2	1	–	–
purple-headed brown	–	–	1	–	–	–	–	–	–	–	–	–

* For dates of swarms see Table 2.

42.1% of the males and 76.9% of the females are green. This difference is highly significant, $\chi^2_{(1)} = 820.6$ ($P < 0.001$).

The relative frequency of brown and green males (but not females) also varies significantly between swarms, as shown in Table 4. For example, the difference in frequency of brown and green males in Swarms 1 and 6 is highly significant, $\chi^2_{(1)} = 127.0$ ($P < 0.001$), while in the females $\chi^2_{(1)} = 0.001$. There is, however, no statistical difference in relative frequencies between swarming and non-swarming *H. nitidulus*.

Local information.

The Luganda name for *H. nitidulus* is nsenene. The grasshopper is extremely well-known in Buganda and when it is swarming it is much sought after for food. The grasshoppers are usually collected from around lights. The wings and legs are removed and the bodies fried in their own fat. In Buganda, most people are permitted to eat nsenene, but in West Nile District illegitimate children may not eat them because it is thought that they may die or at least catch a bad cough. There are many different beliefs about the origin of the swarms. Thus, some people say they come "from the Sudan", others "from the west", while others may be more specific, for instance "from a hill near Masaka". The association of swarms with rain is also well-known and the term "nsenene rains" may mean either one of the two rainy seasons or a light drizzle (in contrast to the more frequent violent thunderstorms).

Some languages in East Africa have different words for each of the colour forms. In Buganda, the green form is called kulumbisi, meaning raw, uncooked, or as green as a raw mango. The brown form is called kulunkalu, meaning dry, or kulusanja, meaning like a dried banana leaf. Kulubazzi, one of the names for the purple-striped form, means, in effect, that when one is

found one stands a greater chance of getting more within a limited period— a perfectly sound biological observation in view of the low relative frequency of this form. The purple-headed green form is called nnangira, meaning prince. I have been unable to discover a name for the purple-headed brown form, but as shown in Table 3, it is extremely rare. Purple-striped and purple-headed green forms are sometimes confused, and elsewhere in Uganda they are often collectively referred to by words meaning king or leader.

Swarming and polymorphism.

The occurrence of swarming and of colour polymorphism in any orthopteran immediately invites comparison with locusts. But in fact the similarities between *H. nitidulus* and locusts are slight and the differences striking. Unlike locusts, swarming in *H. nitidulus* occurs at predictable times of the year. Hopper bands are apparently not formed (KEVAN and KNIPPER, 1955), but hoppers have rarely been observed in the field. The polymorphism in colour is evidently of the strictly genetic kind (FORD, 1945), and not the so-called "continuous polymorphism" (KENNEDY, 1961) of locust hoppers. It is not known if immature *H. nitidulus* are polymorphic: all those I have seen were green. No morphometric differences between swarming and non-swarming *H. nitidulus* have been found, although slight differences in behaviour are claimed (KEVAN and KNIPPER, 1955). No difference has been found in the degree of polymorphism in swarming and non-swarming *H. nitidulus,* but, in males, some conspicuous differences between swarms occur (Table 4).

The origin and subsequent movements of the swarms are unknown. Local information on this point is too diverse to be reliable, and the fact that *H. nitidulus* is chiefly nocturnal makes observation difficult. All that can be said is that great numbers appear relatively regularly and especially when it is wet. One cannot be certain that there is aggregating behaviour, although is has been claimed (KEVAN and KNIPPER, 1955); the grasshoppers might simply be present in large numbers without any tendency to seek each other out.

H. nitidulus is difficult to breed in captivity and nothing is known of the genetic control of the polymorphism. Mating between forms has been seen, but not often enough to test for randomness. The polymorphism is probably determined by multiple alleles and it could be maintained either because heterozygotes have a greater fitness than homozygotes or because the fitness of the forms varies with their frequency in the population. Polymorphism of this kind, in which there are one or two common forms and a series of relatively rare contrasting forms, occurs in a variety of animals that occur at high population densities, including snails and cercopid bugs (OWEN, 1963). In *H. nitidulus,* all the forms may be cryptic: the green and the brown matching green and brown backgrounds, and the others, all three of which have some purple, matching grass leaves and stems that are pigmented with anthocyanins. The association of the brown form with males and the green with females is peculiar and difficult to explain; possibly selection acts differently in the two sexes.

Acknowledgements.

D. R. Ragge helped with the nomenclature of the tropical African *Homorocoryphus.* Many people in Uganda contributed "local information", some of which I have used.

Bibliography.

CHOPARD, L. & KEVAN, D. K. McE. (1954). Orthoptera-Ensifera from northern Kenya and Jubaland. — Trans. Roy. Ent. Soc. London *105,* 315-353.

FORD, E. B. (1945). Polymorphism. — Biol. Rev. *20,* 73-88.

KENNEDY, J. S. (1961). Continuous polymorphism in locusts. — In "Insect polymorphism", ed. J. S. KENNEDY, London: The Royal Entomological Society.

KEVAN, D. K. McE. & KNIPPER, H. (1955). Zur Systematik, Biologie, insbesondere Schwarmbildung und Morphometrie afrikanischer *Homorocoryphus* (Orth. Tettigon. Conocephalidae). — 1. Veröff. Überseemuseum Bremen *2,* 277-318.

OWEN, D. F. (1963). Similar polymorphisms in an insect and a land snail. — Nature *198,* 201-203.