OCCURRENCE OF *CHORTHIPPUS PARALLELUS* (ZETT.) f. *MACROPTERA* (ORTH., ACRIDIDAE) IN BRITAIN.

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Up till last year I have found two published records of the macropterous form of *Chorthippus parallelus* (Zett.) from Britain. The first (H. Campion, 1923) describes a female specimen from Looe, Cornwall, taken in September, 1922; this is the specimen mentioned by M. Burr (1936: 109). Another female, in the Lucas collection of British Orthoptera at Oxford, was taken in the New Forest, 17.x.24 (W. J. Lucas, 1925: 86). Also Sansome and La Cour (1935: 420) mention the occurrence of the macropterous form in their experimental material, but it is not clear whether any of these were taken in the wild state or whether all were bred during their experiments.

The terminology of this form is confused; Campion (*loc. cit.*) prefers the name var. *explicatus* de Sélys, but Lucas (*loc. cit.*) uses the older name var. *montanus* Charp. However, as the difficulty about the identity of the specimen Charpentier described, mentioned by Campion, still remains, while it is probable that de Sélys' description of var. *explicatus* actually refers to *Chorthippus longicornis* (Latr.), it seems best to ignore both names, and to refer to the form simply as *C. parallelus* f. *macroptera*.

In the course of taking random samples from *C. parallelus* colonies in the early autumn of last year, both in the Oxford district and in the Reigate district of Surrey, I found f. *macroptera* to occur in seven out of a total of sixteen colonies studied. In all thirty macropterous specimens were taken, of which eight were males and twenty-two females; the detailed records are as follows:—

Locality.	Habitat.	Date.	Total. ♂	Total. ♀	f. *macroptera*. ♂	f. *macroptera*. ♀
Hell Coppice, Bucks.	Wet meadow ...	12.ix.41	61	70	3	1
Oakley Wood, Bucks.	Hayfield	12.ix.41	123	111	4	7
Shabbington Wood, Bucks.	Wet meadow ...	15.ix.41	64	50	1	2
Oakley Wood, Bucks.	Rough grass, roadside	15.ix.41	47	47	–	1
Boars Hill, Berks. ...	Grass heath over Lower Greensand	18.ix.41	116	92	–	4
Colley Hill, Surrey ...	Dry chalk grassland	22.ix.41	27	27	–	2
,, ,, ...	,, ,, ...	24.ix.41	9	3	–	1
,, ,, ...	,, ,, ...	27.ix.41	11	9	–	3
Kingswood, Surrey ...	,, ,, ...	3.x.41	2	2	–	1
	Total		460	411	8	22

It is doubtful how much significance attaches to the absence of macropterous males from the later records, as such males are far less easily distinguished from the normal form than are the macropterous females, and it is possible that males of intermediate wing-length may have been overlooked, and only the most conspicuous cases recorded. This is the more probable, as the amplitude and length of both wings and elytra in macropterous females from the last three localities were appreciably less than in those of the earlier records, so the degree of macropterism of the males might be expected to be correspondingly less conspicuous. However, H. Karny (1913: 36) mentions specifically that macropterism in *C. parallelus* occurs especially in the female.

Besides these records of my own two other cases of the occurrence of this form in 1941 have come to my notice. Miss S. G. Budge, of the University College of Wales, kindly informs me that she took one male and five females in two localities in the Aberystwyth district in September, 1941, and Hewlett (1942) records the capture of a single female in the Ashford district of Kent in the same month.

This comparative abundance of *f. macroptera* in Britain in 1941, when there have been so few previous records, invites speculation as to the factors responsible for a sudden increase of the incidence of macropterism. The literature on the subject is not very extensive, but there is a general opinion that the incidence is mainly controlled by environmental factors, though there is little agreement about the exact nature of the latter. Sansome and La Cour (*loc. cit.*), for instance, found that the character (macropterism) did not segregate clearly, suggesting that genetic control of its incidence is at best only partial; they concluded that a long period of development, such as in the wild state would be associated with adverse environmental conditions, probably dampness and low temperature, was most favourable to its occurrence; they also found macropterism associated with unspecified abnormal development of the gonads. Creighton and Robertson (1941) studied macropterism in an allied North American species, which they call *Chorthippus longicornis* [Latr.]; this they claim is identical with *C. parallelus,* on the authority of Hebard (1936). Dr. B. P. Uvarov, in a personal communication, informs me, however, that the species they describe is *Chorthippus curtipennis* (Harris), which is confined to N. America; he disagrees with Hebard's conclusion that all three names refer to the same species. The species is at any rate closely related to our

C. parallelus, but they found macropterism correlated with high temperature and a consequently short period of development, in contrast to Sansome and La Cour. W. Ramme (1931) found a clear correlation between macropterism in the Tettigoniid *Metrioptera roeselii* (Hagenb.) and hypo-development of the gonads; he presented evidence that the incidence of macropterism in *Metrioptera brachyptera* (L.) and *M. roeselii*, and also in *C. parallelus* (which he calls *C. longicornis*), *C. longicornis* (which he calls *C. montanus* Charp.) and *Chrysochaon dispar* (Germ.), is greatest in damp localities with tall vegetation and a low ground-temperature, and in seasons when the peak period of development for Orthoptera (May-June) is cold and wet. He raises the question whether wet and cold are the direct factors in production of macropterism, or whether they might not act indirectly in predisposing to a parasitic infection, which would then lead to hypo-development of the gonads and to formation of long wings; the latter possibility is favoured by the small percentage incidence of the form, even in favourable years, in all the species he considers. He quotes the opinion of Zacher (1917: 6) that in the genus *Metrioptera* hygrophily is correlated rather with increased tendency to brachypterism than to macropterism; however, this conclusion, based on the differences of typical habitat shown by normally long-winged and short-winged species, has not the same relevance to the question of occurrence of macropterism in a normally brachypterous species as have the more direct observations of Ramme.

The general conclusion from this discussion is that environmental factors, and more especially general seasonal effects, perhaps to a greater extent than local conditions, are mainly responsible for producing an abnormal number of macropterous individuals in a typically brachypterous species. That such general rather than local conditions have given rise to last year's abundance of f. *macroptera* in *C. parallelus* seems more probable, since the records are from such widely separated localities and diverse habitats; the foregoing table shows this clearly in my own case, while Miss Budge's records were from two hillsides with incomplete vegetation cover, and Hewlett's was from the chalk. This rules out any possibility of correlation with a particular type of habitat. Possible general climatic factors in the abundance of the form are on the one hand the cool weather of most of May, though in my experience this was not very marked, and on the other the prolonged spell of hot and dry weather towards the end of June, which seems, however, rather

late for a maximal effect on the developing insects. Perhaps both of these factors could have been responsible, the cool weather of early May resulting in delayed hatching, with consequent extension of the main period of development into the hot, dry June weather; it will be remembered that Sansome and La Cour found a correlation with protracted development, though on the other hand Creighton and Robertson suggest hot, dry weather favours rapid development. In this connection it is noteworthy that all last year's records are within the period September 3rd to October 3rd; the two previous British records are also from September and October, and de Sélys (1862: 147) says that the macropterous form ('var. *montanus*') is met with towards the middle and end of the season. Unfortunately in my own case no comparable collecting was done earlier in the season by which a correlation with time of year could be checked, but Miss Budge tells me that her September records were the only ones in a period of random sampling of *C. parallelus* colonies from July to September. Finally, the regularly small percentage incidence of the macropterous form in every colony of my records bears out Ramme's similar observation, and I am inclined to agree with him that this suggests that a parasitic infection, liability to which may be enhanced under abnormal climatic conditions, is the most likely factor for the production of macropterism. This probability would perhaps have been enhanced if I had been able to confirm his correlation of macropterism with hypodevelopment of the gonads, but this was only suggested to me after my specimens had dried, so, although I was able to confirm the absence of egg-pods or prominently developed ovaries in the abdomen of seven females after soaking them in water, I could not make out the structures clearly enough to conclude that the gonads here, or in a single male similarly treated, were truly hypoplastic or atrophic, as Ramme describes them.

An interesting feature of both males and females of the macropterous form is the peculiar and variable venation of the elytra. The evolutionary significance of this phenomenon, which is shown by the macropterous forms of many normally brachypterous species of Orthoptera, and its relevance to Dollo's principle of the irreversibility of evolution, were the basis of a controversy between Karny (1913, 1914) and Puschnig (1914). Karny described the type of reduction of wing structure undergone by brachypterous Acrididae and Tettigoniidae, pointing out the irregularity of venation, especially transverse venation, and the greater reduction of the distal end

of the elytron relative to the proximal one. He claimed that these characters were reproduced in the macropterous forms of brachypterous species, *e.g.* in the macropterous form of *C. parallelus,* and he therefore described the condition as secondary macropterism, in contrast to the primary macropterism of normally fully-winged species such as *Euchorthippus pulvinatus* (F.W.) or *Chorthippus albomarginatus* (De Geer). In this way he distinguished between atavism, shown by such macropterous forms as reproduce the typical venation and relative proportions of normal macropterous species, and secondary macropterism, in which the differential reduction undergone by the wings of brachypterous species is reproduced in their macropterous forms. Puschnig did not consider this conception was in accordance with Dollo's law, and held that Karny's examples did not establish clearly the distinction claimed; he regarded all as cases of atavism. In the particular case of *C. parallelus* he held that Karny's comparison between the venation of the macropterous form and that of *E. pulvinatus* and *C. albomarginatus* was not valid; he pointed out that Fischer had recognised two degrees of macropterism in *C. parallelus,* an intermediate β form with elytra covering only two-thirds of the abdomen and a fully-winged γ form (see de Sélys, *loc. cit.,* for a similar distinction, in which he describes the β form as var. *montanus* Charp. and the γ one as his var. *explicatus*). Karny had described specimens of the β form, and Puschnig did not consider this comparable with fully-winged *E. pulvinatus* and *C. albomarginatus*; in comparing the γ form with these species he concluded that, though Karny's distinctions were apparent, yet the differences were not great enough to exclude the possibility of atavism. In his reply Karny (1914) did not admit that the β form was not comparable with *C. pulvinatus* and *C. albomarginatus,* as he included them all in his macropterous category, but in any case he considered the differences shown by form γ as well as form β, especially in respect of the disproportionately small apical part of the elytra, as conclusive for his point of view. Zeuner (1929) supported Puschnig's general view that such cases are atavistic, suggesting the possibility of fossil prototypes, now extinct, nearer to the macropterous forms than are modern macropterous species, in connection with his work on macropterism in the genus *Metrioptera*.

Both the irregular transverse venation and the different proportions of the apical part of the elytra are apparent in my own specimens, both male and female. It is noteworthy that none of these has elytra as short as two-thirds the length of the abdomen, the

lengths in the females varying from a good three-quarters of the abdomen length to well over this length, and in the males always exceeding that of the abdomen, with the lower wings correspondingly well developed in each case. This suggests that the distinction of the β and γ forms made by Fischer and followed later by de Sélys is not very rigid.

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