

CLINAL INTERGRADATION OF *HESPERIA COMMA*
COLORADO (HESPERIIDAE)

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Hesperia colorado (Scudder) was treated as a separate species from *H. harpalus harpalus* (Edwards) and *H. harpalus ochracea* Lindsey (MacNeill, 1964). This paper demonstrates that *H. colorado* intergrades clinally with another subspecies of *H. harpalus* near *ochracea*. Since *H. colorado* has priority over *H. harpalus*, *harpalus* can no longer be used as the species name. Higgins and Riley (1970) and C. D. MacNeill (unpublished) now consider these American taxa to be subspecies of *Hesperia comma* (Linnaeus), therefore I will use the names *H. comma colorado* and *H. comma ochracea*.

The Arkansas River Valley in Lake and Chaffee Counties, Colorado, was chosen for study because its gradual descent towards the plains provided a relatively even environmental gradient allowing intergradation of *H. comma*, which evidently is continuously distributed along the river. Six stations were chosen at about equal distances along the river (Table 1).

The population of *H. comma* from Salida to Cotopaxi, referred to below as *H. c. ssp.*, represents an undescribed subspecies differing from *H. c. ochracea* in having a more yellowish ochre-yellow ventral ground color, and in having the ventral hindwing spots silvery white and forming an acute chevron as in *H. c. colorado*, whereas *H. c. ochracea* often has this band differently shaped and often ochre-suffused.

Results

Wing pattern. *H. c. colorado* is darker than *H. c. ssp.* in ground color and darkness of the ventral front wing tornus. Fig. 1 shows the specimens used as color grades from light to dark. Table 1 demonstrates the cline of ventral hind wing color from mostly black overlain with greenish ochre scales in *H. c. colorado*, to mostly yellow in *H. c. ssp.*

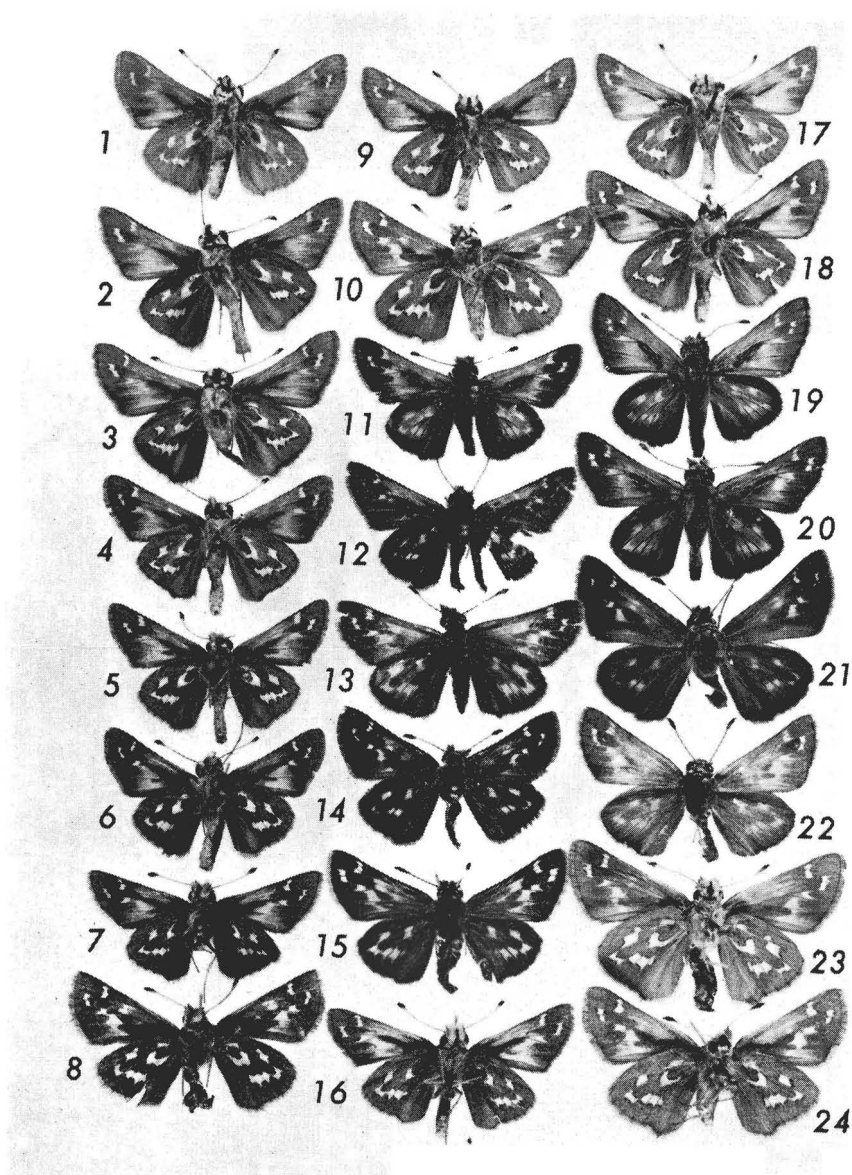
There is considerable variation in *H. c. colorado*, much more than in *H. c. ssp.* The dorsal ground color of *colorado* varies from light to dark. The ventral forewing tornus varies from nearly solid black to ochre (darker in females). The dorsal forewing apical spots are usually reddish brown but are rarely whitish in males and occasionally whitish in females. The ventral hindwing is rarely green in males, and occasionally green in females, but usually has yellowish ochre scales of variable

TABLE 1. Number of specimens per color grade and average color grade for each locality. Mileage refers to the distance downstream along the Arkansas River from the Tennessee Pass locality.

| Mileage and Locality | Sex | Number of Specimens Per Color Grade | | | | | | | | Average Color Grade |
|---|-----|-------------------------------------|----|----|----|----|----|---|---|---------------------|
| | | Color Grade | | | | | | | | |
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| 0 mi., near Tennessee Pass, 10400' | ♂ | — | — | 4 | 8 | 13 | 18 | 4 | — | 5.21 |
| | ♀ | — | — | — | 3 | 12 | 6 | 3 | 1 | 5.48 |
| 0 mi., near Tennessee Pass (reared) | ♂ | — | — | 3 | 1 | — | — | — | — | 3.25 |
| | ♀ | — | — | 1 | 3 | 3 | — | — | — | 4.29 |
| 14 mi., Mt. Massive Trout Club, 9400' | ♂ | — | 2 | 5 | 16 | 8 | 1 | — | — | 4.03 |
| 22 mi., 1.6 mi. N. of Granite, 9100' | ♂ | — | 2 | 10 | 8 | 2 | 2 | — | — | 3.67 |
| | ♀ | — | — | — | — | 1 | — | — | — | 5.00 |
| 28 mi., near Pine Creek, 8800' | ♂ | — | 2 | 1 | — | 1 | — | — | — | 3.00 |
| | ♀ | — | — | — | 1 | — | — | — | — | 4.00 |
| 39 mi., near Buena Vista, 8500–9200' | ♂ | — | 2 | — | 1 | 3 | — | — | — | 3.83 |
| 61–84 mi., Salida to Cotopaxi, 6600–7200' | ♂ | 6 | 23 | 12 | 1 | — | — | — | — | 2.19 |
| | ♀ | — | 1 | 3 | 2 | 1 | — | — | — | 3.43 |

darkness over a black ground color. Rarely the underside is somewhat mottled. The ventral hindwing band is an acute chevron in most males but in only about a third of the females. One female had this band with scattered black scales. The ventral hindwing fringe sometimes has darker spots at the ends of veins. Variation of *H. c. ssp.* is similar except that ground color and ventral hindwing color is less variable, and the silver chevron is sometimes less silvery white than in *colorado*.

At least part of the darkness of *H. c. colorado* is genetic, because the



Figs. 1-24. *H. comma* adults. Figs. 1-8 have the underside color referred to in Table 1 using those same numbers. *H. c. colorado*: 5-7 ♂, 8 ♀, 9 ♂, 10 ♀, 11-12, ♂, 13-15 ♀, all near Tennessee Pass, 9-28 August. *H. c. ssp.*: 1 ♂ (6 mi. W Villa Grove, Saguache Co., Colorado, 9 August 1969); 3 ♂ (Spring Creek, Fremont Co., Colorado, 15 August 1965); 19 ♂ (3 mi. SW Cotopaxi, Fremont Co., Colorado, 3 August 1965); 20 ♂ (Querida, Custer Co., Colorado, 1 September 1962); 21 ♀ (Spring Creek, Fremont Co., Colorado, 7 August 1969); 22 ♀ (Silver

TABLE 2. Number of antennal shaft segments of males.

| Number of Segments | Number of Specimens at each Locality | | | | | |
|--------------------|--------------------------------------|------------------------|---------|------------|----------------|--------------------|
| | Tennessee Pass | Mt. Massive Trout Club | Granite | Pine Creek | E. Buena Vista | Salida to Cotopaxi |
| 16 | 5 | 4 | 1 | 1 | — | — |
| 17 | 4 | 4 | 7 | 2 | 4 | 2 |
| 18 | 1 | — | 2 | 1 | 2 | 5 |

ventral ground color remained greenish on a black background in 4 males and 7 females which were reared indoors at about 20°C. The reared individuals were slightly larger, had greener ventral color (few wild individuals have green scales), and the upperside was somewhat lighter, than wild-caught *colorado*.

Genitalia. There are slight genitalic differences between *H. c. colorado* and *H. c. ssp.* In males the uncus is usually narrow in *H. c. colorado*, and is occasionally narrow but often broader in *H. c. ssp.* This character is also clinal. MacNeill (1964) stated that the penis of *H. c. colorado* had a unidentate rostellum, but I found that about 10% of both subspecies have a unidentate (versus a bidentate) rostellum. The female lamella postvaginalis is so variable individually that I cannot detect interpopulational differences; it is certainly no broader in *H. c. colorado*, and is sometimes narrower than in *H. c. ssp.*

Antennae. Antennal shafts are longer in *H. c. ssp.* (and *H. c. ochracea*) than in *H. c. colorado*, but this character is also clinal at least for males (Table 2). The 4 reared *colorado* males all had 16 segments, so this low number may be genetically inherited. The female antenna has a white ring at the base of the club in 80–90% of *H. c. ssp.* but only in 50% of *H. c. colorado* (16 of 32). The 2 females from Pine Creek and near Granite have almost a complete ring.

Early stages. *H. c. colorado* has fewer micropyle spines than *H. c. ochracea*. In *colorado*, 4 eggs had 4 spines, and 4 had 5 spines. In *ochracea*, 3 had 4 spines, 9 had 5 spines, and 5 had 6 spines. The larvae and pupae of both are almost identical to each other (Scott, 1974) and to *H. c. harpalus* (MacNeill, 1964). The laboratory developmental pe-

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Park, Custer Co., Colorado, 1 September 1962); 23 ♀ (Kuntz Gulch, Fremont Co., Colorado, 26 August 1971). Intergrades: 2 ♂ (2 mi. E Buena Vista, 17 August 1971); 4 ♂ (Mt. Massive Trout Club, 16 August 1971); 16 ♀, 17–18 ♂, 24 ♀ (N of Granite, 16 August 1971).

riod of *H. c. colorado* is much shorter than that of *H. c. ochracea*, apparently through genetic adaptation to high-altitude (Scott, 1975).

Foodplants. In the laboratory, *H. c. colorado* and *H. c. ochracea* larvae feed on many different grasses (Scott, 1975). In nature, *H. c. ochracea* 1 mi. N of Cheesman Reservoir, Jefferson Co., oviposits on many different plants: 3 eggs were found on *Arenaria fendleri* (Caryophyllaceae) plants without inflorescences (which resemble grass), 1 egg on *Bouteloua gracilis* leaf, 3 eggs on *Andropogon saccharoides* leaves, and 8 eggs on *Carex* sp. leaves. A female at Nighthawk, Douglas Co., laid 1 egg on *B. gracilis* leaf. These eggs were distinguished from other *Hesperia* by the basal flange. It is possible that *H. comma* oviposits on any plant resembling a grass, and it may even oviposit on plants of other forms, which were not searched thoroughly. Because of broad larval tolerance and random oviposition, it is unlikely that *H. c. ochracea* is restricted to one larval host.

Mate-locating behavior. *H. c. colorado* and *H. c. ssp.* have the same mate-locating system. Males perch throughout the day on stones and other ground objects, and dart out at passing objects in search of females. This behavior occurs mainly on hilltops, where most males were collected except near Tennessee Pass, where males perched on top of mine spoils and on top of prominent banks of roads, which were evidently substitutes for hilltops. Copulating pairs of *H. comma* were found at 1029 and 1159 hours, at Cripple Creek, Teller Co., and at 1300 hours (all 24-hour ST) north of Granite, Lake Co., all on hilltops.

Other characters. MacNeill (1964) lists *H. c. colorado* as having fewer apiculus segments, longer eyelashes, and paler prothoracic tibial spines. The number of apiculus segments proved too variable (one *H. c. ssp.* had only 1–2 segments apparent ventrally) to find interpopulational differences, and significant differences between *H. c. colorado* and *H. c. ssp.* were not found in the other two characters.

Discussion

This paper describes intergradation of *H. c. colorado* only with *H. c. ssp.*, but I believe *colorado* also intergrades with *H. c. ochracea* and *H. c. harpalus*. At higher elevations west of the continental divide, populations contain individuals resembling *colorado*, *harpalus*, and individuals intermediate in wing pattern. *H. c. ssp.* occurs along the Arkansas River southward and in the San Luis Valley, and it intergrades phenotypically with *H. c. colorado* in western Conejos Co. *H. c. ochracea* occurs in "typical" form (it is quite variable) along the foothills of the Front Range. At higher elevations in Teller, Park, Jefferson, and Boulder

Counties, individuals become darker and with the white ventral spots less ochre and more in an acute chevron, characteristics of *colorado*. A population at Cripple Creek, Teller Co., is mostly referable to *H. c. ssp.* but has some *H. c. ochracea* and some *H. c. colorado* admixture. The situation in the Front Range of Colorado is complicated by great variability. It is my opinion that the Colorado specimens of *H. comma* "*manitoba*" (MacNeill, 1964) are part of the Front Range *H. comma ochracea-colorado* populations, and that the name *manitoba* should be applied only to populations north of Colorado.

Summary

H. c. colorado intergrades clinally with a subspecies of *H. comma* near *ochracea* in several wing and structural characters. At least one of these characters and duration of developmental stages differ when the two taxa are reared in identical conditions; the high altitude *H. c. colorado* therefore apparently differs genetically from the lower altitude *H. c. near ochracea*.

ACKNOWLEDGMENT

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