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STUDIES IN NEARCTIC DESERT SAND DUNE ORTHOPTERA.
PART XV. EREMOCHEIROGRAPHY OF SPANIACRIS
WITH BIOECOLOGICAL NOTES

Ernest R. Tinkham

ABSTRACT.—Four decades of the author’s records indicate that Spaniacris deserticola (Bruner) is confined within the periphery of the Colorado Desert. It is usually found, near or within a few hundred feet of sea level, marking the shore line of ancient Lake Cahuilla (except for the Dale Lake record). The preferred host plant is Coldenia palmeri growing on the lower fringes of bajadas, with C. plicata on drift sand being second in preference. Spaniacris can tolerate sand and rock temperatures of 60 C. (believed to be a maximum for Colorado Desert life). Mating takes place at that and lower temperatures. When they are disturbed while on the tops of host plants, their flight is low and direct and of short duration, and they come to rest on the torrid soil for long periods of time. The female, much larger than the male, can sustain the male in flight while mating. The study verified spatial longevity of Spaniacris at Indio, California, after approximately 70 years and for the Kane Springs area after 52 years.

Spaniacris deserticola (Bruner, 1906), one of the rarest of Nearctic Desert grass-hoppers, was based on a single female collected at Indio by H.F. Wickham.

In 1931, Morgan Hebard (1937:376) instructed me to make special efforts to locate S. deserticola. Late in the afternoon of 25 August 1931, a large colony was located on a low sand ridge some ten miles east of Coyote Wells and about a mile or so east of Plaster City, California. A torrid day had been spent hunting for the elusive creature on the blistering mesas. One had to blink constantly to keep one’s eyes somewhat moist, and it was so hot that the ubiquitous grass-hopper Trimerotropis p. pallidipennis flew from the top of one creosote bush to another. At 8:00 that night, after sundown, it was still 122 F in El Centro. Hebard records that I collected 13 males and 7 females for him that day and that my brother collected 12 males and 9 females for me. In 1940 the colony was still there, and on 14 August I took 8 males and 10 females. In May 1961 I could not find any trace of the colony. During those intervening years the Highway Department had made a barrow pit out of the sand ridge and had destroyed the habitat.

During the period 1949-1973 I took 2 males and 1 female in early June 1953 at or near the mouth of Palm Canyon at a location northward and across Highway 111 from the Smoke Tree Ranch (both locations had disappeared by 1972 due to residential developments) and P. H. Timberlake took a female here on 24 June 1952 and a male on 21 June 1953.

On 22 May 1954, Dr. John Goodman and I were collecting on the east side of dry Dale Lake, 25 miles east of Twenty Nine Palms and found a female nymph, probably in the last stadium, on barren playa, where sand drifted across the gravel road. In May 1973 inspection showed this area so blasted and eroded by violent sand storms, that the only surviving vegetation was some ancient, dying creosote with their crowns supported, like mangroves, on long exposed roots. It is believed that this colony has been exterminated. It was the only one at a considerable elevation, as all others lie close to sea level.

On 14 June 1964, I examined a rather level sweep of sand (air temperature 119 F) well covered with sand mat (Col.endia plicata) some miles west of Rice, California, and one several miles east of the turnoff to the Iron Mountain Pumping Station. The first plant examined contained a female Spaniacris quietly resting among the leaves not more than several inches above the torrid sands.

On 21 June 1964, along the old highway about 4 miles west of Thousand Palms, I found a single male. On 29 July 1974 I reexamined this area with sand mat margining the south edge of the road and scattered on the sand but could find no Spaniacris, although that week I had located six new colonies some miles east of Thousand Palms.

On 29 June 1970 Jim Davis took a pair of Spaniacris in Thousand Palms Canyon. The next day I found Spaniacris at that locality confined to Coldenia palmeri bushes bordering several hun-

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dreds of feet of an old gravel road near the base of the gravelly hills. I took 2 females and one male. Associated were: *Anconia integra* on *Atriplex canescens* var. *linearis* and *A. polycarpa*; *Xeracris minimus* on sandpaper weed (*Petalonyx thurberi*); *Cibolacris parviceps* on the road and *Tytthotyle maculata*, the Malpaius lubber, nearby among the boulders of the brief bajada at the foot of the hills. One male was taken there 1 July 1971, and one male and one female on 3 July 1972; there were no *Spaniacris* there in 1973, a very dry year. In 1974 this area was designated Colony No. 6. (I shall report on Colony No. 6 later.)

On the hot evening of 11 June 1973, Jim Davis and I made a night collecting trip along the roads to the Borrego Desert. One female *Spaniacris* was taken on the road 6 miles west of Salton City, just east of the radar tower; one pair was taken one mile west of the tower; and one crushed female was taken two miles west. In the arroyo area of a broad Pleistocene valley, about 13.5 miles southeast of Borrego Springs by road and within half a mile of Highway 78, another female was found on the paved road at night. In the late evening of 10 Aug. 1974, I surveyed the adjacent arroyo area, both sides of the road, but found no evidence of *Spaniacris*. The Borrego area, based on the parched conditions and poor showing of flowers, apparently got little of the daylong drizzle that drenched Coachella Valley on 7 Jan. 1974.

Theodore J. Cohn contributed some of his collection records as follows: "Imperial Co., Ca., 3 mi. E. Plaster City, at the Oyster Beds Turnoff, 25 June 1965, T. J. Cohn, 1 male. 2 females. On ground near road around noon, hot as a firecracker. I have stopped there many times since and have never seen them again. Lots of *Anconia* around in other years.

"Sonora, Mexico, 22.3 mi. SE San Luis Rio Colorado, 20 June 1965, T. J. Cohn, No. 25. Base of sand dunes but not in them. 1 juv. female, last instar, *Xeracris* and *Coniana* also found here. These are the first set of dunes east of San Luis.

"Sonora, Mexico, 76 mi. SE San Luis Rio Colorado (14 mi NW Los Vidrios), 14 June 1966, T. J. Cohn, No. 16. Very sparse vegetation on moderately sandy soil, not far from stabilized dunes. This was around a corral a few hundred yards south of the road, near the next set of dunes, 1 female. Lots of what I think is *Coniana* here."

The sand dunes 22.3 miles SE San Luis are in large part in Arizona; the International fence terminating on some rocky hills astride the International Boundary. The best dunes are in Arizona immediately north of these hills. I have collected there on many occasions but have never found evidence of *Spaniacris*. This should be the best location to discover *Spaniacris* in Arizona. At the 76-mile location, a high ridge of aeolian dunes sweeps far inland into the area from the southwestern coastal regions.

Notes on the 1974 Survey

Colony No. 1. Found, 25 July 3 miles north of Indio, California, on Monroe Street on *C. palmeri* on the north side of the dyke protecting the Coachella Valley branch of the All American Canal within fifty feet of the paved road. The Colony was at the southern edge of a considerable bajada that gently slopes down from the Indio Hills over an area of many miles. This location is directly south of the Curtis Desert Palms Oasis, whose existence is threatened by the huge Massey Rock and Sand gravel pit. The plant life is typical of that described fully under No. 2 below but is not as extensive. Thus, the presence of *Spaniacris deserticola* for Indio was verified almost 70 years after Bruner described it in 1906; I have not been able to find the date of Wickham's collections prior to 1906.

Colony No. 2. That afternoon, at the powerline crossing of Washington Street, 4 miles north of Interstate 10 and about 10 miles northwest of Indio. I found a much larger colony, here designated No. 2. The location was similar to that of No. 1, representing the southern edge of the long bajada margining the south side of the Indio Hills. The desert vegetation consists of shrubs, living ephemerals, and the dead skeletons of spring ephemerals.

The desert shrubbery was composed of many widely scattered *Colenia palmeri* growing along the narrow, poorly paved powerline road as well as along the margins of a shallow dry-wash with fewer scattered clumps of creosote (*Larrea divaricata*), sandpaper weed (*Petalonyx thurberi*), Burrobush (*Franseria dumosa*),
and even more rarely encelia (Encelia farinosa), desert sweet (Bebbia juncea), cheesebush (Hymenoclea salsola) and California dalea (Dalea californica). Living ephemerals were: inflated stem (Eriogonum lamatum), Spanish needle (Palofoxia linearis), velvet rosette (Psathyrotes ramosissima), Stillinia spinulosa, and Tidestromia oblongifolia; all but Tidestromia were in bloom. Dry spring ephemerals were: desert gold (Eragrostis censeens), forget-me-nots (Cryptantha costata and maritima), Thomas buckwheat (Eriogonum Thomasi), brown-eyed primrose (Oenothera claraefolmis), blazing star (Mentzelia multiflora), and perhaps others. The presence of the flowering ephemerals in July and August on the blazing Colorado Desert can be explained only by the slow drizzling rain (1.56 inches) on 7 Jan., which penetrated to at least three feet. On 29 July, I found damp sand one foot down. Although this soil moisture was a great boon in reviving dying shrubs (transsects anywhere will show 65-75 percent dead or partly dead), germination of ephemeral seeds was poor because of the cold January weather. The deep penetration of moisture accounts for the flowering of Palofoxia and Eriogonum in midsummer and undoubtedly was responsible for breaking the diapause of Spaniarius and other acridid eggs.

On 25 July the two-acre area surveyed (approx. 100 by 80 yds.) contained at least 6 pairs of Spaniarius of which I took 3 males and 2 females, leaving the rest for propagation. Next day, 26 July, 4:15 to 5:00 pm, slightly hazy, temperature 45 C, soil 57 C. Quite a few adults noted but none taken.

On 17 Aug., a hot wind was blowing from the southeast. At 5:00 pm, air temperature was 44 C, soil 54 C; 5:20 pm, air 44 C, soil 53 C. Photographed Spaniarius with Tri-X film. Found Conionia snowi and for the first time Anconia integra female on Coldenia palmeri. Xeracris minimus also sometimes found but more often taken from Petalonyx thurbiri.

On 20 Aug., 5:00 to 6:30 pm, air 38 C, soil 54 C. Found only a few pairs in the original two-acre area. Extended the colony southeastward for 3:10 mile, where I found two pairs, and westward across Washington Street at least 100 yards, where I found two more pairs, one pair in copula, at 6:30 pm. Total area covered by Colony No. 2, at least one half mile in length and about 100 yards in width. Photographed the species with Panatomic-X film as Tri-X was much too fast for glaring light of the desert.

On 24 Aug., 5:30 to 6:30 pm visited the site with Chas. Neeley, photographer. At 5:30 pm, air 41 C, soil 51 C. First male found within a few feet of the road. One area four feet square formed by two contiguous C. palmeri plants held two females and one pair mating; this is the greatest concentration ever found for this species. On this date the original two-acre area contained eight females and nine males despite the fact that three males and two females were removed on 25 July. Since that date all specimens left for propagation of the species. Little change in vegetation noted since 25 July. Fairly hot, slight breeze from the west.

On 18 Sept., 1:15 to 2:00 pm, air 41 C, soil 51 C. One male found near road, one female at least 200 feet away. This female recognized by the slightly shorter tegmina. Trimerotropis p. pallidipennis present for the first time this summer; four females noted. These had probably migrated into the area as no nymphs of any acridids had been noted previously.

On 29 Sept., 1:15 to 2:00 pm, fairly hot wind, temperature: air 39.5 C, soil 52 C. Examined all C. palmeri bushes in the original two-acre area. On the 91st plant the female noted on 18 Sept. was found and some distance away on the 104th plant found a pair, in copula, missed on 18 Sept. Did not find the male found 18 Sept. near the road, which had been at least 200 feet away from the others. It is obvious that Spaniarius is quite localized in its movements especially in the late summer.

On 4 Oct., brisk west wind, air 31.5 C, soil 54 C on sunny side of a C. palmeri plant in wind-sheltered position. Examined about 120 plants; apparently only one female surviving at this late date; this one, the one noted on 18 and 29 Sept., was still in the same area. I found female by waving my net back and forth near each plant. While doing so, I was aware of the slightest movement of something dropping an inch or two from the end of a branch to the ground. This female was hiding under the plant on the sandy
soil. This was the first time I had observed this habit and the first record of this species for October.

On 11 Oct., 11:20 to 11:40 am, much cooler. Had time only to check over those bushes mostly likely to hold Spaniaca is perched on top of plant as they almost always were. Found none; believe colony had died out for 1974. On this late date vegetation was surprisingly like that noted in late July, with E. inflatum, Palofoxia linearis, and P. ramosissima still blooming, but Stillingia has been dead and brown since mid-September.

Colonv No. 3. Located 25 July, about one mile northwest of Colony No. 2, on the south side of Washington Street as it swings west to join the east end of Ramon Road at the turnoff to Thousand Palms Canyon. The colony comprised about 600 yards of C. palmeri on the east and west slopes of a gentle hill with a few plants of Dalea californica and D. emoryi here and there. The road crosses the south marginal area of the Indio Hill’s bajada. The 300 yards of the east slope contained at least five pairs of Spaniaca; one pair taken; west slope at least two pairs; one pair taken. When disturbed this species never flies to another C. palmeri bush but always alights on the very hot soil. Flight is low and direct, the wings showing rather deep azure. On the food plant it usually orients the long axis of its body parallel to the rays of the sun so that usually only the face is exposed to the full effect of the very hot sun. Under the circumstances this reduces exposure to the minimum, and the very long legs help elevate the body from the extremely hot soil tempartures. Spaniaca is not wary: the cautious photographer can move the macrolens of his camera to within 8 inches of the grasshopper. Trimerotropus p. pallidipennis seldom permits approach closer than 10 feet.

Colonv No. 4. Found 29 July, located just east of the Thousand Palms Canyon Turnoff. About one-fifth of an acre of C. palmeri fairly widely scattered with a few creosote interspersed: 2:30 pm, air 37°C; (had been overcast in am), soil 58°C. This small area (100 x 100 ft) revealed at least 9 females and 11 males, some of which were on very hot ground. Most of the females were on the plants. While I was taking temperature readings, one pair, in copula, sat on a rock (58°C) for at least five minutes without showing any signs—as other acridids quickly do—that the rock was hot. Evidence seems to indicate that Spaniaca can tolerate more heat than can any other animal living on the torrid Colorado Desert. Temperature one foot above soil level was 45°C. Still on margin of the bajada.

Colonv No. 5. Found 25 July, one half mile west of Turnoff to Thousand Palms Canyon, 4:30 to 5:00 pm, air 45°C, soil 55°C. Margin of the same bajada but sandier than in previous colonies. Flora: C. palmeri with scattered creosote, D. californica, cheesebush, Dictoria canescens, Atriplex c. linearis, and dead sand verbena (Abronia villosa). One pair in copula, female could fly only a few feet with the male. Took mating pair and left 2 males and one female.

Colonv No. 6. Visited once on 25 July. This is the location mentioned previously under dates of 1970-1973, within the mouth of Thousand Palms Canyon. Observed 1 female and 1 male perched on C. palmeri along margin of old gravel road previously described. Did not disturb. Noted Anconia integr a on Atriplex c. linearis, Xeracris minimus, and flushed a female Typhothyle maculata out of luxuriant creosote bush. No temperature readings were made on the first day of 1974 survey.

On Saturday afternoon, 27 July, I continued my Spaniaca survey. Driving northward on Washington Street and then westward, I passed colonies 2, 3, and 4, then turned right on Thousand Palms Canyon Road to pass Colony 6 and reach the Dillon Road junction in about four and one-half miles. En route I examined 400 yards of fine habitat of C. palmeri on both sides of the road about 1.5 miles north of Paul Wilhelm’s Oasis, but found no specimens. As this was about as fine a habitat as I had seen, I wondered why no Spaniaca. Apparently, since it is so rare, localized, and sedentary in habits and because this location is several hundred feet higher than Colony 6, it has not been able to penetrate up through this rather broad and low canyon.

A survey of Dillon Road from the Thousand Palms Canyon junction (approximately 600 feet elevation) southeasterly 11 miles to where sand is first encountered at about sea level, revealed no Spaniaca.

Colonv No. 7. Shortly beyond, at 11.7
miles from the Dillon-Thousand Palm Canyon junction, I examined 200 yards of C. plicata and found on one plant one male Spaniacris and 1 female Coniana snowi resting on top of the low bush within one foot of each other. Air temperature at 6:00 pm, 45 C with hot wind blowing, 44 C when calm, leaf surface 44.2 C. This location was 3.6 miles northwest of freeway and about 5 miles northwest of Coa chella.

Both sides of Dillon Road, edged with sparse patches of Coldenia palmeri and C. plicata, were examined from Colony No. 7 to the junction with Interstate 10 (3.4 miles) and no Spaniacris were found.

On 29 July, I examined old Highway 99 (now Varner Road) from Thousand Palms west to Garnet Hill (13.3 miles) and found no trace of Spaniacris on Coldenia palmeri and C. plicata, which often formed nice colonies along the margin of the road.

On 10 Aug. I drove along Highway 86 to the Kane Springs area, then westward on Highway 78, but failed to find evidence of Spaniacris other than at Colony No. 8, noted below.

Colony No. 8. At about 7.5 miles from Kane Springs, 6 miles northwest of the junctions of Highways 78 and 86, I examined 100 yards of C. plicata growing on south sandy side of the road and found a female Spaniacris that flew about 30 feet, its azure wings showing in low direct flight, to land on the bare clay soil typical of the area. Later I examined a small flat wash with C. plicata, creosote, and smoke tree (Dalca spinosa) about six miles northwest of Kane Springs that admirably fits Hebard’s (1937:377) location where he took this species. Nothing was found here.

Because of drought conditions there was very little Coldenia west on Highway 78 and what there was occurred chiefly at the sea level line some 6 to 7 miles west of the Kane Springs junction. Late that night, at about 10:30 pm, I examined by Coleman lantern light the area immediately east of the radar tower where Spaniacris had been encountered on the night of 11 June 1973, but found nothing. I had examined about 10 acres of this area in late afternoon of 20 July 1974; but, although it was in interesting habitat, I could find no Spaniacris. Farther on, 4 miles west of Salton City, I examined 300 yards of roadside Coldenia plicata with Coleman lantern and found nothing but Coniana snowi. I had also examined this area on July 20.

Summary and Conclusions

Biology. The adult Spaniacris is now known from early June until early October. Records of nymphs in May represent the two last nymphal stadia. No small nymphs have ever been found. The number of ova laid per female is small, so the population potential is likewise small.

Habits. The low direct flight of rather short duration is diagnostic for the genus. During flight the wings appear darker azure than they appear on close inspection. Flight is almost always from the top of the Coldenia plants to the desert soil, where they will rest immovable many minutes, seemingly able to tolerate perfectly the torrid soil temperatures. Spaniacris is not a wary grasshopper and can be slowly and easily approached to within six inches for macro lens photography. However, quick lateral movements will alarm them and cause flight. The female of this species is probably the only grasshopper that can sustain flight, carrying the male, while mating. I never failed to find mating pairs in the larger colonies during afternoon and late evening hours. No observations were made in the early morning. Mating was observed from late July to late September. Oviposition was not observed. During the hotter portions of the day, from late morning until late evening, females oriented themselves so that the long axis of the body was parallel to the rays of the sun. In such positions only the front of the long face was exposed to the full effect of the rays. Only on rare occasions, and that in the late evening, did I observe males and females resting on the shady side of their host plant (Fig. 4).

Habitat. The marginal fringes of great bajadas, where the soil is partly of rock, sand, and clay, seem to be the preferred habitat. Spaniacris has been taken in purely drift sand locations near Rice (Figs. 1 and 2), Dale Lake, and the northwestern Sonora, Mexico (records of Dr. Colm). The preferred altitudinal habitat appears to be at or slightly above the sea level contour line in the Colorado Desert; no captures have been made below sea
Figs. 1-8. Habit and habitat photographs of Spaniacris deserticola: 1. Habitat of drift sand, with C. plicata in foreground, some miles west of Rice, Ca., 14 June 1964, 119°F in shade; 2. Female resting in top of C. plicata at Fig. 1 locality; 3. Female (by Chas C. Neeley), 24 Aug. 1974, late evening, at Colony No. 2; 4. Female resting on C. palmeri in shade of setting sun, Colony No. 4, 29 July 1974, taken with Vivitar Strobe Flash No. 292 with white cloth filter; 5. Female on hot gravelly soil, Colony No. 2, 20 Aug. 1974, soil surface 54°C; 6. Male, Colony No. 6, 30 June 1970; 7. Mating pair, Colony No. 4, 29 July 1974, resting on rock surface, 58°C, 2:15 pm; 8. Habitat, Colony No. 4, C. palmeri in foreground; some Creosote in background, looking north up Thousand Palms Canyon, 29 July 1974, 2:30 pm. All photographs taken by Ernest R. Tinkham except No. 3, which is by Chas. C. Neeley.
level. The only records of considerable elevation (± 1000 feet) appear to be the captures at Dale Lake and near Rice. There are no records for sand dune situations. Thus, the sea level contour represents the ancient shore line of Pleistocene fresh water Lake Cahuilla, which dried up hundreds of years ago to leave the salt deposits of the Salton sea depression before flooding in 1903. It is obvious, because Spaniacris is still largely confined to the old beach line, that its powers of dissemination must be rather poor. This seems partly accounted for by its sedimentary habits (as noted under Colony No. 6), by its low egg potential, by the restricted habitat of its chief host plant (C. palmeri), by the torrid temperatures, by the great aridity of its habitat, and, perhaps, by other factors as well.

Host Plants. Spaniacris appears to be strictly confined to Coldenia palmeri and C. plicata. The Palmer coldenia seems to be the preferred host because its distribution is closely related to the sea-level beach line of ancient lake. Other factors in the choice of host plants appear to be the size and greater height of C. Palmeri, which provides green foliage all summer long, and the edaphic conditions which provide greater protection than the sand (inhabited by C. plicata) for the eggs during drought-induced diapausas. Very little is known about the diapause in the eggs of desert acridids. On the other hand, sand appears to be a poor medium for the protection of eggs, especially if laid close to the sand surface.

Temperature Tolerance. Spaniacris appears to tolerate torrid soil and rock temperatures of 140 F (60 C), as portrayed by the mating pair in Photo 7, without exhibiting any of the signs of intolerance (such as the lifting of tarsi) that most other desert acridids would soon portray under such situations. Its extremely long legs (for an acridid) must be partly responsible for this heat tolerance. Thus, evidence seems to indicate that Spaniacris can tolerate higher temperatures than any other life form associated with the Colorado, our hottest desert.

Spatial Longevity. The evidence provided by Colonies 1 and 8 indicates that Spaniacris has survived in the Indio area for 75 years, and in the location a few miles northwest of Kane Springs for 50 years, which is more than half the time of American occupation of the territory. However, in the areas near Dale Lake and Palm Springs and west of Thousand Palms there is evidence that the destructive practices of man have extirpated three colonies of Spaniacris within the past two decades. These practices include scraping off large areas of desert shrubbery, asphalt paving of huge areas, and many other methods well known to conservationists, all of which helped produce the increasing droughts and sandstorms of the past two decades. It is also apparent that Spaniacris survived many millennia in the Colorado Desert before the advent of the white man.

Faunal Designation. Spaniacris appears strictly confined to the Colorado Desert, its zonal distribution being confined largely to the old beach line of Pleistocene Lake Cahuilla, which is also at sea level.

Orthopteran Associates. The chief associates are: Coronia snowi especially on sandier habitats dominated by C. plicata; Xeracris minimus, showing a preference for Petalonyx thurberi; and, rarely, the saltbush grasshopper (Anconia integrata), which prefers Atriplex spp. Also present are soil-dwelling species such as the Arrayo Grasshopper (Cibolacris parviceps), the ubiquitous Trimerotropis p. pollidipennis, rarely the Malpais lubber (Typhonotholyte maculata) as in Colony 6, and the ground mantid (Lianucutia minor).

Enemies. Since the 1974 survey demonstrated that many colonies exist along road margins favored by C. palmeri and (where sandier) C. plicata, evidence indicates that many Spaniacris are crushed by passing cars, especially at night, when there seems to be considerable nocturnal activity among desert acridids. As the crested lizard is strictly herbivorous, there seems to be no evidence that it would feed on Spaniacris; but the presence of zebratails and, rarely, sand dune lizards of the genus Uma in sandy habitats where C. plicata is growing may pose a threat to the early stages of Spaniacris, about which nothing is known.

References
Hebard, M. 1937. Studies in Orthoptera which