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Author: Bidau, Claudio J.

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Curious orthopterological errors of a great naturalist: William Henry Hudson

CLAUDIO J. BIDAU

Universidad Nacional de Rio Negro, 8336 Villa Regina, Rio Negro, Argentina. Email: bidau50@gmail.com

This paper is dedicated with love to Valeria Ximena Rodríguez on the occasion of her 27th birthday

Abstract

I analyzed chapter VIII of William Henry Hudson’s “The Naturalist in La Plata”, a popular book published in 1895. Herein the famous naturalist ornithologist and writer relates many observations made by him in his youth in a region of Buenos Aires, Argentina, accounts of a large number of natural phenomena especially pertaining to animal life. Chapter VIII is called “Mimicry and Warning Colours in Grasshoppers”. Although very interesting by virtue of Hudson’s considerations of aposematism and Batesian mimicry in grasshoppers and katydids, this chapter contains essential errors of identification of the orthopteran species he discusses.

Key words

aposematism, Batesian mimicry, Orthoptera, Zoniopoda tarsata, Chromacris speciosa, Scaphura nigra, wasps

Introduction

This historical sketch is based on analysis of a chapter of a famous popular book, “The Naturalist in La Plata”, Hudson 1895, by the renowned anglo-argentine naturalist and author William Henry Hudson. Of his comments on wildlife in La Plata, chapters VIII to XV are dedicated to the description and discussion of many observations of the behavior of insects and spiders made by the author in the field. Most of the observations are quite accurate, interesting and delightful to read for a lay reader as for the scientist. However, I have found in chapter VIII (“Mimicry and Warning Colours in Grasshoppers”) a series of curious errors in the identification of orthopteran species which I will try to disentangle in this paper.

I will first introduce the naturalist and then explain and discuss the problem. Since some of the terms used and people named in this paper may be unfamiliar to readers, I have added some notes to help comprehension.

The naturalist.—William Henry Hudson (Guillermo Enrique Hudson in Argentine literature) (Fig. 1) was born (4th August 1841) in the Estancia “Los 25 Ombúes”, near Arroyo (creek) “Las Conchitas”, in the borough of Quilmes, today a completely urbanized area of Buenos Aires province, Argentina. His parents were Daniel Hudson and Katherine Kimble, who had arrived in Argentina from the USA in 1833, both 31 years of age. Daniel was born in Marblehead, Massachussets, Katherine in Berwich, Maine, she a descendant of Mayflower puritans. All their sons were born and raised in Argentina. They lived in the Estancia “Los 25 Ombúes” until 1846, when Daniel Hudson decided to abandon sheep breeding and installed a “pulperia” in Chascomús, then a small village some 120 km south of Buenos Aires. They returned to “Los 25 Ombúes” in 1856 where Katherine died.

The adolescent William was already an experienced horse rider in the gaucho style beginning when he was 6 years old. Now he worked as a cowboy and at other rural and physical demanding activities. He started to study the local flora and fauna, which he continued later in many travels to the heart of the country.

Horses were a fundamental part of his life, and he tells us in one of his book, “A Hind in a Richmond Park”, how horse riding made him think better and faster. He was a keen observer of natural and human scenarios and extremely fond of gauchos and their lifestyle. William became a keen observer of birds and their habits, publishing his ornithological work in the Proceedings of the Royal Zoological Society. He came to be respected by local and foreign naturalists, including Charles Darwin, who in his own youth, during his transcendental initiatory voyage, also became fascinated by the Argentine pampas and Patagonia.

After Daniel Hudson’s death the family dispersed. William’s sister Maria stayed in the house, but his elder brother went to England. This brother was essential to the informal scientific and philosophical growth of William, through their long conversations on Darwin and evolution, which moulded most of William’s vision of the world as a naturalist. The following years found him going from estancia to estancia, living the life of a gaucho. After a brief stay in Uruguay in 1868 where he became involved in the civil war between “whites” and “reds” and after several more years in Buenos Aires, he emigrated to England on 1 April 1874, never came back. He became a British subject in 1900. He married Emily Vingrave, a woman several years older than him who became his lifelong companion.

In London he also wrote the first of a long series of books, The Purple Land That England Lost (1885). He produced many ornitho-

1 “estancia” is equivalent in Spanish to the English term “ranch”, and is used mostly in Argentina and Uruguay. It usually refers to an expanse of land devoted to the breeding of cattle or sheep. In fact, Hudson’s father started in Argentina as a sheep farmer.

2 “Los Veinticinco Ombúes” means in English “The twenty-five ombu trees”, the number of these tree-like plants growing in the Hudson’s estancia. The ombú (Phytolacca dioica, Phytolaccaceae) is a herbaceous plant of arboreal habit, reaching 18m in height and almost 5m in diameter. Its leaves produce several poisonous compounds which make it immune to the attack of grasshoppers and other herbivorous insects.
logical studies, including two volumes with the famous ornithologist Philip Lutley Sclater (1829-1913) on Argentine Ornithology (1888, 1889) and British Birds (1895), and later achieved well-deserved fame with his books on the English countryside, including Hampshire Day (1903), Afoot in England (1909) and A Shepherd’s Life (1910), which helped foster the back-to-nature movement of the 1920s and 1930s. His most famous books are probably the novel Green Mansions 1904 and the autobiographical Far Away and Long Ago (1916).

Towards the end of his life, Hudson moved to Worthing in Sussex, England. He died on 18 August 1922 at 81 years of age. His grave is in Broadwater Cemetery in Worthing, Sussex. Several biographies of Hudson are available, those of Arocena (2003) and Ronner (1986) being the most advisable. Also, since he was a very prolific writer, several bibliographies have been compiled (e.g., Payne 1977). Many of his books can be found online at the website of Project Gutenberg.

The problem.—Hudson’s observations in this book were made in the southern portion of the La Plata district in what is now Buenos Aires province. This region corresponds to the eastern humid pampas (pampa meaning in quichua language, open space or country) and, as Hudson indicates in the first chapter, “...it forms in most part one continuous plain, extending on its eastern border from the river Parana, in latitude 32 degrees, to the Patagomian formation on the river Colorado, and comprising about two hundred thousand square miles of humid, grassy country.” The climate is temperate and “...nature is neither exuberant nor grand...” (Hudson 1985 in the book’s Preface). Perhaps because of this lack of grandeur, the naturalist’s detailed observations on the Love’s fauna are a pleasure to read: a supposedly dull landscape is transformed by his writing into a land of marvels. Most of the material in his book had already been published in natural history journals and general interest magazines of that time.

He starts chapter VIII, Mimicry and warning colours in grasshoppers, as follows: “There is in La Plata a large handsome grasshopper (Zoniopoda tarsata), the habits of which in its larva and imago stages are in strange contrast, like those in certain lepidoptera, in which the caterpillars form societies and act in concert. The adult has a greenish protective colouring, brown and green banded thighs, bright red hind wings, seen only during flight. It is solitary and excessively shy in its habits, living always in concealment among the dense foliage near the surface of the ground.”

The genus Zoniopoda Stål, 1873, belonging to the family Romaleidae of the Acridoidea is widespread in South America and includes 10 species in two taxonomic groups (Carbonell 2007; Eades et al. 2012). Z. tarsata (Serville, 1831) (= Acridium cruentatum Blanchard, 1843) (Fig. 2A) has the largest geographic distribution, occupying the whole territory assigned to the genus, i.e., east of the Andes from 15° to 35° southern latitude (Carbonell 2007).

Hudson’s brief description of the grasshopper leaves little doubt it was indeed Z. tarsata. Compare with the description of the chromatic characters mentioned by Carbonell (2007) [numbers in parentheses refer to the color nomenclature scheme of Smith 1975]: “General coloration of the pronotum and tegmina yellowish-green, varying in different specimens from olive-yellow (52) to lime-green (59). Legs banded with black, red (11) and yellow (56). Antennae black. Head: dorsal and lateral areas red (11); front partially yellow (56) on surface of rugae; fastigium and interocular area mostly black; clypeus, labrum and mandibles black; labial and maxillary pulpi yellow, or yellow with black bands in different individuals. Pronotum and meso-metapleurae with green rugae (52, 59) on black background. Pronotum is in some specimens uniformly colored (as in Fig. 10), in others it has yellowish-green longitudinal bands where rugae and background are of the same color, alternating with bands that look darker by having green rugae on a black background.”

However, the next considerations by Hudson are patently incorrect: “The young [sic] are intensely black, like grasshoppers cut out of jet or ebony, and gregarious in habit, living in bands of forty or fifty to three or four hundred; and so little shy, that they may sometimes be taken up by handfuls before they begin to scatter in alarm.”

Z. tarsata nymphs are as colorful and conspicuous as adults (Fig. 2B), and not gregarious. In fact, what Hudson misidentified as Z. tarsata nymphs must correspond to nymphs of another widespread genus of romaleid grasshoppers: Chromacris Walker, 1870. It comprises nine species and several subspecies, according to its last revision, distributed in humid areas of the American tropics from Mexico to Argentina (Roberts & Carbonell 1982). The species Chromacris speciosa (Fig. 3b) is one possessing the largest geographical distribution within the genus: it includes Colombia, Venezuela, Guyana, Brazil, Ecuador, Peru, Bolivia, Paraguay, Uruguay and Argentina. In the region surveyed by Hudson one frequently finds C. speciosa and Z. tarsata in the same habitat. Nymphs of C. speciosa are black with red and some white markings (Roberts & Carbonell 1982). Nymphs of Chromacris species are highly gregarious (Pretto-Malca 1968; Turk & Barrera 1976). The gregarious immature stages of Chromacris form large groups upon their food plants (Fig. 3A) and their shiny and contrasting black coloration suggests they are unpalatable or poisonous to predators, being thus a case of aposematism or warning coloration, produced through natural selection as originally proposed by Alfred Russel Wallace (Wallace 1879; Poulton 1890; Joron 2003).

Hudson continues: “Their gregarious habits and blackness—of all hues in nature the most obvious to the sight—would alone be enough to make them the most conspicuous of insects; but they have still other habits...”

3 Philip Lutley Sclater (1829-1913) was a prominent English biologist. Among many scientific feats in 1858 he established six zoogeographic regions of the world which he named Palaearctic, Nearctic, Neotropical, Aethiopian, Indian, Neotropical, and Australasian. These denominations are still in use.

4 Quichua (also Quechua) is a very important family of native South American languages, still spoken today in its several intelligible dialects, by millions of inhabitants of Bolivia, Argentina, Chile, Peru, Ecuador, and Colombia. It dates back at least to the Inca period. In quichua, grasshopper is spelled “Ch’arika”.

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Fig 1. William Henry Hudson.
which appear as if specially designed to bring them more prominently into
notice. Thus, they all keep so close together at all times as to have their
bodies actually touching, and when travelling, move so slowly that the
laziest snail might easily overtake and pass one of their bands, and even
disappear beyond their limited horizon in a very short time.” Obviously
the naturalist was struck by the fact that these apparently defenseless
young Chromacris made themselves so obvious to potential preda-
tors, a characteristic behavior of aposematically colored animals.

Although not actually a color, black is often a warning ‘color’ in
insects, perhaps because it increases visibility by contrast against
green foliage (Joron 2003).

Hudson almost correctly interpreted (despite his misidentifica-
tion of the species) the aposematic nature of the black coloration
and gregariousness of the nymphs: “They often select an exposed
weed to feed on, clustering together on its summit above the surrounding
verdure, an exceedingly conspicuous object to every eye in the neighbour-
hood. They also frequently change their feeding-ground; at such times
not much experimental work has been done in this respect with this
genus, some indirect evidence points to that conclusion. C. speciosa
feeds preferentially on solanaceous plants. Turk & Barrera (1976)
report its feeding on Cestrum parqui, C. strigillatum, C. lorentziana,
Lycium cestroides, Solarium argentinum and S. verbascifolium (Solana-
ceae), and also on Verbena enceloides (Compositae) and Medicago
sativa (alfalfa, Leguminosae). Solanaceae species are protected from
many herbivores by producing toxic compounds, but some grass-
hoppers, such as Chromacris, are not affected by them (Naskrecki
2004).

A very interesting observation in this respect was made by H.
Radcllyffe Roberts (Roberts & Carbonell 1982): “One of us (H.R.R.)
recently observed 20 to 30 conspicuous nymphs on top of a tussock of grass
two or three meters from a small solanaceous shrub stripped of its leaves,
which suggests that the gregarious behavior is a part of the premonitory
defense.” In well-studied species such as Schistocerca emarginata,
gregariousness and aposematism are related to the feeding of nymphs
on plants that confer gut-content mediated toxicity to predators
This description is extremely confusing. First, Romalea Burmeister, 1838 is a synonym of Romalea Servelle, 1831, a genus of Romaleidae grasshoppers. Romalea is monotypic, its only species being R. microptera (Beauvois, 1817) which is found in North America. Furthermore, the binomen Romalea speciosa has never existed (Eades et al. 2012). In fact, Thunberg named a species of Romaleidae (Thunberg, 1824) as Gryllus speciosus, which was later

Kirby & Spence. William Kirby (1759-1850) was an important British entomologist in his own time. His scientific ideas were typical of that epoch, that is Natural Theology: ‘The author of Scripture is also the author of Nature; and this visible world, by types indeed, and by symbols, declares the same truths as the Bible does by words. To make the naturalist a religious man – to turn his attention to the glory of God, that he may declare his works, and in the study of his creatures may see the loving-kindness of the Lord – may this in some measure be the fruit of my work…’ (Correspondence, 1800). Kirby produced his Introduction to Entomology, as result of a friendship formed in 1805 with William Spence (c. 1783-1860) a British political economist and entomologist; the work appeared in four volumes between 1815 and 1826. Several editions followed. Both scientists were founders of the Society of Entomologists of London and fellows of the Royal Society.

Fig. 3. A. Gregarious black nymphs of Chromacris speciosa perching on a host plant. B. Chromacris speciosa, adult male. For color version, see Plate XII.
transferred to Chromacris (Walker 1870; Lieberman 1935; Roberts & Carbonell 1982). But the description of the grasshopper does not pertain to Chromacris speciosa (Fig. 3B).

Note the chromatic characteristics as depicted by Roberts & Carbonell (1982): “Red winged over most of its range, but in lowland coastal area from Bahia, Brazil, to Uruguay, wings are frequently orange or yellow, and tegmina tend to be green rather than green tinged with red. Yellow-winged individuals readily distinguished from the typically yellow-winged species of the trogon group by entirely black basal half of the first two plaits (anterior or first paired fold of wing) (Fig. 6). In Paraguay, Argentina, and Uruguay wings tend to be orange-red, and yellow markings are tinged with red. In Bolivia, Peru, and Ecuador reduction and variation in leg banding evident. Elsewhere, hind femur almost always has three pale bands and the hind tibia two pale bands. Specimens from Ecuador and Peru lack hind tibial bands, and hind femur usually has a strong proximal band, median band may be weak or absent, and distal band almost always absent.”

Furthermore, Chromacris species do not mimic wasps, and there is no wasp genus with the name Pepris. Hudson is obviously referring to new world spider-hunting wasps (tarantula hawks) of the genus Pepsis Fabricius, 1804 of the family Pompilidae, a family which includes at least 133 described species (Vardy 2000). Vardy says: “For sheer variety of size and colour, the spectacular wasps of the genus Pepsis Fabricius, 1804, including 133 known species, are unrivalled by any aculeate group in the world. Their diversity of colour approaches that of butterflies, often with extreme variation between sexes and within species; the members vary from the gigantic, brassy-haired females of the P. sumptuosa group whose astonishing size (65 mm long) instantly commands respectful attention, to the slender, comparatively diminutive (11 mm long), brilliant green males of P. purpurea. The members of this genus, making their nests in burrows in the ground and provisioning them exclusively with mygalomorph spiders (usually Theraphosidae, i.e., tarantulas), are found everywhere in the New World from the USA and West Indies to Chilean and Argentine Patagonia; in all habitats from rainforest to desert, and in the High Andes reaching altitudes of around 3,400m.” (Fig. 4A).

The Batesian mimics of the tarantula hawks are indeed orthopterans, but from another suborder, Ensifera Chopard, 1921 (including crickets, katydids and wetas) not Acridomorphs. They belong to the subfamily Phaneropterinae of the Tettigoniidae.

According to Hudson’s description of the orthopteran mimic of the wasps found in La Plata, he is almost undoubtedly referring to Scaphura nigra (Thunberg, 1824), an extraordinary phaneropterine tettigoniid (Fig. 4B). Mimism must not be confused with aposematism as a whole, as described above. At least there are three uses of the term mimetism: Batesian, Mullerian, and Waismanian (Pasteur 1982). We are concerned here with a clear case of Batesian mimicry (Bates 1862, 1863) in which a mimic resembles another species which is unpalatable for different reasons. It should be noted that, usually, the mimic resembles an aposematic model. This is the case of the humble katydid Scaphura (mimic) and the dangerous wasps Pepsis (models)6; it is worth noting that other katydids are mimics of wasps (e.g., Aganacris spp., Grant 1958, and see Nickle this issue), but these do not occur in Argentina.

Furthermore, S. nigra is a polymorphic mimic of wasps. Del Claro (1991) demonstrated that three morphs of S. nigra mimicked three different species in Brazil. This author identified in laboratory–bred S. nigra nymphs, three morphs (also found in the field) that mimic wasps of three different species. The ‘Pepsis’ morph is a mimic of Pepsis wasps (Pompilidae). This is certainly what Hudson described.

In chapter three of his book “Contributions to the Theory of Natural Selection” (1871, a compilation of former essays), devoted to mimicry in the animal kingdom, Alfred Russel Wallace writes (p. 98): “There is a genus of small spiders in the tropics which feed on ants, and they are exactly like ants themselves, which no doubt gives them more opportunity of seizing their prey; and Mr. Bates found on the Amazon a species of Mantis which exactly resembled the white ants which it fed upon, as well as several species of crickets (Scaphura), which resembled in a wonderful manner different sand-wasps of large size, which are constantly on the search for crickets with which to provision their nests”. As we have seen, the tarantula hawks hunt spiders, not crickets! Another little error in the Scaphura story.
Two other morphs resemble, respectively, Polistes (Vespidae) and Entypus (Pompilidae) wasps. Ressemblance between tettigoniid mimics and wasp models was constated in coloration, morphology, times of activity, use of substrate, and behavior. This extraordinary Batesian mimicry polymorphism has been hypothesized by Del Claro (1991) as resulting from density-dependent selection.

Discussion and conclusions

This paper is obviously not intended to discredit Hudson, just to correct some mistakes pertaining to my favorite research organisms: species of Orthoptera I know fairly well from years in the field, including most of the regions Hudson explored. Indeed, I have great admiration for this notable self-taught naturalist. Hudson was not only a keen observer of nature, he was also compassionate with all living beings and reflected philosophically and authoritatively about their origins and habits. He was amazed and delighted by what we call now biodiversity: aesthetic pleasure in its contemplation was as important to him as scientific knowledge.

Furthermore, he was a pioneering conservationist, as these opening lines from his book show: “During recent years we have heard much about the great and rapid changes now going on in the plants and animals of all the temperate regions of the globe colonized by Europeans. These changes, if taken merely as evidence of material progress, must be a matter of rejoicing to those who are satisfied, and more than satisfied, with our system of civilization, or method of outwitting Nature by the removal of all checks on the undue increase of our own species. To one who finds a charm in things as they exist in the unconquered provinces of Nature’s dominions, and who, not being over-anxious to reach the end of his journey, is content to perform it on horseback, or in a wagon drawn by bullocks, it is permissible to lament the altered aspect of the earth’s surface, together with the disappearance of numberless noble and beautiful forms, both of the animal and vegetable kingdoms. For he cannot find in it his heart to love the forms by which they are replaced; these are cultivated and domesticated, and have only become useful to man at the cost of that grace and spirit which freedom and wildness give. In numbers they are many—twenty-five millions of sheep in this district, fifty millions in that, a hundred millions in a third—but how few are these human-caused depletions of the most precious thing upon Earth: life.

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