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NOTES ON THE BIOGEOGRAPHY AND DORSAL COLORATION OF *CICINDELA AMARGOSAE* DAHL (COLEOPTERA: CARABIDAE)

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ABSTRACT.—The widely distributed and fragmented populations of the tiger beetle *Cicindela amargosae* are documented for dorsal coloration, elytral maculation, habitat, and adult escape behavior. Currently, there are 2 recognized subspecies, *C. a. amargosae* and *C. a nyensis.* The analysis of populations indicated that the variation in dorsal coloration did not coincide with the accepted subspecific criteria for this species, thus illustrating the difficulty in applying a subspecific category unequivocally to tiger beetles.

Key words: Cicindela amargosae, *tiger beetle, subspecies, phenotypic variation, habitat.*

Cicindela (Cicindelidia) amargosae Dahl is a polytypic species associated with grass margins of moist, often alkali-encrusted areas of drainages in southern Oregon, western Nevada, and eastern California (Fig. 1, Table 1). There are 2 recognized subspecific forms: *Cicindela a. amargosae* and *C. a. nyensis* Rumpp. Dahl (1939) described *C. willistoni amargosae* from "four miles north of Furnace Creek, Death Valley, Inyo County California." This subspecies was separated from other geographical forms of the *C. willistoni* group by the combination of bright blue-green dorsal coloration, maculation pattern reduced to an apical lunule, and elytral punctation (Dahl 1939). Interestingly, Dahl (1939) believed this species to be a subspecies of *C. willistoni* even though *C. willistoni pseudosenilis* W. Horn was sympatric at the type locality. In a study of the Death Valley, California, tiger beetles, Rumpp (1956) elevated *C. amargosae* to specific rank based on the observations that it did not interbreed with *C. w. pseudosenilis* at the type locality and there was a lack of hybrids. Utilizing color and body length as diagnostic criteria, Rumpp (1956) described *C. amargosae nyensis* from "1.6 miles south of Springdale, Nye County, Nevada." In addition to the allopatry from the nominate form, this subspecies was characterized by its matte-black dorsal coloration, "softer" elytra relative to the nominate form, and smaller overall body length. Various authors have considered *C. amargosae* to be a subspecific form of *C. senilis* G. Horn (Boyd et. al 1982, Werner 1994); however, Leffler (1979) presented distinguishing morphological and geographical attributes for the 2 species. Apart from studies by Dahl (1939) and Rumpp (1956), *C. amargosae* has received little attention in entomological literature except for Leffler (1979), who included this species as part of the Pacific Northwest tiger beetle fauna, and Freitag (1999), who listed all populations for this species outside Death Valley as *C. a. nyensis.*

In a geographic outline of the populations of *C. amargosae,* Rumpp (1956) found *C. a. amargosae,* along with *C. w. pseudosenilis* and *C. californica pseudoerronea* Rumpp, isolated along the natural springs associated with the alkali flats north of Furnace Creek, Death Valley, California. *Cicindela a. amargosae* was not found downstream of Furnace Creek at Saratoga Springs, even though *C. w. pseudosenilis, C. c. pseudoerronea,* and a 3rd species, *C. n. nevadica* LeConte, were present (Rumpp 1956). Interestingly, Rumpp's tiger beetle collection at the California Academy of Sciences includes a series of *C. a. amargosae* collected at Saratoga Springs in 1963. Rumpp (1956) found *C. a. nyensis* associated with the intermittent channels of the Amargosa River near Springdale, Nye County, Nevada. Although the Death Valley and Springdale populations are in close proximity to one another (<80 km), small mountain ranges apparently are geographical barriers between the 2 type localities. Rumpp (1956) believed that populations connected to the Springdale and Furnace Creek populations

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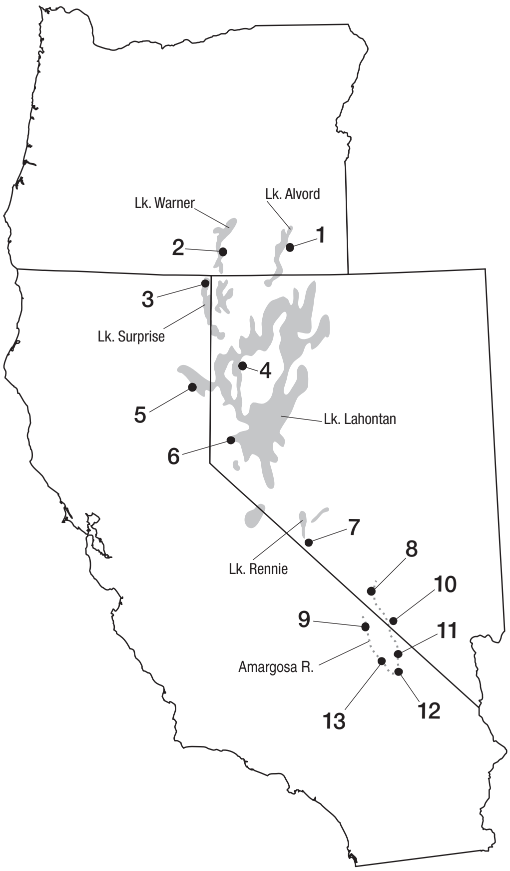

Fig. 1. Known populations of *Cicindela amargosae* and pluvial lakes (numbers correspond to Table 1).

by the Amargosa River would have individuals expressing a variety of dorsal coloration indicative of hybridization. Accordingly, the populations downstream of Springdale at Ash Meadows, Nye County, Nevada, were categorized as "hybrid," inasmuch as individuals matched the description of both subspecific forms (Rumpp 1956; Table 2). In addition, Rumpp (1956) considered as "hybrids" populations from northwestern Nevada and adjacent California that exhibited dorsal coloration described as "black, green and bronze." Rumpp (1956) apparently was unaware of *C. amargosae* populations outside California and Nevada; however, Leffler (1979) examined populations from Lake and Harney Counties, Oregon, all of which were placed as *C. a. nyensis.*

During a study of the current distribution of *C. amargosae* in 2002 and 2004, I made numerous observations that contradicted Rumpp's (1956) assertion that dorsal color variation was due to hybridization. Because most cicindelid taxonomy relies solely on morphological characters to determine subspecific status, the consideration of ecophenotypic characters and their role in cicindelid color expressions (Pearson and Vogler 2001, Schultz 2001) is often left unexplored. The objective of this study is to review the current distribution and habitat of *C. amargosae* populations throughout its range while evaluating the correlation between distribution and dorsal coloration and maculation.

METHODS AND MATERIALS

I reevaluated the criteria utilized by Rumpp (1956) to differentiate the subspecific forms of *C. amargosae*. These include (1) geography and allopatry, (2) dorsal coloration and elytra maculation, (3) habitat and adult escape behavior, and (4) total body length. To evaluate each of these criteria, I collected individuals of *C. amargosae* from locations throughout the species range. In addition to specimens captured in the field, pinned material including the type of *C. a. nyensis* and paratypes of *C. a. amargosae* were examined from the California Academy of Sciences Collection (San Francisco, California).

RESULTS AND DISCUSSION

Geography and Allopatry

Vestiges of the ancient lakes that once occupied the Great Basin offer an understanding of the present-day distribution of *C. amargosae* (Fig. 1). Leffler (1979) believed that *C. amargosae* inhabited the shores of pluvial Lake Lahontan and associated lake basins. The reduction of these pluvial lakes in post-Pleistocene times to smaller remnant lakes (Reheis 1999) can be considered a valid explanation for the widespread and fragmented distribution of current populations in the northern half of the species range. Historically, it is likely the localized distribution of the Death Valley, California, populations had a much more widespread range along the shores of pluvial Lake Manly, which at one time was close to 161 km long (Sharp and Glazner 1997). Populations close to Tecopa, Inyo County, California, are associated with remnants of ancient Lake Tecopa, which occupied the area south of Death Valley until 500,000 years ago (Sharp and Glazner 1997).

TABLE 1. Known populations of *Cicindela amargosae* (arranged north to south).

	Location	Source
1.	OR: Harney Co., Alvord Hot Springs	MGKC, CSUC[a]
2.	OR: Lake Co., Crumb Lake	Leffler 1979[b]
3.	CA: Modoc Co., Surprise Lake	CASC[c]
4.	NV: Wascoe Co., Gerlach	CASC, MGKC[d]
5.	CA: Lassen Co., Honey Lake	CASC, MGKC
6.	NV: Washoe Co., Truckee Meadows	LaRivers 1946
7.	NV: Esmeralda Co., Fish Lake	CASC
8.	NV: Nye Co., Springdale	CASC, MGKC
9.	CA: Inyo Co., Death Valley Nat. Mon., Furnace Creek	CASC, MGKC
10.	NV: Nye Co., Ash Meadows NWR	CASC, MGKC
11.	CA: Inyo Co., Shoshone	CASC
12.	CA: Inyo Co., Tecopa Hot Springs	CASC
13.	CA: Inyo Co., Death Valley Nat. Mon., Saratoga Springs	CASC

[a]Colorado State University Collection, Fort Collins, CO
[b]Literature sources only
[c]California Academy of Sciences, Golden Gate Park, San Francisco, CA
[d]Michael G. Kippenhan Collection, Portland, OR

The Death Valley and Tecopa populations, along with populations not directly associated with pluvial Lake Lahontan, such as Springdale and Ash Meadows, Nye County, Nevada, may have arrived via watercourses originating from the shores of pluvial lakes and are currently associated with the Amargosa River. The Fish Lake, Esmeralda County, Nevada, population is associated with remnants of pluvial Lake Rennie.

In June 2004 I searched for suitable habitats along Highway 140 between Lakeview, Lake County, Oregon, and Denio, Humbolt County, Nevada, for additional populations of *C. amargosae.* Even though this area has small remnants of pluvial lakes and alkali areas, such as Bog Hot Valley, I discovered no populations of *C. amargosae.* Due to (1) the large areas of inhospitable habitat between the fragmented suitable habitat and populations of *C. amargosae,* and (2) the general limited dispersal abilities of *Cicindela* sp. (Pearson and Vogler 2001), it appears unlikely that gene flow exists between populations north of the Inyo County, California, and Nye County, Nevada, populations.

Dorsal Coloration and Elytral Maculation

Dorsal coloration and the extent of elytral maculation are common morphological characters used in identifying and separating adult tiger beetles and have traditionally been used to define subspecies (Pearson and Vogler 2001). Such is the case with *C. amargosae,* where Rumpp (1956) characterized *C. a. amargosae* as "green" and *C. a. nyensis* as "black" without providing evidence regarding evolutionary implications of these 2 color forms. In an ecological role, color, elytral maculation, and ventral setae function as the primary mechanisms by which adult tiger beetles regulate body temperature (Schultz and Hadley 1987, Pearson and Vogler 2001). While *C. a. amargosae* and *C. a. nyensis* exhibit a very small degree of variation in elytral maculation and no difference in ventral setae, it is the dorsal (Table 2) and ventral (Table 3) coloration that demonstrates a marked degree of separation. While studies of the thermoregulatory performance of *C. amargosae*'s color morphs have yet to be undertaken, the southwestern United States tiger beetle *Cicindela hornii* Schaupp can be utilized as a model, as populations of this species have individuals expressing similar morphs of green, blue, or black dorsal coloration. Interestingly, Schultz and Hadley (1987) found that the 3 color morphs of *C. hornii* illustrated no significant difference in regard to heat gain from shortwave radiation. Therefore, assuming that the green and black dorsal coloration of *C. amargosae* have similar thermoregulatory performance as the color morphs of *C. hornii,* evolutionary forces outside thermoregulation have resulted in the expressed variation of dorsal coloration in *C. amargosae.*

When populations of *C. amargosae* are examined, it becomes clear that most populations have individuals expressing numerous dorsal color morphs (Table 2). Rumpp (1956) believed that populations expressing coloration of both subspecies were "hybrid," including individuals with dark green dorsal coloration found at Honey Lake, Lassen County, California, and

TABLE 2. Dorsal coloration and number of specimens of *Cicindela amargosae* examined and relative percent of dorsal coloration.

			Dorsal coloration				
Location	Collection	Total #	Blue	Green-blue	Green	Dark green	Black
Alvord Hot Springs	CSUC, MGKC	164				2 (1%)	162 (99%)
Surprise Lake	CASC	4					4 (100%)
Honey Lake	CASC, MGKC	43				3 (7%)	40 (93%)
Gerlach	CASC, MGKC	30				25 (83%)	5 (17%)
Fish Lake	CASC	26					26 (100%)
Springdale	CASC, MGKC	41				1 (2%)	40 (98%)
Ash Meadows	CASC, MGKC	73	7 (10%)	35 (48%)	5 (6%)		26 (36%)
Furnace Creek	CASC, MGKC	188		128 (68%)	59 (31.5%)		1 (0.5%)
Saratoga Springs	CASC	14	2 (14%)	5 (36%)	1 (7%)		6 (43%)
Shoshone	CASC	3					3 (100%)
Tecopa Hot Springs	CASC	59	7 (12%)	13 (22%)	7 (12%)		32 (54%)

Gerlach, Wascoe County, Nevada. Apparently, any connection in geologic time between the drainage of Honey Lake and Gerlach with Furnace Creek appears unlikely (Reheis 1999). In addition, the dark green dorsal coloration is associated with bronze ventral coloration, which is not found in any of Rumpp's (1956) other so-called "hybrid" populations, and therefore the plausibility of hybridization as a source of color expression in these populations is in question.

The character state of elytral rigidity was utilized by Rumpp (1956) when differentiating *C. a. amargosae* and *C. a. nyensis.* An initial analysis of living adult specimens indicates a correlation between elytral color and elytra rigidity; however, while this characteristic's potential as a quantifiable factor in subspecific determination is apparent, a method of measurement has yet to be devloped.

An additional consideration not discussed by Rumpp (1956) is the dorsal coloration of sympatric tiger beetle species. Schultz (1986) documented convergent dorsal coloration for numerous populations of *C. oregona* LeConte and *C. tranquebarica* Herbst in the southwestern U.S. In each instance the dorsal color of each species corresponded with its associated substrate color; as a result, numerous subspecific names have been attributed to these populations. An examination of sympatric species present at the above sites indicates similar color forms (Table 4). For example, at Furnace Creek, the 3 species that inhabit the open alkali flats, *C. a. amargosae*, *C. c. pseudoerronea,* and *C. w. pseudosenilis,* all exhibit iridescent dorsal coloration varying from green to dark blue and may represent a case of convergent evolution.

Habitat and Adult Escape Behavior

The habitat of *C. a. amargosae* at Furnace Creek, the type locality, consists of narrow rivulets where trickling water passes through alkali-encrusted soil. This area is conspicuous due to the lack of vegetation and to the alkali encrustations that make the soil covering completely white (Fig. 2), creating blinding reflections during periods of sunlight. At this location *C. a. amargosae* adults are encountered along the exposed waterways where their green dorsal coloration makes them conspicuous on the alkali surface. When disturbed, adults took off in strong flights between 2 m and 6 m in a relatively straight pattern. Individuals would most often fly toward open, moist soil and were active upon landing.

The type locality of *C. a. nyensis* at Springdale, Nevada, is part of the broad flood plain of the Amargosa River and is covered with alkali-resistant plants, leaving only small areas (<12 cm^2) of bare ground. A large portion of the area is covered by standing water during the seasonal period of adult activity (March to May). The open areas are characterized by dark, muddy soil with little or no evidence of alkali development. Adults of *C. a. nyensis* occur at the base of vegetation patches or on open areas, often in standing water. When disturbed, individuals took off in a short (<2 m) flight that was erratic in direction. These flights are characterized by sharper, vertical ascents terminating with the individual dropping back into the grass, most often with no post-landing movement. This behavior probably arose from the necessity to clear grass when ascending and landing in areas that are partially concealed by

TABLE 3. Ventral coloration and specimens of *Cicindela amargosae* examined.

Location	Genae	Proepisternum	Metaepisternum	Abdomen	Femur
Alvord Hot Springs	dark blue-green to purple	black with blue-green to purple reflections	black with blue-green to purple reflections	black with blue-green to purple reflections	black with blue-green to purple reflections
Gerlach	green with copper reflections	dark green to purple with strong copper reflections	dark green to purple with strong copper reflections	green to blue to blue-purple	dark green with copper reflections
Springdale	dark blue-green to purple	black with blue-green to purple reflections	black with blue-green to purple reflections	black with blue-green to purple reflections	black with blue-green to purple reflections
Furnace Creek	blue-green to blue to purple	purple to blue-green with strong green reflections	purple to blue-green with strong green reflections	purple with dark blue-green reflections	black with strong dark reflections

TABLE 4. Dorsal coloration of associated species of *Cicindela* found at Furnace Creek, Inyo. Co., California; Gerlach, Wascoe Co., Nevada; and Alvord Hot Springs, Harney Co., Oregon.

Location	Species	Dorsal coloration
Furnace Creek	*Cicindela californica pseudoerronea*	green-blue to dark blue
	Cicindela willistoni pseudosenilis	green to dark green
	Cicindela a. amargosae	green to purple
Gerlach	*Cicindela willistoni echo*	bronze-brown
	Cicindela h. haemorrhagica	brown to black-brown
	Cicindela a. amargosae	dark green to black
Alvord Hot Springs	*Cicindela tenucincta*	brown-green to brown
	Cicindela h. haemorrhagica	brown to black-brown
	Cicindela willistoni echo	bronze-brown
	Cicindela terricola imperfecta	brown-green to brown
	Cicindela amargosae nyensis	black

Fig. 2. Habitat of *Cicindela amargosae* at Furnace Creek, the type locality, Death Valley National Monument, Inyo Co., California.

grass, thus offering a relatively high level of immediate cover. This location is interesting in that as the season progresses (June) and adult activity declines, the dry soil is covered by a thick layer of alkali crust.

The habitat and habit of populations of *C. a. nyensis* outside the type locality were determined to have similar characteristics. Approximately 80 km downstream from Springdale, the habitat of the Ash Meadow population is almost identical to Springdale and is also associated with the Amargosa River. The habitat of Alvord Hot Springs is characterized by drainages from hot springs, which form large pools of standing water on the playa (Fig. 3). During June 2002 and 2004, I often observed adults of *C. a. nyensis* at Alvord Hot Springs standing in shallow water in the cover of vegetation. When disturbed, most individuals preferred to stay within close proximity of the wet, grassy areas with short, erratic flights. Adults that flew into the open playa were active upon landing and soon returned to the vicinity of the water. Honey Lake appeared similar to Alvord Hot Springs; however, since only 1 specimen was encountered, observations are inconclusive. Due to a lack of water runoff on the playa, no suitable habitat or specimens were located at the Modoc County location in June 2004. However, the description of this habitat, as well

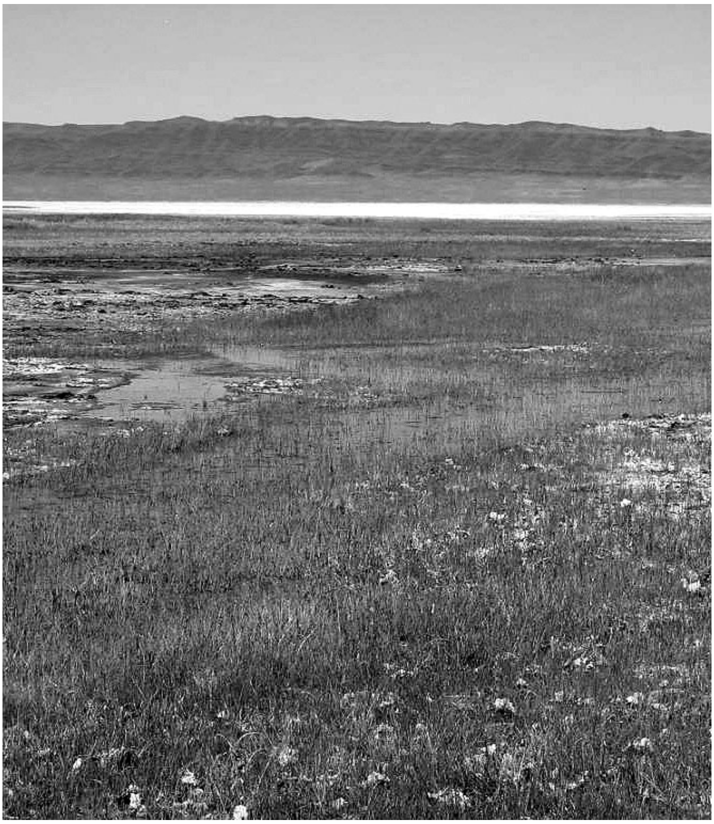

Fig. 3. Habitat of *Cicindela amargosae nyensis* at Alvord Hot Springs, Harney Co., Oregon.

as adult behavior (Smith and Bronson 2003), appears similar to the Alvord Hot Springs site.

The Gerlach population occurs in a habitat that can best be described as intermediate to Furnace Creek and Ash Meadows. This location is characterized by a large, open expanse of alkali-encrusted soil bordered by very dense vegetation and small areas of standing water. Here, adults of *C. amargosae* were encountered at the edges of vegetation and flew into the open expanses of alkali. This area did not have the total lack of vegetation as did Furnace Creek, but the open areas were much more exposed than either Springdale or Alvord Hot Springs. Similar to Gerlach, the Tecopa locality is also characterized by a large, open alkali area bordered by dense vegetation, and this location also supports individuals exhibiting color of both subspecies (Table 2). Neither the Fish Lake nor Saratoga Springs locations were examined during the course of this study.

Total Body Length

Lengths of adults were also utilized by Rumpp (1956) to differentiate *C. a. amargosae* (average length male = 11.4 mm, $n = 23$; female = 12.2 mm, $n = 46$) and *C. a. nyensis* (average length male = 10.4 mm, $n = 23$; female = 10.9 mm, $n = 27$). Average length of adults at the Gerlach was 11.3 mm ($n = 11$) in males and 12.1 mm ($n = 6$) in females.

CONCLUSIONS

Based on the analysis of the current populations of *C. amargosae,* I conclude that dorsal color does not necessarily correlate with geographical distribution of subspecific forms as defined by Rumpp (1956), and, in fact, most populations have individuals expressing a variety of colors (Table 2). The correlation between color and overall body length is consistent throughout the range of *C. amargosae,* with green dorsal coloration coinciding with larger average length, whereas black dorsal coloration occurs in individuals of smaller average body length. Even though the Gerlach population is unique for the high percentage of individuals with dark green dorsal and copper ventral coloration (Tables 2, 3), this population is best assigned to the nominate subspecies based on its elytral rigidity, elytral maculation, and overall body length.

Whatever the biological function of the specific colors, there is no doubt that selection is producing convergence in color patterns and color pattern variation among *C. amargosae* populations. It is conceivable that isolated populations of *C. amargosae* could lose morphs through drift such that the monomorphic populations of *C. amargosae* are a result of stochastic rather than deterministic processes. The hybrid populations of Rumpp (1956) are those that retain the original genotypic variation for color pattern and presumably remain under some sort of stabilizing selection (T. Schultz personal communication). Therefore, the interpopulation variation of dorsal coloration is more likely a result of an evolutionary response to ecological factors rather than hybridization. Instances such as those described here for *C. amargosae* illustrate the complexity of coloration as expressed in adult *Cicindela.*

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