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# THE LIFE HISTORY AND ECOLOGY OF THE PINACATE BEETLE, *ELEODES ARMATUS* LECONTE (TENEBRIONIDAE)

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ABSTRACT

*Eleodes armatus* LeConte, the pinacate beetle, occurs throughout the warm deserts and intermontane valleys of the southwestern United States and northwestern Mexico. It is a scavenger, feeding mainly on plant and animal detritus, and it hides in rodent burrows during times of temperature extremes. Adult activity peaks in the fall but it may occur at any time of the year. Females produce several hundred eggs per season and adults may live for more than 1 year. Larvae are fossorial and require 9 months to develop.

The broad ecological, geographical, temporal and dietary range of this beetle may be in part attributable to its defense mechanisms (repugnatorial secretions and allied behavior) against vertebrate predators.

On the black earth on which the ice plants bloomed, hundreds of black stink bugs crawled. And many of them stuck their tails up in the air. "Look at all them stink bugs," Hazel remarked, grateful to the bugs for being there.

"They're interesting," said Doc.

"Well, what they got their asses up in the air for?" Doc rolled up his wool socks and put them in the rubber boots and from his pocket he brought out dry socks and a pair of thin moccasins. "I don't know why," he said, "I looked them up recently—they're very common animals and one of the commonest things they do is put their tails up in the air. And in all the books there isn't one mention of the fact that they put their tails up in the air or why."

Hazel turned one of the stink bugs over with the toe of his wet tennis shoe and the shining black beetle strove madly with floundering legs to get upright again. "Well, why do you think they do it?"

"I think they're praying," said Doc.

"What!" Hazel was shocked.

"The remarkable thing," said Doc, "isn't that they put their tails up in the air—the really incredibly remarkable thing is that we find it remarkable. We can only use ourselves as yardsticks. If we did something as inexplicable and strange we'd probably be praying—so maybe they're praying."

—John Steinbeck
Cannery Row

On a warm evening in late May 1981, on the Glamis Sand Dunes west of Yuma, Arizona, several colleagues and I observed the activities of an unusually large population of tenebrionid beetles. Enormous numbers of these insects emerged from the mouths of kangaroo-rat burrows (*Dipodomys* spp.) just after sundown to forage on the dune surface. A cursory survey of the dunes around camp with the aid of a lantern revealed the presence of an especially dense aggregation in one nearby swale where the beetles were feeding on the blossoms of an ironwood tree (*Olneya tesota*). While several species of tenebrionid were present on the dune, the preponderance of individuals belonged to a large, common species, *Eleodes armatus* LeConte.

This beetle occurs throughout the warm deserts and intermontane valleys of the southwestern United States. In northern Mexico it is known by the familiar name "pinacate," meaning acrobat or tumbler, because of its propensity for standing on its head when disturbed. In Sonora there is even a mountain range, the Pinacates, named for these beetles. Although conspicuous in our southwestern deserts, little has been written on its biology. Ahearn & Hadley (1969) and Ahearn (1970) demonstrated that the beetle effectively reduces transpiratory water loss through discontinuous respiration, regulated tracheal air flow and low cuticular permeability. Thomas (1979) reported on the relationship between population abundance and climatic variables, especially the availability of moisture. Over the past decade I have had opportunity to observe the behavior and to quantify certain aspects of this beetle's ecology in the Mojave and Sonoran deserts.

## Methods

Populations of *E. armatus* were censused using grids of pitfall traps from 1971 to 1975, and again in 1981. Details are given in Thomas & Sleeper (1977). Grids of 50 traps were located at the following sites: Nevada: Rock Valley, Nye Co.; Moapa Valley, Clark Co.; Mormon Mesa, Lincoln Co. Arizona: Beaver Dam, Mojave Co. The beetles were marked individually and released at these sites.

Smaller pitfall grids of 10–20 traps were operated at the following sites: Nevada: Potosi Pass, Clark Co.; Blue Diamond, Clark Co. Arizona: Tucson, Pima Co.

Larvae and pupae were reared by Mr. Paul J. Franco, technician with the Rock Valley Ecology project, from adults obtained at the Rock Valley site.

Living beetles were maintained in captivity in terraria and fed fresh carrots, leaves of desert plants, or starved, to determine food preferences and the effects of starvation on longevity and fecundity.

## Morphology and Taxonomy

The adult of *Eleodes armatus* is an elongate, shiny black, flightless beetle. It has long legs and semifused elytra. Average live weight of 57 individuals was .884 gm. Females tend to be slightly larger than males and reach a length of 3.5 cm, often weighing over a gram. Otherwise there is little sexual dimorphism.

*Eleodes armatus* can be distinguished from the majority of its congeners by the presence of a sharp spine on each femur. The few species which also have spines on the meso- and metafemora are found in Baja California, Mexico. There are three subspecies of *Eleodes armatus*. Their distributions are shown in Figure 1. The observations reported here were made on the nominal subspecies, *Eleodes armatus armatus*.

## Immature Stages of *Eleodes armatus*

Eggs. Elliptical, pearl-white; uniformly ca. 1.5 mm length. Mean number of eggs dissected from 12 gravid females, 193.8 (range 52–428).

Mature Larva. Body elongate, cylindrical, thickened moniliform, slightly dorsoventrally compressed; length 39 mm, width 4 mm; pale tan with darkly sclerotized claws

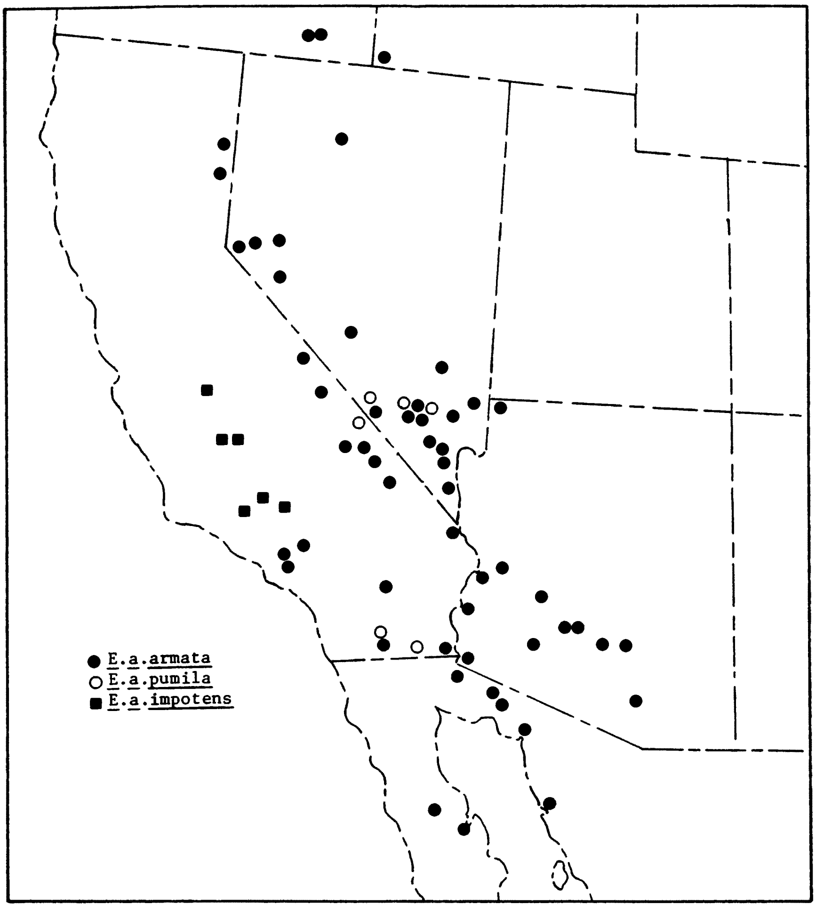



Fig. 1. Distribution of *Eleodes armatus* and its subspecies.

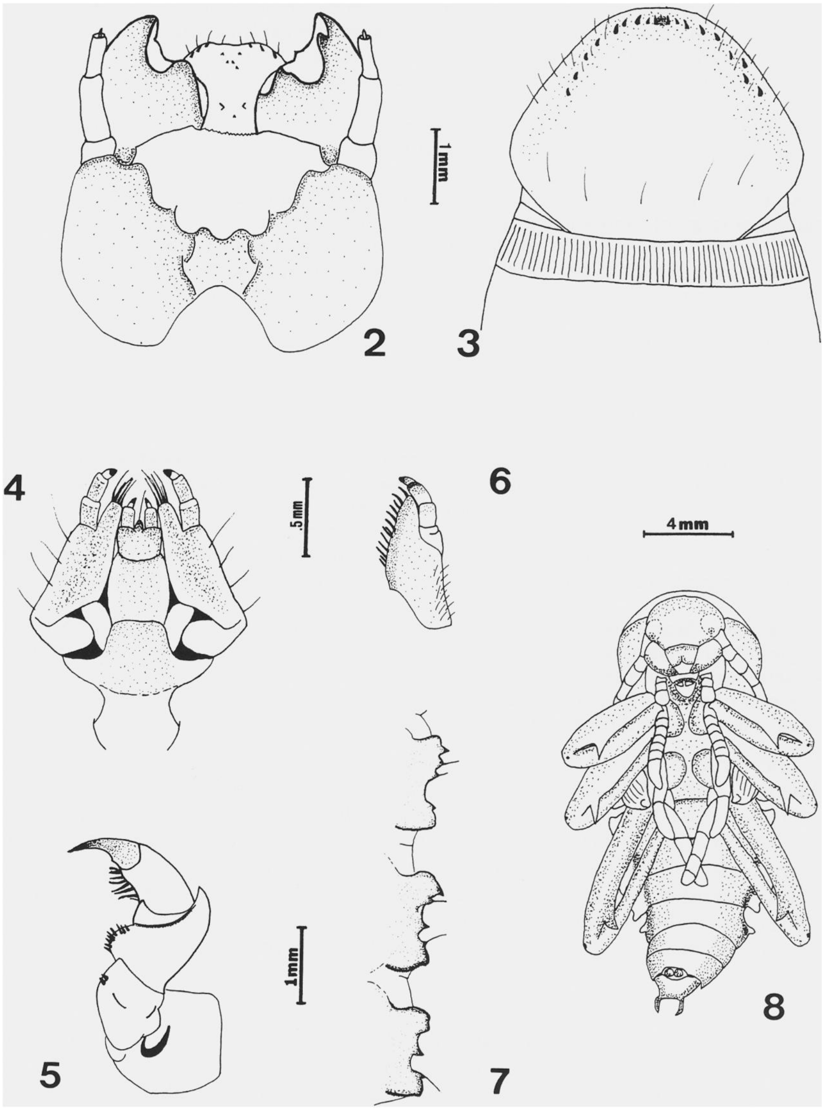
and mandibles. Prothoracic legs noticably more robust than meso- and metathoracic legs.

Head: Cranium well sclerotized, subquadrate (Fig. 2); distinctly wider than long, ratio 13:21; glabrous dorsally, sparsely setose laterally and ventrally; lacking ocellar lenses. Epicranial suture irregular, lyre-shaped; stem short, arms bifurcating just before antennal angles.

Pedicel of antenna globular, nearly twice as thick as scape; scape cylindrical, 2.3 times longer than wide; last antennal segment weakly clavate, 1.7 times longer than wide, bearing a small sensory peg at apex.

Clypeus with weakly deflexed, slightly less sclerotized epistomal lobe (anteclypeus); bearing 4 setae, one at each posterior angle of epistomal lobe and one on each side of middle on sclerotized postclypeus. Epipharynx with weak, irregular set of minute cusps located mesially (Fig. 2). Labrum weakly emarginate anteriorly and bearing two rows of setae; first row on anterior margin; second row submarginal, just posterior to first row; each row with 7 or 8 thick, golden setae.

Mentum pentagonal (Fig. 4), sides concave for reception of maxillary cardo. Labium




Figs. 2–8. *Eleodes armatus,* larval and pupal morphology. 2, head capsule, ventral view, maxillae and labium removed. 3, pygidium, dorsal view. 4, labium and gulamentum, ventral view. 5, left prothoracic leg, ventral view. 6, left maxilla, ventral view. 7, pupal gin-traps, abdominal segments. 4–6, right side, dorsal view. 8, pupa, ventral view.

simple. Hypopharyngeal sclerome pentagonal, concavely excavated, base thickened, dorsal angles weakly produced. Cardo with two well-sclerotized plates; mala and stipes contiguous, cylindrical, well sclerotized. Tip of mala setose and bearing a double row of curved spines (Fig. 6), on its mesial edge.

Left mandible sulcately excavated aborally; ventral aboral margin with single cusp; dorsal aboral margin broadly explanate; right mandible weakly excavated aborally; ventral aboral margin without accessory cusp; dorsal margin sinuate.

Thorax: Anterior margin of pronotum and posterior margin of all thoracic nota golden brown, weakly, longitudinally striate. Prothoracic coxae contiguous; coxae of meso- and metathorax distinctly separate. Each trochanter bearing pair of subapical spines on ventral margin. Ventral margin of each femur and tibiotarsus bearing row of 4–9 (usually 5) spines or coarse setae (Fig. 5).

Abdomen: Posterior striated band of each tergum weakly infuscated. Pygidium (9th abdominal tergum) subtriangular in lateral view; flattened dorsally with scattered setae; an apical, sclerotized tubercle subtended by a pair of short thick spines and flanked on each side by a marginal row of short, thick, socketed spines, 6–10 in each row (the number varying both between individuals, and between sides of the same individual) (Fig. 3).

Pygopods of 10th abdominal segment angularly tumescent, with 14 or 15 strong, thick setae.

PUPA. Dull, yellowish-white; unsclerotized except for apices of mandibles, angles of femora, tips of urogomphi and minute points on gin traps (abdominal lamellae). Length 20 mm (Fig. 8).

Head: Flattened, elongate. Eye spots discernible as minute pink spot at center of mild protuberance at base of each antenna. Labial palps robust, 3-segmented, free. Antennae free, each positioned between profemur and prothoracic pleuron, 11-segmented.

Thorax: Prothorax with domed notum; notohypomeral margin entire with sparse setae. Each femur with robust, preapical, spinose tooth. Elytra arising from basal pronotal angles; divergent, feebly striated. Epipleural fold distinct except at very base and very tip.

Abdomen: Segments 1–6 with lamelliform lateral gin-traps. Anterior and posterior margins of lamellae darkened, microcrenulate; lateral margin irregularly serrate, bearing 1–3 seta-bearing spicules (Fig. 7).

A pair of small pygopods on either side of anus. Pygidium with pair of terete, sclerotized, sharp-tipped urogomphi.

The larva of *Eleodes dentipes* Eschscholtz was described and figured by Blaisdell (1909), *E. letcheri vandykei* Blaisdell and *E. pimeloides* Mannerheim by Hyslop (1912), *E. tricostata* Say by McColloch (1918), *E. suturalis* Say by Wade & St. George (1923), and *E. opaca* Say and *E. carbonaria* Say by St. George (1925). The larvae of these *Eleodes* species are very similar. The descriptions and accompanying figures indicate that there are slight but distinct differences in the number and arrangement of pygidial spines. The pupa of *E. armatus* is readily distinguished by the well-developed femoral armature.

## DISTRIBUTION AND HABITAT

*Eleodes armatus* is commonly encountered in the Mojave and Sonoran deserts along with an array of other ground-dwelling tenebrionid beetles. Its distribution includes the San Joaquin Valley of central California and the western Great Basin Desert along the rain shadow of the Sierra Nevadas as far north as southeastern Oregon (Fig. 1). I have collected the species as far south as Punta Cirrio on the coast of Sonora, Mexico. I have not seen a record from Utah, but the species undoubtedly occurs in the vicinity of St. George. The easternmost extension of the range appears to be in the vicinity of Tucson, Arizona. It was not among the species of *Eleodes* reported at a site in southwestern New Mexico by Smith & Whitford (1976).

The beetle was common at all census areas in Arizona and Nevada which included mixed Creosote-Bursage, pure Creosote, Saltbush and Yucca-Blackbrush communities (Table 1). It was enormously abundant on the Glamis Sand

Table 1. Relative abundance of *Eleodes armatus* in different desert habitats.

| Study area | Habitat | Trap-nights | Tenebrio-nids | % *E. armatus* |
|---|---|---|---|---|
| Tucson | Creosote | 4,400 | 704 | 22.8% |
| Beaver Dam | Creosote | 2,600 | 681 | 13.5% |
| Rock Valley | Creosote-Bursage | 43,700 | 4,699 | 4.4% |
| Mormon Mesa | Creosote-Bursage | 2,600 | 200 | 2.0% |
| Blue Diamond | Creosote-Bursage | 1,440 | 99 | 16.2% |
| Potosi Pass | Yucca-Blackbrush | 1,440 | 60 | 5.0% |
| Moapa Wash | Saltbush | 2,600 | 359 | 4.2% |

Dunes where the vegetation consists of Palo Verde and Ironwood. I have also collected this species in a Sagebrush habitat near Ely, Nevada. These localities differ markedly from one another in some aspect of climate, edaphic character or vegetational composition, indicating a broad ecological tolerance within desert or semiarid habitats. It is apparently restricted from higher elevations. It was not among the tenebrionids inhabiting Pinyon-Juniper communities surveyed by Tanner & Packham (1965) in Nye Co., Nevada, or by Kramm & Kramm (1972) in Riverside Co., California.

## Abundance and Seasonality

*Eleodes armatus* has its peak adult abundance during fall with a lesser peak in spring, though it may be found at any time of the year (Fig. 9). At the Tucson site, beetles were captured as late as mid-December. Larval stages were found at the Rock Valley site in both May and December, indicating that the beetle overwinters in both adult and larval stages. Potential longevity is not known, but two adult beetles marked in the fall of 1971 were recaptured alive in the fall of 1972, thus some beetles live more than a year in the wild.

In captivity *E. armatus* lays eggs continuously. In the wild, gravid females were found during spring and fall, and most oviposition probably occurs during these peaks in activity. Complete development of immature stages required a minimum of 9 months in the laboratory.

Calculations of population density using mark-recapture methods at Rock Valley during the summer of 1972 provided an estimate of 134 individual beetles per hectare (Thomas & Sleeper 1977). This is equivalent to 75 sq. m. of space for each adult, a far lower density than that indicated by observations on the Glamis Dunes in 1981, but indicative perhaps of normal population levels in open desert.

*Eleodes armatus* is one of the most conspicuous of tenebrionid beetles, not because it is particularly abundant, but because it is more frequently encountered during the daytime. The majority of North American desert tenebrionids are primarily if not strictly nocturnal. During the autumn peak in activity the beetles are often encountered in numbers during daylight hours. In all instances observed by me, though, temperatures were cool or skies overcast. Hadley (1970) found that tethered *E. armatus* were unable to withstand exposure to direct sunlight and mid-day surface temperatures normal to their habitat in summertime. During 4 yrs of daily, day-time insect surveys at Rock Valley, *E. armatus* was never found active on the surface during the summer months. The beetles seek refuge from high diurnal surface temperatures by retreating

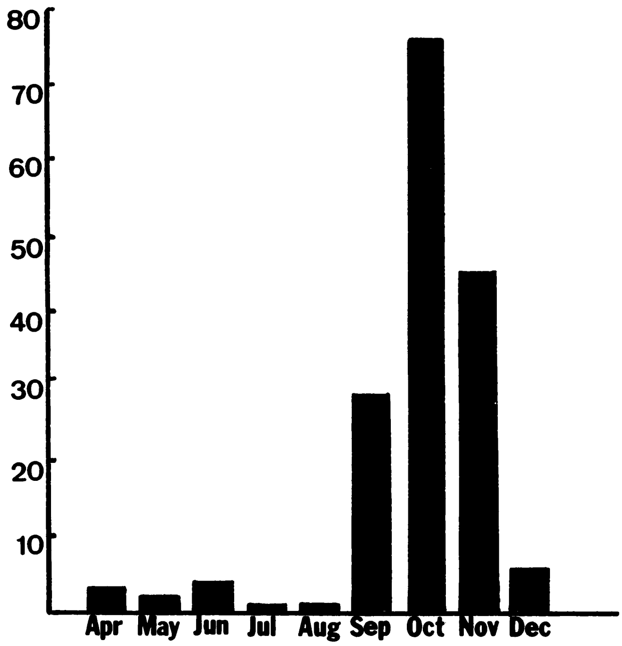



Fig. 9. Monthly pitfall captures of *E. armatus* from desert site near Tucson, Arizona, in 1981 (600 trap-nights/month).

into rodent burrows. One kangaroo-rat burrow excavated on 29 May 1981 contained over 50 individuals.

It would appear that *E. armatus* is primarily nocturnal during the summer months with a shift to diurnal or crepuscular activity during the cooler months. Interestingly, Ahearn (1970) demonstrated that *E. armatus* is less tolerant of high tempratures than some of its strictly nocturnal counterparts, *Cryptoglossa verrucosa* (LeConte) and *Centrioptera muricata* LeConte. The greater flexibility exhibited by this beetle with respect to diel and seasonal activity may be largely attributable to its defense against vertebrate predators.

## Behavior

Defense. Perhaps the most conspicuous behavior exhibited by *E. armatus* is its defensive posture of head-standing. Folk-tales of desert Indians held that the beetle was listening to the spirits (Jaeger 1950). The posture is defensive however, almost certainly aposematic, and therefore analogous to the posturing behavior of skunks. The beetle is able to spray a repugnatorial fluid for a distance of several inches. Some species of *Eleodes* neither spray nor posture (Tschinkel 1975*a, b*). *Eleodes armatus* does both though it does not have to assume the headstand to spray, furthermore, the beetle does not usually spray if handled gently. The defensive fluids are secreted from a pair of anal glands and have been identified in *Eleodes* spp. as analogs of benzoquinones (Tschinkel 1975*b*). Slobodchikoff (1978) documented the efficacy of this defense against vertebrate predators. Doyen & Somerby (1974) have described a complex of beetle species that have evolved as morphological and behavioral mimics of *Eleodes*.

Some natural enemies are able to overcome *Eleodes* defense. A particularly interesting account involves the predatory mouse, *Onychomys torridus* reported by Eisner (1966). The mouse pounces on the beetle and grasping with the forepaws jams the beetle tail first into the sand. Held in this position the beetle is killed and eaten.

I have found that the desert hairy scorpion, *Hadrurus arizonensis* Ewing, feeds readily on *E. armatus*. The beetle is captured by the legs and held in the scorpion's pedipalps with the tip of the abdomen pointed away. The scorpion stings the beetle, usually between abdomen and thorax. After a few minutes the scorpion uses its pedipalps to break the beetle in half and eats the internal organs. This feeding behavior is quite distinct from the manner in which *H. arizonensis* feeds on other insects (Bub & Bowerman 1979).

MATING. Copulation was observed frequently among captive beetles. A pheromone may be involved (Haverfield 1965), but evidence for this is indirect. Encountering a female the male beetle mounts from behind, over the dorsum, and grasps the female's body with his meso- and metathoracic legs. The female often attempts to dislodge the male and struggles to escape. The male sometimes counters by flipping over on its back, rendering the female unable to use her legs for leverage. When the female ceases struggling the male strokes her antennae with the prothoracic legs attempting to induce receptivity. After a few seconds of antennal stroking the male slips backwards over her dorsum to bring his abdominal terminus into coital position. He everts his aedeagus and probes the female's terminus. This action often provokes the female to attempt escape again, but the male persists, alternately stroking her antennae and probing with his aedeagus until she permits intromission or escapes.

OVIPOSITION. Egg laying was observed only in captivity. The female probes the soil surface with her antennae. Selecting a suitable site she moves forward bringing her abdominal terminus into position and extrudes the ovipositor. With rapid side-to-side motions, using the tip of the ovipositor as a rasp, she makes a shallow excavation in the soil. Pressing her ovipositor into this depression a slight tremor of her body signals injection of an egg (or eggs) into the soil. Moving forward a few centimeters the process is repeated. One female was observed to repeat this prodedure 86 times in succession during a period of ca. 20 minutes before stopping to feed. The significance of this behavior is that it serves to scatter the larvae spatially. *Eleodes* and other tenebrionid larvae are known to exhibit cannibalistic behavior under crowded conditions (Allsopp 1980).

## DIET AND FEEDING PREFERENCES

In captivity beetles lived up to 30 days without food. Diet appeared to be quite catholic; dog-food, apple cores, lettuce, carrots and dry corn meal were readily accepted. Papp & Pierce (1960) report *E. armatus* attacking stored grain. Kramm & Kramm (1972) describe *Eleodes* beetles as essentially scavengers, feeding opportunistically as they wander through their habitat. I have observed *E. armatus* feeding on the blossoms of ironwood (*Olneya tesota*), fruits of boxthorn (*Lycium andersonii*), and leaves of saltbush (*Atriplex confertifolia*) in the wild. It seems likely that the shed parts of deciduous desert shrubs are a primary food source for this beetle. A number of freshly captured individuals were dissected and their gut contents examined. In all specimens the gut contents were a greenish-brown fluid. Under magnification this material was found to consist of a suspension of plant epidermal tissue, macerated beyond species recognition. In several of the specimens there were also small amounts of insect parts. Since these specimens were captured in pitfall traps their gut contents reflected, in part, debris found by the beetles in the traps.

In order to test dietary preferences, starved individuals were offered counted numbers of fresh green leaves from different desert plants. Blades of grass, the leaves of *Lycium andersonii* and *Lycium pallidum,* and the green twigs of *Ephedra nevadensis* were accepted and eaten. The leaves of *Prosopis* sp. and *Larrea tridentata* were refused. Beetles starved to death in the presence of these leaves. Rhoades (1977) has demonstrated that the resins of creosote bush are feeding deterrents to many insects.

## Summary and Conclusions

Most desert tenebrionid beetles are nocturnal scavengers, active during the summer months. Since most deciduous desert shrubs shed their leaves and annual plants die with the onset of hot, dry summer weather, plant detritus is most available and exploited by tenebrionids at this time (Thomas 1979).

*Eleodes armatus,* however, is active at almost any time of the year, with a peak in the fall, well after the summer tenebrionids have ceased activity. Although there may be less plant detritus available at this time, moisture levels are higher because of late summer rains and temperatures are milder, allowing daytime activity. *Eleodes armatus* has one of the broadest geographical, diel and seasonal activity ranges of any desert tenebrionid beetle. This may be in part attributable to its defensive mechanisms against vertebrate predators.

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