

## A TAXONOMIC STUDY OF POPULATIONS OF TIGER BEETLES IN THE *CICINDELA LONGILABRIS* COMPLEX FROM THE BLACK HILLS OF SOUTH DAKOTA

S. M. Spomer

Department of Entomology  
208 Entomology Hall  
University of Nebraska  
Lincoln, NE 68583-0816  
sspomer1@unl.edu

**ABSTRACT**—Three phenotypes within the *Cicindela longilabris* complex are present in the vicinity of the Black Hills in South Dakota: Laurent's boreal long-lipped tiger beetle, *Cicindela longilabris laurentii*; the prairie long-lipped tiger beetle, *Cicindela nebraskana*; and a third phenotype that shares characteristics of both species. By comparing morphological and ecological characteristics between these three phenotypes, I was able to separate *C. longilabris* and *C. nebraskana* using ventral and proepisternal color, presence or absence of a middle band on the elytra, elytral luster, labral width:length ratio, and hind tarsal length. Somewhat less useful characters were labral color and total length. The third phenotype was often not assignable to either species and probably represents hybrid populations, showing gene flow (introgression and recombination) between *C. longilabris* and *C. nebraskana*, as individuals were often found in overlapping prairie/boreal habitats at intermediate altitudes.

**Key Words:** Cicindelidae, hybridization, taxonomy

### INTRODUCTION

There are 24 or 25 species of tiger beetles reported from South Dakota (Kirk and Balsbaugh 1975; Backlund et al. 2005; Spomer et al. 2008), including one subspecies that is endemic to the Badlands (Spomer 2004). Two closely related species, *Cicindela longilabris laurentii* Schaupp and *C. nebraskana* Casey, are both reported from the Black Hills (Backlund et al. 2005; Weins and Krueger 2005). Laurent's boreal long-lipped tiger beetle, *C. longilabris laurentii*, is found throughout the Rocky Mountains from New Mexico to Canada, with disjunct populations occurring in the White Mountains of Arizona and the Black Hills of South Dakota (Pearson et al. 1997). It is found in meadows or grassy areas with nutrient-poor, acidic soils in or near coniferous forests (Pearson et al. 2006). It is variable in color, but Black Hills specimens are usually dark brown/bronze, with up to three white marks on each elytron, including a fairly distinct middle band. Spanton (1988) characterized a population he referred to as *C. longilabris* in the Black Hills as being "lightly marked." Ventrally, they are usually metallic blue-green, and both sexes have white labra. This species

is considered to have a spring-fall activity pattern, but are often seen in mid- to late July at higher elevations in the Black Hills.

The prairie long-lipped tiger beetle, *C. nebraskana*, is a species found throughout western North America, including the Great Plains. As its common name suggests, it is found on treeless or near treeless prairies with rich soils (Pearson et al. 2006). It is black, both dorsally and ventrally (rarely with a slight purplish reflectance ventrally), and has smoother and shinier elytra than *C. longilabris*. The labrum of the male is white, while that of the female is black or dark brown. It is also a spring-fall species, but most records are from spring.

A third phenotype is also present in the Black Hills. Individuals of this form have characteristics of both *C. longilabris* and *C. nebraskana* and cannot be identified with certainty. They are usually unmarked like *C. nebraskana* but have coloration more like *C. longilabris* (e.g., metallic blue-green ventrally). They occur on prairie hilltops within Ponderosa pine forests and seem to be more common in the lower-elevation southern Black Hills. There are several possibilities as to the identity of this third phenotype: (1) they are variants of *C. nebraskana*, with metallic undersides, (2) they are unmarked

variants of *C. longilabris* (typically marked *C. longilabris* are also found in the Black Hills), (3) they are a third, undescribed species, (4) they are part of a hybrid population between *C. longilabris* and *C. nebraskana*, or (5) they are intergrades between two subspecies of one species, *C. longilabris* (thus, *C. nebraskana* would be a synonym of *C. longilabris*).

From a conservation and taxonomic viewpoint, it is important to determine the identity of these beetles. Although not rare in the Black Hills, *C. longilabris* is disjunct from the populations inhabiting the Rocky Mountains. At this point, it is unknown if these Black Hills populations are genetically distinct from their Rocky Mountain counterparts. In contrast, *C. nebraskana* does not appear to be disjunct in South Dakota but nevertheless is a rare beetle in South Dakota and Nebraska (Backlund et al. 2005; Brust and Hoback 2005), so identification is crucial before conservation steps can be taken to ensure its survival.

The objectives of this study were to compare morphological, ecological, and behavioral characteristics between *C. longilabris*, *C. nebraskana*, and the unknown phenotypes in the Black Hills and vicinity. Key characteristics were determined for the two species, and an identity, based on these characteristics, was given to the unknown populations.

## MATERIALS AND METHODS

Two trips were made to coincide with the spring-fall adult activity of *C. nebraskana* and *C. longilabris*: May 11-14 and September 6-8, 2006. The following sites were visited in May: Wilson Ranch (Sioux County, NE), Robinson Flats (Fall River County, SD), Cottonwood Springs (Fall River County, SD), Ft. Meade Bureau of Land Management (BLM) Recreation Area (Meade County, SD), Boundary Gulch (Crook County, WY, and Lawrence County, SD), and McNenny Fish Hatchery (Lawrence County, SD). The same sites were visited in September, along with an additional site in the Bear Lodge Mountains (Crook County, SD) and Timon Campground (Lawrence County, SD).

Attempts were made to collect all specimens seen, and these were either preserved in 70% EtOH or kept alive in glassine envelopes. Third-stage larvae of presumed *C. longilabris* complex species were dug up from Wilson Ranch, Robinson Flats, and Ft. Meade BLM Recreation Area and transferred to terraria with their native soil. Three pairs of live adults of *C. nebraskana* (Wilson Ranch) and the Robinson Flats population were set up in

terraria with soil and grasses from their native habitat in an attempt to start a colony. These were fed mealworms (*Tenebrio* sp.) and wingless "fruit" flies (*Drosophila melanogaster*) and watered daily.

Soil samples from Wilson Ranch, Robinson Flats, and Boundary Gulch were analyzed at the University of Nebraska-Lincoln for various nutrients (C, N, P, and K), pH, and organic matter.

A small sample (1 to 6 adults) from Wilson Ranch, Robinson Flats, Boundary Gulch, Ft. Meade BLM Recreation Area, and McNenny Fish Hatchery, as well as an outgroup of *C. longilabris longilabris* Say from Ontario (provided by M.L. Brust) were killed in 95% EtOH and sent to Alfried Vogler in London for DNA analysis.

After adults from the rearing attempt died, they were pinned and allowed to dry. These specimens, along with those from the collections of Scott Weins (Spearfish, SD), Doug Backlund (Pierre, SD), Matt Brust (Lincoln, NE), and the author, were examined to determine the following data: locality, altitude (if known), habitat (if known), date of capture, sex, labrum color, total length (tip of labrum to tip of abdomen, unless genitalia were everted; then, tip of elytra), meta (hind) tarsus length, presence or absence of middle band, humeral lunule, apical lunule, dorsal color, ventral color, proepisternum color, and elytral luster or reflectance (shiny, dull, or intermediate). In addition, metatibia:metatarsus ratio was determined for a small sample of adults, as was labrum width:length ratio, and an estimation of setal density on the metathoracic sternite was made. Measurements were made with an Olympus SZH10 stereomicroscope and a metric miniscale (Bio-Quip Products, Gardena, CA).

Typical *C. nebraskana* were examined from Harding County, SD (1 specimen), Ziebach County, SD (2 specimens), Scotts Bluff County, NE (2 specimens), and Sioux County, NE (34 specimens). The site in Sioux County (Wilson Ranch; 3 mi. N, 8.5 mi. NW of Harrison) is probably very close to the locality where Casey collected his type series (M.L. Brust, pers. comm.). These were compared to what was determined to be *C. longilabris* (based on literature, several morphological characters, habitat, altitude, etc.) to try to determine defining, or key, characteristics of each species. Individuals from each population were then rated on these characteristics in an attempt to categorize populations as *C. nebraskana*, *C. longilabris*, both, or hybrids/intermediates between the two.

For metatibia:metatarsus ratio, metatarsal length, and labrum length:width ratio comparisons, additional specimens from outside the Black Hills area were used. These

included *C. l. longilabris* (Ontario, New Brunswick), *C. l. laurentii* (Colorado, New Mexico, Wyoming, Utah), *C. l. longilabris* × *C. l. laurentii* (Manitoba), *C. l. perviridis* Schaupp (Idaho, Washington, Oregon, California), and *C. nebraskana* (Montana, Colorado, Saskatchewan).

In all, 215 specimens were examined. Of these, 120 were from the Black Hills (Fall River, Custer, Pennington, Meade, and Lawrence counties, SD, and Crook County, WY), 53 were from nearby counties in Nebraska, Wyoming, and South Dakota within 100-150 miles from the Black Hills, and 42 were from other states and provinces.

GPS coordinates were taken at visited sites with a Garmin eTrex Vista™.

## RESULTS AND DISCUSSION

Spatial representation of sites is shown in Figure 1 and listed in Table 1. A more detailed description of these sites is given in Appendix 1.

### Morphologically Separating *C. nebraskana* from *C. longilabris*

Pearson et al. (2006) and Leffler (1979) list the following differences, summarized in Table 2.

As indicated in Table 1, ventral and proepisternal color (black vs. metallic greens, blues, purples, etc.), presence or absence of a middle band, and elytral luster were the most useful characters for distinguishing the two species. Other important characters were hind tarsal length and labral width:length ratio. Labrum color was not as consistent, with only 79% of female *C. longilabris* having white labra, while 5% of female *C. nebraskana* also had white labra (in contrast, Spanton [1988] reported 44.8% of female *C. nebraskana* had light-colored labra and 90.3% of female *C. longilabris* had white labra). In total length, male *C. nebraskana* averaged 1.0 mm shorter than *C. longilabris*, but females of both species only varied by 0.5 mm (13.8 mm for *C. nebraskana* vs. 14.3 mm for *C. longilabris*).

### Morphological Measurements

**Metatibia:Metatarsus Ratio.** Leffler (1979) reported that the metatibia:metatarsus ratio was a good distinguishing character for *C. longilabris* and *C. nebraskana*, but his specimens of *C. nebraskana* were from the Pacific Northwest and a form he considered to be a separate subspecies, *C. n. chamberlaini* Knaus. He stated that the

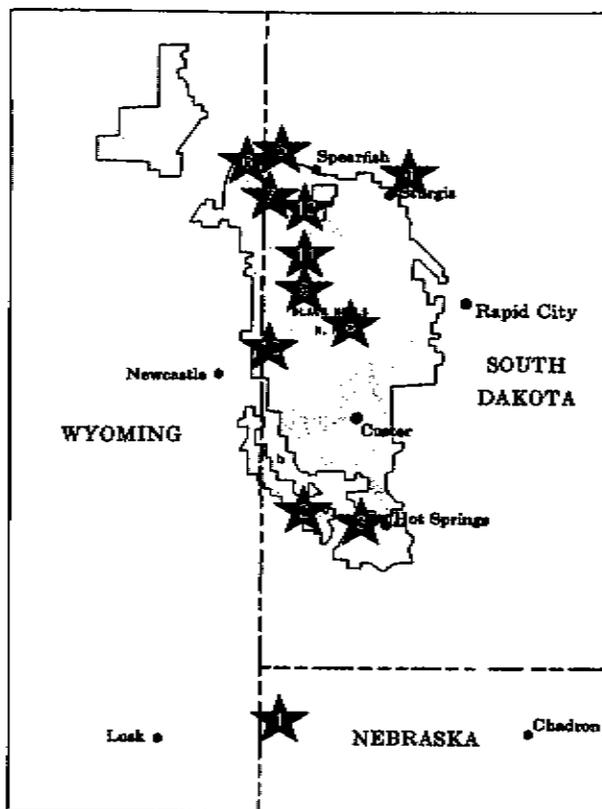


Figure 1. Map of Black Hills and vicinity. Outlined areas are Black Hills National Forest. Numbers correspond to collection sites listed in Appendix 1.

ratio was always less than 0.99 (most were 0.95 or less) for *C. nebraskana* and greater than 1.00 for *C. longilabris*. I measured a sample ( $n = 10$ ) of Nebraska *C. nebraskana*, South Dakota *C. longilabris* ( $n = 10$ ), Rocky Mountain *C. longilabris laurentii* ( $n = 7$ ), Manitoba *C. l. longilabris* × *C. l. laurentii* ( $n = 9$ ), and *C. l. perviridis* ( $n = 9$ ). Ratio means were 0.996 for *C. nebraskana* (range of 0.97 to 1.04), 0.974 for South Dakota *C. longilabris* (range of 0.92 to 1.03), 1.02 for Rocky Mountain *C. l. laurentii* (range of 0.95 to 1.08), 0.984 for Manitoba *C. l. longilabris* × *C. l. laurentii* (range of 0.89 to 1.17), and 0.92 for *C. l. perviridis* (range of 0.82 to 1.02). Because of the large amount of variability, I concluded that the metatibia:metatarsus ratio was not a good character for separating the two species. However, while examining the ratios, I noticed what appeared to be a difference in hind tarsal lengths, which led to the discovery of *C. nebraskana* having shorter hind tarsal lengths than *C. longilabris* (and females having shorter hind tarsi than males in both species, which was unexpected). Hind tarsal lengths were as follows: *C. nebraskana* (male,  $n = 14$ , 4.8 mm; female,  $n = 22$ , 4.7 mm), South Dakota *C. longilabris* (male,  $n = 17$ , 5.4 mm;

TABLE 1  
MORPHOLOGICAL COMPARISONS OF *C. NEBRASKANA* (NEBRASKA AND SOUTH DAKOTA),  
*C. LONGILABRIS* (BLACK HILLS), AND BLACK HILLS POPULATIONS OF "UNKNOWN"

Taxon	Length (mm)		Hind tarsus length (mm)		Labrum color (%)							
					White		Brown/Mottled		Black		Ventral color (% black)	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
<i>C. nebraskana</i>	12.9	13.8	4.8	4.7	92	5	8	39	0	56	100	100
	(17, 0.1)	(22, 0.0)	(14, 0.0)	(22, 0.0)								
<i>C. longilabris</i>	13.9	14.3	5.4	5.1	100	79	0	21	0	0	6	0
	(17, 0.1)	(16, 0.2)	(17, 0.0)	(15, 0.1)								
<b>Site of unknown identification</b>												
Ft. Meade BLM Recreation Area	13.0	13.9	5.0	4.8	100	17	0	17	0	67	50	67
	(6, 0.1)	(6, 0.1)	(6, 0.0)	(6, 0.1)								
McNenny Fish Hatchery	13.3	13.8	4.9	4.9	100	0	0	67	0	33	33	0
	(3, 0.1)	(3, 0.1)	(3, 0.1)	(3, 0.1)								
Robinson Flats	13.3	14.0	5.0	4.7	100	14	0	71	0	14	7	29
	(15, 0.1)	(7, 0.3)	(14, 0.1)	(7, 0.1)								
Cottonwood Springs	13.6	14.0	5.0	4.7	100	13	0	63	0	25	0	0
	(10, 0.1)	(8, 0.2)	(9, 0.1)	(8, 0.1)								
Boundary Gulch	13.6	13.9	5.2	4.8	100	50	0	33	0	17	0	0
	(6, 0.1)	(6, 0.1)	(5, 0.2)	(6, 0.1)								
Timon Campground	14.3	14.3	5.4	5.1	100	100	0	0	0	0	0	0
	(2, 0.2)	(2, 0.5)	(2, 0.0)	(1, 0.0)								
Black Fox Campground	14.0	15.3	5.4	5.3	100	100	0	0	0	0	0	0
	(2, 0.4)	(2, 0.2)	(2, 0.1)	(2, 0.0)								
Moon Campground	12.5	14.2	5.1	5.2	100	100	0	0	0	0	0	0
	(1, 0.0)	(3, 0.4)	(1, 0.0)	(3, 0.0)								
Keough Draw	13.8	—	5.4	—	100	—	0	—	0	—	0	—
	(2, 0.2)		(2, 0.1)									
Deerfield Lake	14.0	13.8	5.5	5.1	100	100	0	0	0	0	0	0
	(1, 0.0)	(2, 0.2)	(1, 0.0)	(2, 0.1)								
Terry Peak	14.7	15.4	5.4	5.3	100	100	0	0	0	0	0	0
	(1, 0.0)	(2, 0.1)	(1, 0.0)	(2, 0.1)								
Taxon	Middle band presence (%)		Proepisternum color (% black)		Luster (%)							
					Dull		Shiny		Intermediate			
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀		
<i>C. nebraskana</i>	8	0	100	100	0	0	92	100	8	0		
<i>C. longilabris</i>	88	86	6	0	81	93	0	0	19	7		
<b>Site of unknown identification</b>												
Ft. Meade BLM Recreation Area	17	0	67	67	0	0	100	100	0	0		
McNenny Fish Hatchery	0	0	33	0	0	0	100	100	0	0		
Robinson Flats	13	0	7	29	0	0	100	100	0	0		
Cottonwood Springs	0	0	0	0	0	0	100	100	0	0		
Boundary Gulch	33	50	0	0	50	67	17	0	33	33		
Timon Campground	50	100	0	0	50	100	0	0	50	0		
Black Fox Campground	100	100	0	0	100	100	0	0	0	0		
Moon Campground	0	100	0	0	0	67	0	0	100	33		
Keough Draw	50	—	0	—	100	—	0	—	0	—		
Deerfield Lake	100	100	0	0	100	100	0	0	0	0		
Terry Peak	100	100	0	0	100	100	0	0	0	0		

Note: Numbers in parentheses are number of individuals (*n*) and standard error of the mean (SE).

TABLE 2  
MORPHOLOGICAL DIFFERENCES BETWEEN THE PRAIRIE LONG-LIPPED TIGER BEETLE,  
*C. NEBRASKANA*, AND THE BOREAL LONG-LIPPED TIGER BEETLE, *C. LONGILABRIS*

<i>C. nebraskana</i>	<i>C. longilabris</i>
Elytral punctures irregularly arranged, not in distinct, transverse rows; few, thus appearing shiny	Elytral punctures in distinct, but sometimes, wavy, transverse
Ratio of metatibia length/metatarsus length <0.99	Ratio of metatibia length/metatarsus length $\geq$ 1.0
Black dorsally and ventrally	Metallic purple to green ventrally
Thin middle band only, if any marks present	Maculated, with up to 3 distinct marks on the elytron
Female with dark or partially dark labrum	Female with white labrum

Note: From Pearson et al. (2006) and Spanton (1979).

female,  $n = 15$ , 5.1 mm), Rocky Mountain *C. l. laurentii* (male and female combined,  $n = 8$ , 5.2 mm), Manitoba *C. l. longilabris*  $\times$  *C. l. laurentii* (male and female combined,  $n = 7$ , 5.2 mm), New Brunswick/Ontario *C. l. longilabris* (male and female combined,  $n = 10$ , 5.4 mm), and *C. l. perviridis* (male and female combined,  $n = 15$ , 5.4 mm). Only one male *C. nebraskana* had a tarsal length of  $>5.0$  mm, and only two female *C. longilabris* (South Dakota) had a tarsal length  $<5.0$  mm, so tarsal length was a good, consistent character to distinguish the two species.

**Labrum Width:Length Ratio.** A sample of *C. nebraskana* and *C. longilabris* was used to determine the width:length ratio of the labrum. Width:length ratio averaged 1.50 for *C. longilabris* ( $n = 29$ ), while *C. nebraskana* (from Nebraska and from Albany County, WY;  $n = 25$ ) averaged 1.63. Labral width:length ratio for *C. nebraskana* from other states and provinces (Colorado, Montana, Saskatchewan;  $n = 7$ ) also averaged 1.63 but were more variable. This is in agreement with Spanton (1988), who reported that *C. longilabris* had a greater labral length relative to width.

**Hairs on Metathoracic Sternite.** A cursory examination of the hairs on the metathoracic sternite appeared to be denser in *C. longilabris* than in *C. nebraskana*. After examining all specimens, however, it was decided that hair density was too variable to be a useful character.

#### Ecologically Separating *C. nebraskana* from *C. longilabris*

Pearson et al. (2006), Spanton (1988), Wallis (1961), Criddle (1907), and Wickham (1899) list the following ecological characteristics, summarized in Table 3.

For the most part, my observations were consistent with published information on the two species. The Wil-

son Ranch site (true *C. nebraskana*) was open, shortgrass prairie at about 1550 m elevation. Typical *C. longilabris* (from Timon Campground, Deerfield Lake, Moon Campground, Keough Draw, Black Fox Campground, Terry Peak) were from altitudes of 1768-1951 m. Boundary Gulch (about 1463 m+, with habitat more similar to higher-altitude sites) had individuals that appeared to be true *C. longilabris*, along with individuals that had *C. nebraskana*-like qualities. Other sites (McNenny, Ft. Meade, Cottonwood Springs, Robinson Flats) were lower in altitude (1067-1280 m), even more so than Wilson Ranch, but had similar habitat as Wilson Ranch, and beetle phenotype was more *C. nebraskana*-like, although some intermediate-looking individuals were found. All three phenotypes tended to fly into the grass when disturbed.

Results of the soil analyses are shown in Table 4. All three samples were classified as silty loam soils. Soil samples from Wilson Ranch were lowest in pH, low in phosphorus (P), highest in potassium (K), organic carbon (C), nitrogen (N), and organic matter. Soil from Boundary Gulch was neutral in pH, high in P, and slightly lower than Wilson Ranch in organic C, K, and N. Robinson Flats was neutral in pH, and lowest in P, K, organic C, and N. These results were fairly consistent with the scant published data, although Boundary Gulch (a *C. longilabris* site) was not acidic. Though the soil from Wilson Ranch (*C. nebraskana* site) was the most nutrient-rich and highest in percentage of organic matter, differences between the three sites were not dramatic.

#### Rearing

Larvae excavated from Wilson Ranch, Robinson Flats, and Ft. Meade BLM Recreation Area emerged as cow path tiger beetle, *C. purpurea audubonii* Le Conte, adults later in 2006 and early 2007. These were

TABLE 3  
 ECOLOGICAL DIFFERENCES BETWEEN THE PRAIRIE LONG-LIPPED TIGER BEETLE, *C. NEBRASKANA*,  
 AND THE BOREAL LONG-LIPPED TIGER BEETLE, *C. LONGILABRIS*

<i>C. nebraskana</i>	<i>C. longilabris</i>
Found in shortgrass prairie grasslands with few or no trees	Found in meadows or grassy areas in open coniferous forests
Prefers nutrient-rich soils; heavy clay soils; Chernozemic (Mollic) soils dominate	Prefers sandy, often nutrient-poor, acidic soils in or around coniferous forests
Prefers bare soil but flies into the grass when disturbed	Found on stony banks, roads, and paths, at some distance from water
	Found at higher altitudes

Note: From Criddle (1907), Pearson et al. (2006), Spanton (1988), Wallis (1961), and Wickham (1899).

TABLE 4  
 SOIL ANALYSIS FROM SELECTED SITES

Site	Total C (%)	Organic C (%)	Organic matter (%) (LOI)	Total N (%)	Bray P (ppm)	K (ppm)	Buffered pH
Wilson Ranch	1.2	1.1	2.3	0.12	11.7	387	6.8
Boundary Gulch	1.1	1.1	1.5	0.08	34.4	174	7.0
Robinson Flats	0.8	0.8	1.5	0.09	9.1	183	7.0

presumed to be *C. nebraskana* (Wilson Ranch) and the unknown beetle (Robinson Flats, Ft. Meade BLM Recreation Area) because they were collected where adults were most numerous. In addition, several of the burrows appeared to be funnel-shaped, which is listed as characteristic of *C. nebraskana* (Pearson et al. 2006). Although the three pairs of adults from Wilson Ranch and Robinson Flats that were transferred to terraria with soil and grasses from their native habitat mated, oviposition was not observed, and no larval burrows resulted. As adults died, they were transferred to 95% EtOH for DNA analysis.

#### DNA Analysis

Samples of *C. nebraskana* and *C. longilabris* were sent to A. Vogler for mtDNA extraction and sequencing. These included *C. nebraskana* from Wilson Ranch, *C. l. longilabris* from Ontario, and unknowns from Boundary Gulch (at least some were *C. longilabris* phenotype), Ft. Meade, Robinson Flats, and McNenny. Preliminary results did not detect differences between any of the populations (A. Vogler, pers. comm. 2007).

#### CONCLUSIONS

Phenotypic determinations of populations from specific sites are shown in Table 5. Individual characters were scored and an overall determination as to species was given. I concluded that many of the populations were not assignable to either one species or the other, and probably represent hybrid populations, showing past gene flow (introgression and recombination) between *C. nebraskana* and *C. longilabris*. This is in contrast to Spanton (1988), who found no evidence of hybridization between the two species. However, Pearson et al. (2006) reported an interspecific copulation sighting in California.

Hybrids are not rare in insects between closely related species. Shaw et al. (1993) discuss a hybrid zone between grasshoppers in Australia, and Rand and Harrison (1989) showed genetic and reproductive differentiation between two species of crickets and their hybrids by soil type. There is a hybrid, or "tension," zone between the swallowtail butterflies *Papilio glaucus* and *P. canadensis* in the Great Lakes region (Collins 1991). A hybrid swarm between the butterflies *Papilio zelicaon nitra*, *P. polyxenes asterius*, and possibly *P. machaon*

TABLE 5  
PHENOTYPIC DETERMINATION OF POPULATIONS, BASED ON ALTITUDE OF SITE, HABITAT,  
AND MORPHOLOGICAL CHARACTERISTICS

Population/Site	Altitude	Habitat type	Total length	Metatarsal length	Labrum color	Ventral and proepisternum color	Middle band	Luster	Overall determination
Robinson Flats	N	N	I	I	N	I	N	N	N/I
Cottonwood Springs State Recreation Area	N	N	L	I	N	L	N	N	I
McNenny Fish Hatchery	N	N	I	N	N	I	N	N	N/I
Ft. Meade BLM Recreation Area	N	N	N	I	N	I	N	N	N/I
Boundary Gulch	N	L	L	L	I	L	I	I	L/I
Deerfield Lake	L	L	L	L	L	L	L	L	L
Timon Campground	L	L	L	L	L	L	L	L	L
Moon Campground	L	L	I	I	L	L	L	I	L/I
Black Fox Campground	L	L	L	L	L	L	L	L	L
Keough Draw	L	L	L	L	L	L	L	L	L
Terry Peak	L	L	L	L	L	L	L	L	L

Notes: N = *C. nebraskana*, L = *C. longilabris*, I = intermediate (hybrid), N/I = intermediate, but tending toward *C. nebraskana*, and L/I = intermediate, but tending toward *C. longilabris*.

*dodi* exists in Cheyenne County, NE, extending at least to Scotts Bluff County, (personal observations). Other well-documented hybrid swarms include the saturniids *Hyalophora euryalus* and *H. gloveri* in the Lake Tahoe area and elsewhere in the Pacific Northwest (Collins 1991, 2007).

Although altitude and habitat tend to separate *C. longilabris* and *C. nebraskana* populations, altitudinal and habitat overlaps have probably provided the means for the two species to hybridize. Boundary Gulch is one such site that showed a large mixture of phenotypes, from typical *C. longilabris* to near *C. nebraskana*. Long-range dispersal of fertile individuals with genes from both species probably resulted in "unidentifiable" populations at lower altitudes, such as McNenny, Robinson Flats, Ft. Meade, and Cottonwood Springs. These populations may not currently receive new gene flow from either species, and have maintained a "hybrid-appearing" phenotype. From my observations, these hybrid-appearing populations are not restricted to the Black Hills but are also found in the foothills of the Rocky Mountains and likely elsewhere. However, there appears to be gene flow between these foothills populations of *C. nebraskana* and *C. longilabris*, which may not be the case at most sites in the Black Hills.

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