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Chromatic Polymorphism and Geophagy: Two Outstanding Characteristics of *Rhammatocerus schistocercoides* (Rehn 1906) Grasshoppers in Brazil [Orthoptera, Acrididae, Gomphocerinae]

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Abstract

A study of coloration in *Rhammatocerus schistocercoides* (Rehn 1906) grasshoppers in natural conditions revealed substantial variability, with evidence of a new case of chromatic polymorphism. Green coloration is much more common in this species than previously assumed. The percentage of green adults, or those with a partially green integument, varied seasonally within the same generation according to the phenology and especially the sexual maturity of the population. The most important coloration change occurred in September, during the sexual maturation period, when the grasshoppers turned progressively from brown to green or partially green. The present study also highlights evidence of a geophagy phenomenon (consumption of large amounts of soil) that has never before been reported in locusts or grasshoppers. This yet unexplainable behaviour was particularly spectacular in terms of its scale. [Keywords: grasshoppers, chromatic polymorphism, geophagy, *Rhammatocerus*, Brazil]

Introduction

Rhammatocerus schistocercoides (Rehn 1906) is a common pest grasshopper in Mato Grosso state, Brazil (Carbonell 1988; Cosenza *et al.* 1990). It was initially thought that the species was limited to this state and neighbouring regions, but there is now evidence that its range encompasses most South American savanna regions around the Amazon. This grasshopper was also recently identified in Peru, Costa Rica, Uruguay (Amedegnato, pers. corr. 1995), Colombia (NRI collections and specimens recently collected by J.A. Jimenez Gomez in the Porto Lopez region) and Rio Grande do Sul state, Brazil (Barrientos 1992).

The species is clearly gregarious and forms dense hopper bands and adult swarms. Its outbreak area in Brazil extends across Mato Grosso from east to west, covering an area known as the Chapada dos Parecis *(sensu lato)*. Although phase polymorphism has been mentioned with respect to this species, it has not yet been demonstrated (Lecoq & Pierozzi Jr. 1994a). In the absence of clearly defined morphological phase characters, *R. schistocercoides* does not merit recognition as a true locust, despite its gregarious behaviour.

Rhammatocerus schistocercoides is univoltine; it lays from late September through October, and the eggs hatch in October and November. Hopper development lasts almost 6 months and the imaginal moult occurs in April. Adults spend the dry season in the immature state and migrate locally for several months, carried by the winds. Sexual maturation is triggered around late August, with the approach of the rainy season (Lecoq & Pierozzi Jr.1994a, 1994b; Launois-Luong & Lecoq 1995a).

This grasshopper, identified by Rehn as early as 1906, has only been at the forefront in the news for about 15 years, since its conventional breeding and outbreak areas in Mato Grosso were colonized and developed by immigrants from southern Brazil. Contrary to general opinion, our recent studies indicated that outbreaks of *R. schistocercoides* are a long-standing phenomenon and not in any way linked with the large-scale farming development that has occurred in the concerned zones since 1980 (Lecoq & Pierozzi Jr. 1995a). Indeed, the only recent phenomenon is the fact that this grasshopper now has an economic impact. A new control strategy against this species is currently considered (Lecoq & Pierozzi 1996).

Rhammatocerus schistocercoides was recently recharacterized by Carbonell (1988). It is a very polymorphic species with many different adult chromatic forms (Carbonell 1988; Launois 1984; Duranton & Launois-Luong 1988; Cosenza *et al.* 1990; Lecoq & Pierozzi Jr. 1994a). Some forms have a uniform light-brown hue, and a few are darker with prominent elytral markings. There can be large black spots on the head and lateral parts of the pronotum (as in the type specimen). The top of the head-pronotum area can be uniformly brown or have a light strip bordered by two darker strips of various intensities. The most melanic forms can have dark cross strips on the top of the hind femur.

The hind femur coloration is a unique feature of all grasshoppers of this species; the internal part is bright blue two-thirds from the base and reddish-orange on the apical third. These bright markings are also found on the hind tibia, which is reddish-orange around the base and bright blue apically. This coloration likely has a protective function against potential predators, as suggested by Dearn (1990). In the field, we have often observed predator wasps *(Pryonix thomae* Fabricius 1775 [Hym. Sphecidae]) hunting over roosting grasshopper swarms. As a wasp approaches the grasshopper, usually from behind, the latter inevitably lifts up its hind legs, revealing the bright blue and orange underlying colors to the wasp.

In Carbonell's investigation (1988), only one grasshopper was found to have light-green coloration in the facial area, on the lateral carinae and sides of the pronotum metazona; no green was noted in all other grasshoppers examined. Nevertheless, several authors have reported a relatively high percentage of green grasshoppers. Green hoppers are commonly observed, even within hopper bands, but the percentages are very low. We previously noted marked between-population variations in the percentage of green (or partially green) adult grasshoppers, but the underlying mechanisms have not yet been clari-

fied (Lecoq & Pierozzi Jr. 1994a). Seasonal green/brown polymorphism has been observed in *Locusta migratoria* and many other locusts and grasshoppers, with green forms prevailing during the rainy season and brown forms during the dry season (Rowell, 1971; Dearn, 1990). However, this could not account for the above-mentioned variations in the percentage of green grasshoppers since *R. schistocercoides is* univoltine, i.e. producing only one generation yearly.

We thus carried out an in-depth field study on the coloration of *R. schistocercoides* adults and assessed this factor in terms of ecological conditions and the physiological status of the grasshopper populations.

Field research carried out from 1992 to 1994 in *R. schistocercoides* outbreak areas of Mato Grosso showed that green coloration is more common than suggested by descriptions in the literature (particularly that of Carbonell 1988), and that the respective percentages of green and brown grasshoppers change over time, in adults of the same generation, via unique mechanisms.

Moreover, these studies highlighted a noteworthy extraordinary geophagous "feeding" behaviour in this grasshopper.

Materials and Methods

Samples of swarming adult *R. schistocercoides* grasshoppers were collected on a regular basis, generally every 2 weeks, at various sites in Chapada dos Parecis, Mato Grosso (Brazil). During September, a key period for coloration changes, samples were collected daily. Voucher specimens are deposited in the Muséum National d'Histoire Naturelle, Paris.

Coloration was classified as follows (Fig.1):

B — for grasshoppers with an overall brown colour and no green markings

V1 — for green coloring limited to facial areas

V2 — identical to V1, but with the green hue extending to lateral and/or back parts of the pronotum

V3 — identical to V2, but with the green hue extending to all or part of the meso- and meta-thoracic epimerons and episternae, the anal zone of the outer wings and the area between the suprainternal and supraexternal carinae of the hind femurs.

Grasshoppers with more extensive green areas are uncommon. Moreover, the presence and absence of large black cephalic and pronotum markings has also been noted. Coloration must be studied on freshly captured grasshoppers since the green markings fade rapidly after death, when they can appear completely brown; this is especially true when the markings are small (V1 and V2).

A total of 3673 grasshoppers were examined from November 1992 to October 1994.

The life cycle of *R. schistocercoides* was also studied from regular samples collected in the field. Since the grasshopper life cycles were identical in 1992, 1993 and 1994 (e.g. the adult moult occurred on the same dates), the results were pooled for these 3 years. Geophagy behaviour in this species was also monitored during these field studies, at different sites and on different dates.

Results

1. Chromatic polymorphism

The percentage of grasshoppers with black pronotal markings was 13.3±5.6% for all studied populations (12.0% in males and 13.8% in females). This percentage remained constant (with a few random sampling variations) throughout the adult life of the grasshopper. Conversely, the percentage of green grasshoppers varied in a quite different way.

The results obtained in 1992, 1993 and 1994 are summarized in Figure 2; September is stressed in this figure on account of the marked coloration changes that occurred during this period.

More than 95% of young adults appearing in April had completely brown integuments. The remaining 5% presented traces of green pigmentation of various sizes. The percentage of brown grasshoppers remained stable through most of the dry season.

As the rainy season drew near, i.e. late August and September, the percentages in the different coloration categories were quickly modified. Adults turned progressively green.

This color change first appeared on the forehead (Class V1). In early September, the percentage of V1 grasshoppers increased from a few percent to around 30-40%. The green coloration then extended towards the back lateral parts of the pronotum, or even covered it, with V2 grasshoppers appearing in large numbers around September 18. The percentage of V2 grasshoppers remained around 50-60% until the end of the month. The meso- and meta-thoracic epimerons and episternae, and, in the greenest grasshoppers (V3), the anal zone of the outer wings and the area between the suprainternal and supraexternal carinae of the hind femurs, turned green. Class 3 grasshoppers were the most numerous during October, and represented 90-95% of the population at the end of that month. This level remained stable until disappearance of the last adults in November.

In the same generation, the respective percentages of completely brown grasshoppers and grasshoppers showing extended green coloration were inversed between the April adult moult and the end of the breeding period, in October and November. The same phenomenon was observed in 1992,1993 and 1994.

This rapid change from brown to green during September occurred at the same time as sexual maturation (Fig. 3). The adults, which had remained immature since their adult moult in mid-April, began their sexual maturation in late August. Vitellogenesis of ovocyte 1 occurred throughout September and the first oviposition took place at the end of that month. Massive deposition of the first eggpods occurred within a few days, between September 28 and September 30, in 1994 (the year studied in the most detail). These two phenomena, i.e. sexual maturation and greening, seemed to be generally linked with the onset of the rainy season, although the rains do not represent the critical factor for ending imaginal diapause.

We have shown that the photoperiod likely has a determining role in the *R. schistocercoides* maturation process (Launois-Luong & Lecoq 1995). The grasshoppers have to spend the dry season in the diapause state, induced by the decreased daylength in April and May at the time of the adult moult. Ovarian development starts again by the end of August, which is in the dry season. In 1994, the first rains only began on September 6, whereas adults had started turning green and maturing sexually in the dry season in late August. Before the first rain on September 4, the percentage of green grasshoppers was already as high as 50% and 20% of females were already undergoing vitellogenesis.

The two phenomena, sexual maturation and greening, are thus likely dependent on the photoperiod, and they regularly occur at the same date every year. Obviously, they must represent adaptations to the onset of the rainy season which has a high likelihood of occurring in September, despite high interannual variability.

2. Geophagy

Rhammatocerus schistocercoides essentially feeds on natural grasses of cerrado and campo-cerrado areas (Cosenza *et al.* 1990). There is mainly extensive damage to rice, maize and sugarcane crops and natural grazing lands. In soybeans, the main crop of Mato Grosso, there is very little grasshopper-related damage.

Our studies on natural food intake confirmed that *R. schistocercoides* regularly consumes both green and dry parts of wild grasses, even when given a choice. A grasshopper was even once observed eating termites. Many times we also observed a very original feeding behaviour involving consumption of large amounts of sand and soil.

Rhammatocerus schistocercoides adults were often observed, either individually or in groups of several dozens of grasshoppers, gathered on the ground with their abdomens lifted up, heads tilted forward with their mandibles scraping and digging the ground. In this position, they were consuming sand and soil particles. Areas occupied by the adult grasshoppers were quickly covered with a mixture of faeces containing plant material and faeces containing sand/soil; the latter could represent, locally, one-third of all of the faeces. Some of the faeces were compounds partly made up of plant detritus and partly of soil. Close visual observations indicated that they were greatly enjoying what could be called a "sand dinner".

Geophagous behaviour is not exceptional for this grasshopper. It has been commonly observed at different locations in various seasons, at the beginning of the rainy season in adult populations of a few months old, and in the middle of the dry season for younger populations. Such soil faeces concentrations have often been observed even when there are no adults around; however, this faeces is very fragile, breaks up easily when touched and naturally disappears with the wind or rain.

In any case, the soil surface was dry and these adults had apparently adequate plant resources close by (cerrado grasses with a large percentage of green parts, sugarcane, etc.). This is therefore not a substitute behaviour, but normal for the species, even when favourable food resources are available.

Thin rootlets are also likely eaten this way, but most of the time the observed adults seemed to only eat soil. Stereo-microscopic examination showed that the sand/soil faeces contained very little plant detritus (except of course for the mixed sand/grasses faeces). It seemed to be chiefly composed of small soil particles and only a small proportion of root fragments were found in it.

Discussion and Conclusion

Data collected during more than 2 years of field research on the coloration of *R. schistocercoides* adults showed that there is much more coloration variability in this species than suggested by prior descriptions based on limited sample sizes.

Green coloration seems to be much more common than previously assumed. The percentage of green adults, or those with a partially green integument, varied seasonally within the same generation according to the phenology and especially the sexual maturity of the population.

The observations, obtained almost daily during some key periods of the life cycle, showed that during one generation, the same grasshoppers turned progressively from brown to green. The most important coloration change occurred in September, at the time of sexual maturation. Similar phenomena have been observed in *Schistocerca gregaria* (Forskål 1775), where sexual maturation of gregarious locusts is accompanied by a color change, from overall pink to bright yellow (Norris 1954). Such coloration modifications linked with sexual maturation are also known in other locust or grasshopper species (Uvarov 1966). More generally, Rowell (1971) and Dearn (1990) reviewed coloration and modifications in acridians. However, to our knowledge, there have been no previous reports of brown to green changes within grasshoppers of the same generation during their adult life. This color modification, although seemingly not dependent on the arrival of the rainy season, probably corresponds to an adaptation to seasonal changes in the grasshopper environment, and especially to the greenness of the vegetation. The overall brown color of grasshoppers going through their adult moult at the end of the rainy season (April) allows them to effectively hide in the straw-colored vegetation during the dry season. Conversely, their change from brown to green at the end of the dry season/onset of the rainy season enables them to mimic the greening vegetation in September and October.

The geophagy phenomenon observed in *R. schistocercoides* also seems unique. Locusts and grasshoppers have already been reported eating bits of sand, but in a limited and anecdotal way (Jago pers. corr.). Duranton (pers. corr.) also noted that desert locusts, *Schistocerca gregaria*, are sometimes observed with their digestive tracts filled with sand, when no vegetation is available. The phenomenon reported here is very different since the adults had favourable food available nearby in all of the observed cases. Furthermore, the scale of the phenomenon was such that geophagy is a valid term to explain it. The overall significance of this behaviour is still unknown and would require further investigation.

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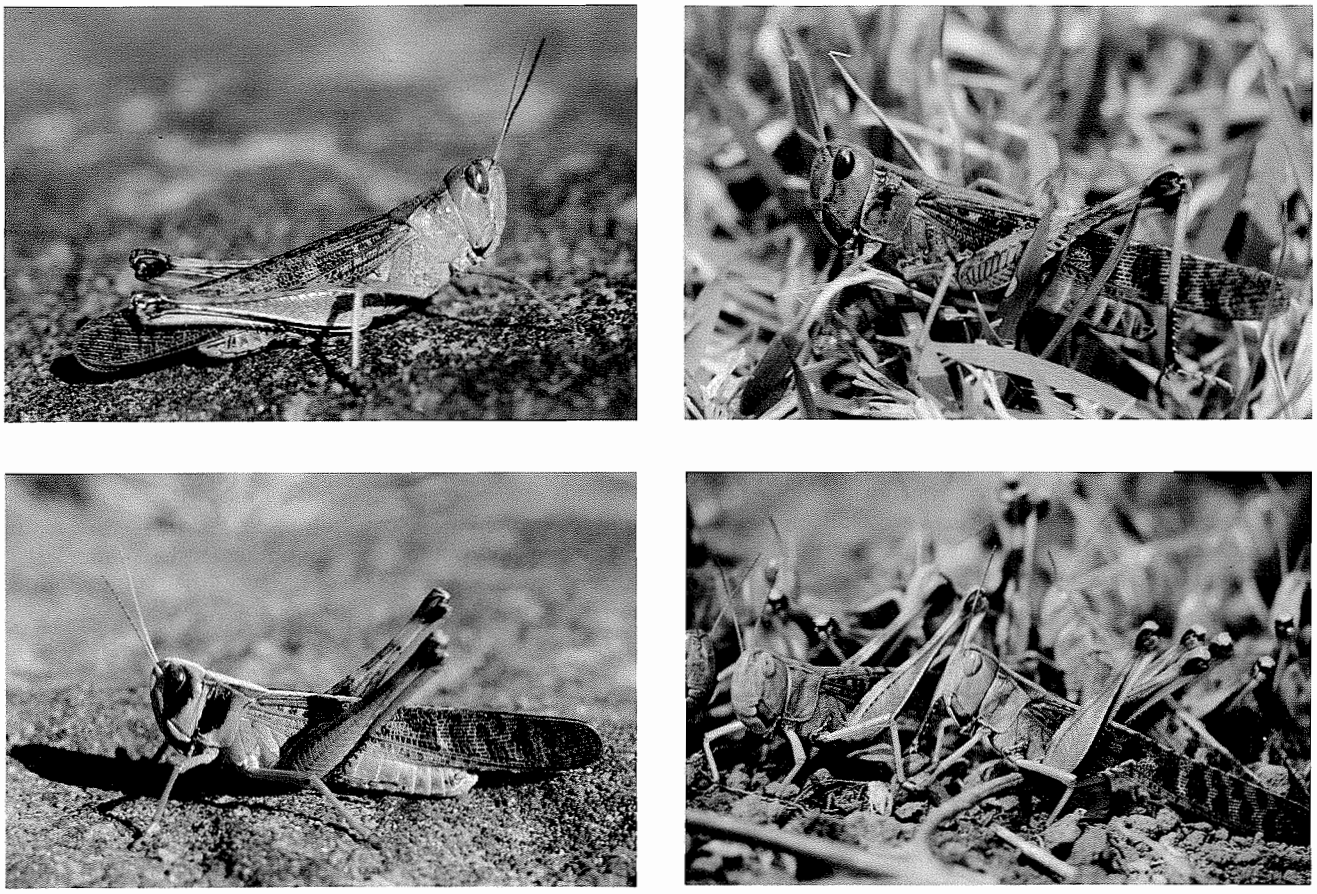

Fig. 1. Some coloration variations in *Rhammatocerus schistocercoides*. **a**, immature brown male. **b**, Immature brown female (form with black spots). **c**, Laying green females. **d**, Old green female.

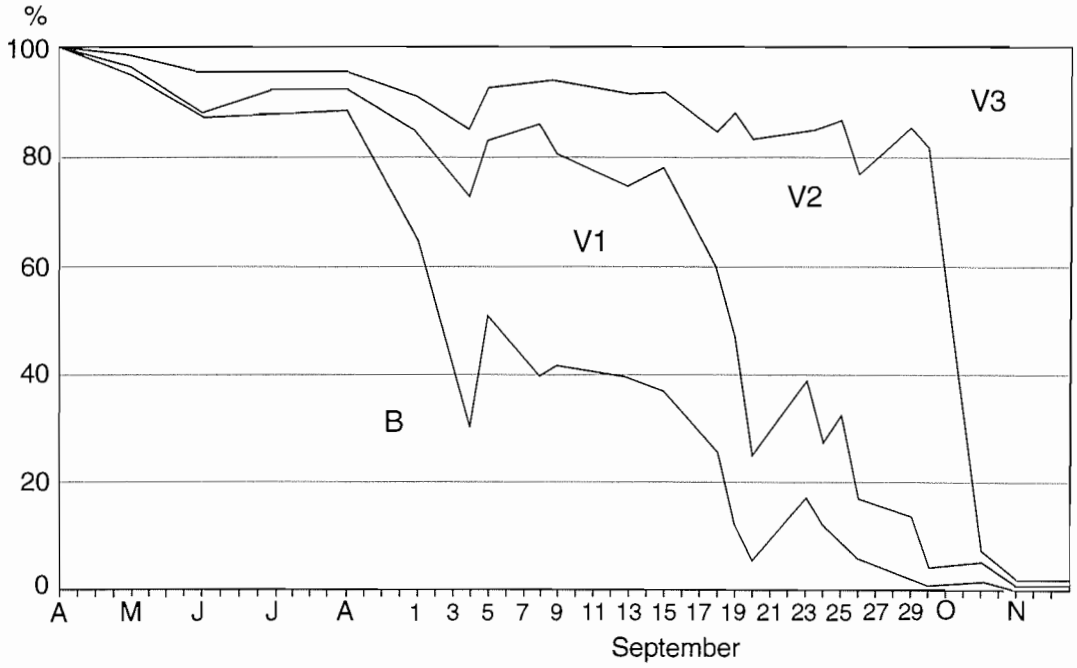

Fig. 2. Variations in adult *R. schistocercoides* coloration in the same generation (all data from 1992,1993 and 1994). **B**, entirely brown grasshoppers. **V1**, **V2**, **V3** grasshoppers with various extents of green coloration (see text).

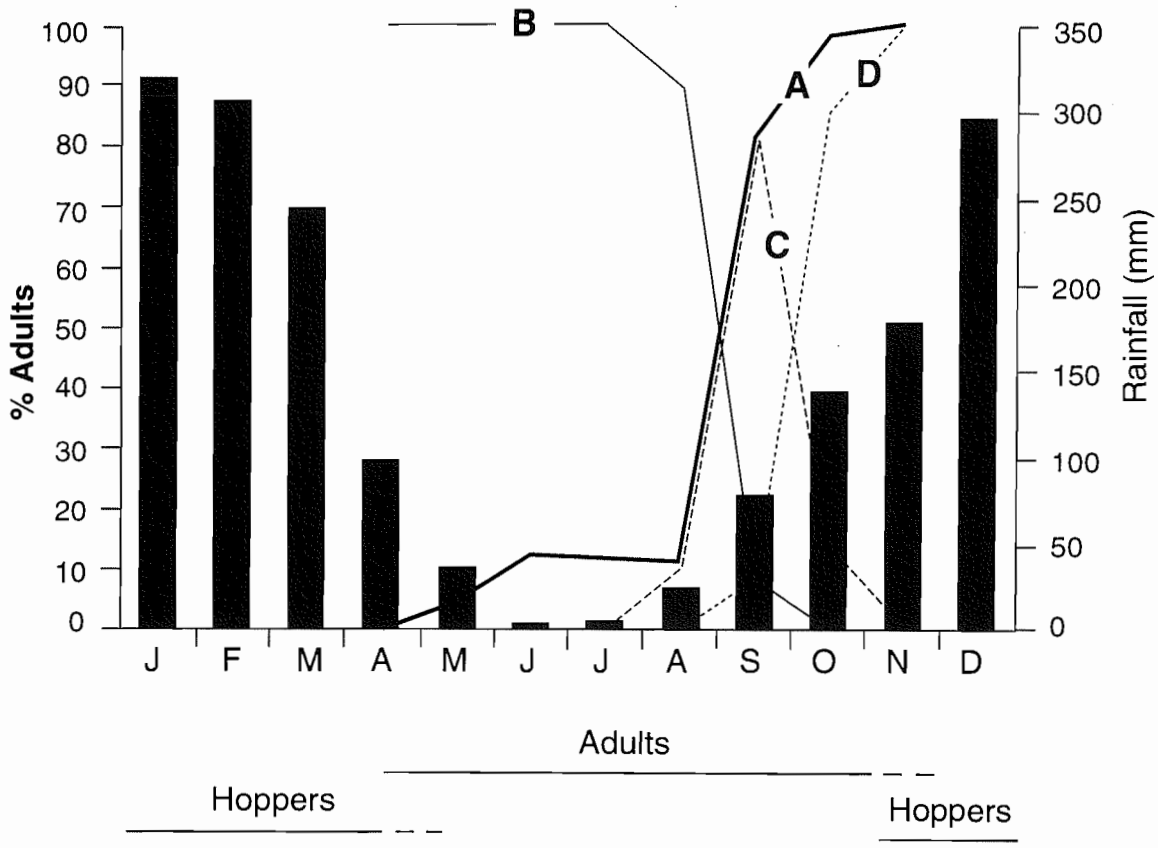

Figure 3. Variations in the percentage of green adults as compared to the sexual maturity status of the population. **A**, green adults (V1, V2 and V3 classes together). **B**, immature females. **C**, nulliparous females in vitellogenesis. **D**, parous females. **Histogram**: rainfall in mm (mean monthly rainfall for the 1983-93 period at the COPRODIA station, Campo Novo do Parecis county, Mato Grosso, Brazil).