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NATURAL HISTORY OF THE SPIDER GENUS *LUTICA* (ARANEAE, ZODARIIDAE)

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ABSTRACT. Spiders of the genus *Lutica* are fossorial inhabitants of coastal dunes of southern California, Baja California and the California Channel Islands. They live in silk-lined burrows concentrated beneath dune vegetation. *Lutica* are sit-and-wait predators that subdue insects that walk near or over burrows. They are sedentary and do not engage in aerial dispersal via ballooning. Adult males abandon their burrows during the late summer and early fall to wander in search of females. Females produce eggsacs and guard them till they die; spiderlings emerge in the spring. Dune trapdoor spiders (*Aptostichus simus*) prey on *Lutica*, while the larvae of a therevid fly are external parasites.

Spiders of the genus *Lutica* are fossorial inhabitants of coastal dunes of southern California, Baja California and the California Channel Islands (Gertsch 1961, 1979; Ramirez 1988). Although described over 100 years ago (Marx 1891), little is known of their natural history. Gertsch (1979) stated that they are nocturnal and come to the surface at night to hunt various beetles and other insects that drop on the sand, and that they spin a loose tubular retreat deep in the cool, moist sand. Gertsch (1961) believed that they probably live for two to three years, with males maturing in the summer or fall, but admitted that little was known about the details of the "... lives and habits of these large, whitish spiders."

George Marx first described the genus *Lutica* from Klamath Lake, Oregon (Marx 1891). Gertsch (1961) corrected the type locality of *Lutica maculata* to Santa Rosa Island, California, and also described three new species: *nicolasia* (San Nicolas Island), *clementea* (San Clemente Island) and *abalonea* (Oxnard, Ventura County). Additional species have been described from India (Tikader 1981), but these taxa are clearly misplaced (Jocqué 1991). Gertsch (pers. comm.) has prepared a revision of *Lutica* based on morphological features, while Ramirez & Beckwitt (in press) have re-defined valid species and determined their phylogenetic relationships based largely on molecular characters. Since these works propose very different species designations than Gertsch (1961), species names in *Lutica* are uncertain at this time.

My study of *Lutica* elaborates on the natural history of this obscure genus.

METHODS

From 1982 to 1987, I collected over 3000 *Lutica* from 20 different dune systems in southern California and Baja California (Fig. 1), including sites on all the Channel Islands except Anacapa (where they are not known to exist), as part of a study of the population genetics and biochemical systematics of this genus (Ramirez 1990). Spiders were collected by sifting dune sand beneath beach vegetation using geologic sieves with a minimum mesh size of 1.0 mm. All specimens were brought back to the laboratory alive, where they were either used for observations or processed for starch gel electrophoresis. Living spiders were maintained in small upright glass or plastic containers or in horizontal glass tubes, partly filled with beach sand. Water was added periodically with either an eye dropper or atomizer. I fed them small arthropods, mainly fruit flies, house flies and beetle larvae (wireworms).

For a mark-recapture experiment with *Lutica* in the field, I marked spiders on the dorsal surface of their abdomens with quick drying scale model paint (Testors Flat White), after first cooling the spiders in a refrigerator for 30 min to make them sluggish and easier to mark. After the spiders were warmed to ambient temperature, there was no visible difference in their behavior.

RESULTS

Burrow construction.—Individual *Lutica* readily constructed burrows in the laboratory after being placed in sand-filled containers. Burrows consisted of silk-lined tunnels in the sand, usually just below the surface and sometimes partly against the side of the glass container. This facilitated the observation (under subdued light) of activities within. Burrows had either open entrances or no entrances.

On two occasions, I observed burrow construction. In one case, the horizontal glass tube occupied by the spider was packed with moist sand in the sealed end. The spider moved about in a space between the sand and the lower side of the glass tube (Fig. 2). It moved its spinnerets from side to side and up and down, cementing fragments of sand together with silk, and slowly moved in a circle as it did so. It sometimes stopped this activity and moved over to the interior of the burrow wall where it pushed forward with its forelegs, pushing back the wall and expanding the burrow. It then resumed its circular spinning activity. I observed the spider until it suddenly halted its activity and did not resume work on its burrow. In the second case, also with a spider in a horizontal glass tube, the spider half-carried, half-pushed a pile of sand toward the entrance of its burrow. Before it reached the entrance, it halted its activities and did not continue.

In the field, burrows were concentrated in and about stands of native dune vegetation, particularly *Abronia maritima* and *Franseria chamissonis*, and extended into the dune amidst litter and the root systems of the plants. On Santa Barbara Island, typical coastal dunes do not exist and these spiders live in the sandy soil and debris below vegetation growing on a sea cliff. While burrow entrances were normally not visible, one could often see small dimples on the open surfaces of vegetated dunes after strong winds. These usually proved to be the entrances of *Lutica* burrows, composed of a delicate sand-covered, flap-like lid; this is consistent with Thompson's (1973) description of burrows on Santa Cruz and San Miguel Islands. Most burrows descended into the sand at about a 45° angle, although some had portions of their length laying horizontally, just below the sand surface. On the other hand, at La Jolla Beach (Ventura County), I found four burrows that descended vertically into the sand. *Lutica* burrows were usually very fragile and quickly fell apart if the sand around them was removed. Individual burrows were usually from 2.5–15 cm in length, though W. Icenogle and I found a burrow that was 25–30 cm long (occupied by a mature female) at Little Harbor, Santa Catalina Island.

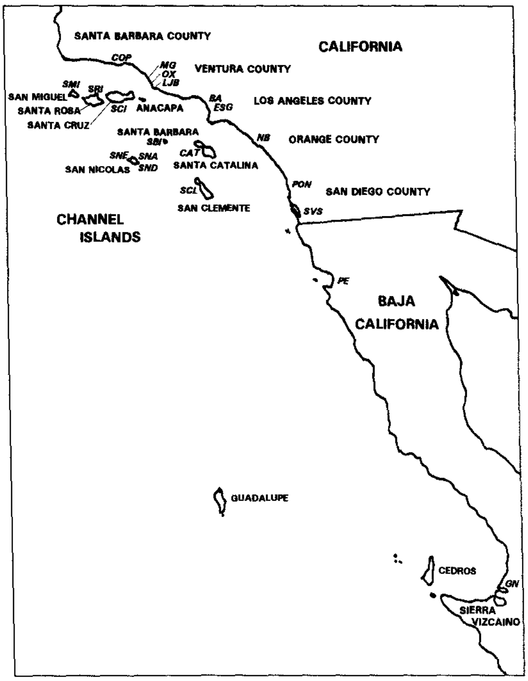

Figure 1.—Map of southern California and Baja California, including the Channel Islands, showing *Lutica* sample sites. Population abbreviations are as follows: Channel Islands - Cuyler Harbor, San Miguel Island (SMI); Southeast Anchorage, Santa Rosa Island (SRI); Johnstons Lee, Santa Cruz Island (SCI); cliffs south of Signal Peak, Santa Barbara Island (SBI); Army Camp Beach (SNA), Dutch Harbor (SND), Red Eye Beach (SNE), San Nicolas Island; Little Harbor, Santa Catalina Island (CAT); Flasher Road Dunes, San Clemente Island (SCL); Mainland - Coal Oil Point Reserve (COP), Santa Barbara Co., California; McGrath State Beach (MG), Ventura Co., California; Oxnard Beach (OX), Ventura Co., California; La Jolla Beach (LJB), Ventura Co., California; Ballona Wetlands (BA), Los Angeles Co., California; El Segundo Dunes, LAX (ESG), Los Angeles Co., California; Balboa Beach (NB), Orange Co., California; Ponto State Beach (PON), San Diego Co., California; Silverstrand State Beach (SVS), San Diego Co., California; Punta Estero (PE), Baja California Norte, Mexico; Guerrero Negro (GN), Baja California Sur, Mexico.

Prey capture.—Once they had constructed burrows in the laboratory, the spiders readily accepted small insects as food. An insect crawling about on the surface of the sand elicited an immediate response. The spider (hanging upside down) would rush about on the "ceiling" of its burrow, possibly trying to locate the exact position of the insect by the vibrations caused by its activities. If the insect suddenly ceased its

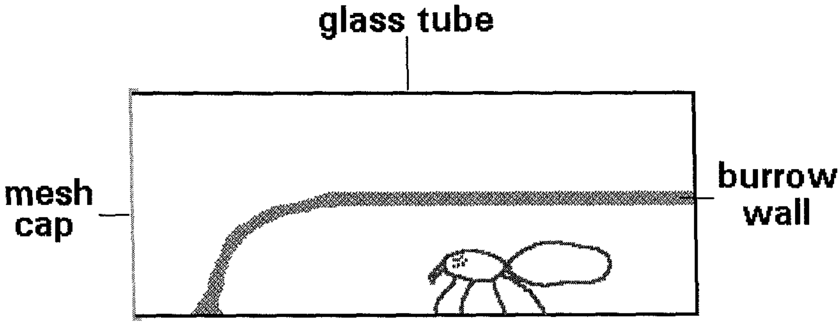

Figure 2.—Profile of horizontal *Lutica* rearing container,showing the orientation of a spider and its burrow. Containers were 2.5 cm in diameter and 9.5 cm long.

movements, the spider would likewise stop its movements and would remain motionless until the insect started moving once again. Once the spider had positioned itself below the insect, it would lunge up and through the wall of the burrow, grab the insect and pull it inside the burrow. Spiders sometimes left their burrow completely to pursue prey that initially escaped; they brought the prey back to the burrow either through the open entrance or through the hole created in leaving the burrow. Once insects ceased to struggle inside the burrow, the spider would leave the insect to patch up the hole in the burrow wall, and would then return to feed on the now dead prey.

While the capture of prey through the burrow wall was typical, spiders sometimes emerged from their burrows at the first sign of prey vibrations and subdued their prey directly, before taking them inside the burrow. Most spiders deposited the prey remains outside the burrow following feeding. Field-collected burrows were always uniformly clean and a prey item was found inside a burrow on only one occasion.

Timing of reproduction.—*Lutica* males molt to maturity and abandon their burrows to wander about in search of females. Based on a master list of collecting records of all *Lutica* specimens (available on request), the earliest record of an adult male is May 11 (1♂, Oxnard Beach, Ventura County, 1968, M. Thompson) and the latest records are November 3 (1♂, Oxnard Beach, Ventura County, 1982, M. Ramirez) and November 4 (1♂, Silverstrand State Beach, San Diego County, 1982, M. Ramirez). The largest number of records and actual numbers of males collected are for September and October. For example, pitfall traps set up in dunes at Pt. Mugu Naval Air Station, Ventura County collected 169 adult male *Lutica* between 31 August–18 October 1981 (C. Nagano & J. Donohue pers. comm.). Thus, the peak of the breeding season appears to be late summer and early fall.

Following mating, females produce eggsacs, though how soon is not known; there then follows the period of spiderling growth and development. My earliest record of brood spiderlings was 15 April (El Segundo Dunes, Los Angeles International Airport, Los Angeles County, 1985), and I collected broods as late as August from both island and mainland populations. Females presumably guard eggsacs and young till they die; of 22 eggsacs or broods collected in 1985 and 1987, 12 were found in burrows along with the shrunken remains of adult females. Since burrows are destroyed during collection, scattering their contents, it is probable that the remains of adult females also may have been present with the other 10 eggsacs/broods.

Dispersal.—Mark-recapture data suggest that non-reproductive dispersal is limited. At Coal Oil Point Reserve (Santa Barbara County), 170 spiders from a single dune were captured on 28 February 1984, marked on the dorsal surfaces of their abdomens and released into the dune from which they were taken. Seventy-seven (45.3%) of 170 spiders collected at that same dune a month later were marked. Assuming the loss of marks by individual spiders due to molts in the intervening period, actual site fidelity was probably greater. However, since I did not have an opportunity to collect in dunes adjacent to the one in which the marked spiders were released, it is not known how many of the marked spiders I failed to recover may have moved to different dunes in the intervening month. Nonetheless, since their burrows were destroyed when the spiders were first collected, it is remarkable that such a large percentage of them stayed in the same dune following release.

Gertsch (1961) stated that *Lutica* do not balloon, as is common among many spiders (Decae 1987), and *Lutica* of all sizes instantly buried themselves in the sand if removed from their burrows. However, while sifting for *Lutica* during Santa Ana wind conditions, I often saw small specimens cling tenaciously to the mesh of the sieve; if they lost their grip, the smallest spiders would sometimes be blown up and out of the sieve. This is a highly unnatural situation, since the spiders do not normally move about at the surface during the day and would certainly not find themselves a foot or more above the sand surface. Dune vegetation is prostrate and I have never seen them climb about in plants. On the other hand, twice during Santa Ana winds, I saw a few immatures and adult females moving about on the surface of the dunes. Since I never observed *Lutica* moving about on the surface on any other occasions, it is possible that the wind had shifted the sand in the area where these spiders had made their burrows, eventually dislodging them. Thus, while they do not engage in ballooning behavior, it may be possible for the smallest instars of *Lutica* to be carried away in high winds.

Predators.—Trapdoor spiders of the genus *Aptostichus* (Cyrtaucheniidae) are the only organisms known to prey on *Lutica*. One member of this genus, *A. simus*, is restricted to coastal dunes in southern California (Chamberlin 1917), including the California Channel Islands, and it lives in silk-lined burrows. In September 1979, W. Icenogle (pers. comm.) found the remains of an adult male *Lutica* (as well as an adult male *Aptostichus*) in the burrow of an adult female *Aptostichus* in a coastal dune near Encinitas, San Diego County. Since only adult male *Lutica* would normally be expected to wander about on the surface of the sand, it is not likely that *Aptostichus* prey on non-male *Lutica*.

Parasites.—Of the thousands of *Lutica* collected over six years, only a single spider was parasitized. In September 1983, I collected three *Lutica* from La Jolla Beach (Ventura County) which were paralyzed. Attached to the abdomen of one of the spiders was a small white larva. The larva eventually consumed the spider from the outside in, but unfortunately died without pupating. E. Schlinger (pers. comm.) identified the larva as that of a therevid fly (Diptera). No Therevidae have been reported previously as spider parasites (Eason et al. 1967; E. Schlinger pers. comm.).

Prey.—In the field, I recovered many *Lutica* with beetle larvae (wireworms) in their chelicerae and found one burrow which contained the dry remains of a wireworm. In the laboratory, *Lutica* readily attacked any small insects or spiders and never rejected any arthropod they were capable of subduing. If many prey items were supplied at once, most *Lutica* attacked and subdued all the arthropods in rapid succession before they began to feed on any of them.

DISCUSSION

Burrow construction.—The fossorial lifestyle of *Lutica* is typical of the Zodariidae, most of which are ground or forest floor dwellers which often construct silken retreats, either burrows or silk-lined bags (Jocqué 1991, 1993). Aside from *Lutica,* the construction of burrows with trapdoors has been reported among the Zodariidae in *Antillorena* (Gertsch 1961; Jocqué 1991), *Capheris* (Hewitt 1914; Jocqué 1991), *Neostorena* (Jocqué 1991) and *Psammorygma* (Jocqué 1991, 1993). Observations of burrow construction have not been reported previously for a zodariid, although Harkness (1977) detailed the construction of a bag-type shelter by *Zodarion frenatum.*

Prey capture.—The prey capture behavior in *Lutica* described herein is the first description of the sub-surface attack sequence of a burrow-dwelling zodariid. Since the orientation of burrows in the field ranged from nearly horizontal to vertical, it is probable that the sub-surface attack sequence described for *Lutica* only applies to those burrows which have at least some portion lying near the surface in a horizontal position, where arthropods can walk across them. With burrows situated at steeper angles, *Lutica* probably come out to attack passing insects, as did some laboratory spiders and as does *Antillorena* (Gertsch 1979).

The sub-surface prey location and attack behavior of *Lutica* strongly parallels that reported for the "purse web" spiders, *Atypus*, *Calommata* and *Sphodros* (Atypidae) (Bristowe 1958; Coyle 1986). These three spiders are all burrow dwellers which construct a tube-like, silken extension of the burrow (the "purse web") that extends along the ground or vertically against a tree or other support. Prey are located when they walk or land on the purse web: the spider locates the position of the prey by its vibrations and once positioned below the insect, it then strikes through the silken tube, slits open the purse web and pulls the prey inside, much as *Lutica* does in its own burrows. However, while only the fangs of purse web spiders are extended though the tube wall to capture prey, *Lutica* may force much or all of its body through the burrow wall to do so. This similarity in attack sequence may be an example of convergence in behavior involving spiders in two very different families, due to the functional similarities of a purse web and a shallowly buried silk-lined burrow.

Timing of reproduction.—The presence of males in the field largely in the summer and fall, coupled with the appearance of spiderlings by the spring, indicates that the production of eggsacs and development of young takes place sometime between fall and spring. Bonnet (1935) noted that many spiders which mature and mate toward the end of the summer produce overwintering eggsacs in the fall, with spiderlings emerging in the spring. Since brood spiderlings were collected in the field as early as April, it would appear that production of eggsacs and subsequent development of spiderlings is consistent with that of other spiders which mature in the late summer. When *Lutica* do reproduce, it is probable that the females guard the eggsacs and developing spiderlings in their burrows till they die, as evidenced by the regular collection of eggsacs or broods along with the remains of adult females.

Dispersal.—Given the isolation of coastal dune systems along the southern California and Baja California coasts (Fig. 1) (Cooper 1967; Powell 1981), knowledge of the extent and timing of inter- and intra-dune dispersal by *Lutica* would be of great value in understanding the structure of their populations and patterns of genetic variation within and among them (Ramirez 1990). On a local scale, a low dispersal rate among different parts of a dune system [typical size 2–10 km^2 (Powell 1981)] might lead to genetic subdivision, and possibly the evolution of microgeographic races (Doyen & Slobodchikoff 1984).

The results of the mark-recapture study suggest that non-reproductive terrestrial dispersal is low. Terrestrial dispersal is probably limited to wandering males and those spiders dislodged from their burrows by the shifting of dune sand. Nonetheless, dispersal on a local scale is apparently effective enough to maintain genetic homogeneity among spiders in dunes on the same beach (Ramirez 1990).

Ballooning is rare in fossorial spiders (Decae 1987) and has never been reported in the family Zodariidae (Jocqué 1993). However, Robinson (1982) has suggested that spider aerial dispersal may sometimes be accidental. More specifically, if a spider is small and light, it is possible that if it loses its hold of the substrate while exposed to wind of sufficient strength, it might become airborne solely due to its favorable aerodynamic characteristics (Glick 1939). This apparently happened with small *Lutica* in my sieves during Santa Ana winds. However, since ballooning spiders depend on wind borne silk threads for lift (Coyle 1983), it is unlikely that *Lutica* travel far even if they do become airborne, since they were never seen to pay out threads of silk into the wind or drop from elevated positions on draglines exposed to the wind, the two means spiders use to accomplish ballooning (Coyle 1983; Decae 1987).

If aerial transport is a regular means of *Lutica* dispersal, one would expect that there would be few dune systems that they would not be capable of invading; yet, they are absent from most of the coastal region between Ventura County and Los Angeles (their absence from the well developed dune system at Pt. Dume is particularly puzzling) and from Anacapa Island, the closest of the Channel Islands to the mainland (Fig. 1). Although Anacapa has no dune system, *Lutica* live on much more isolated Santa Barbara Island in a non-dune habitat. Thus, while it may be physically possible for *Lutica* to become airborne, it is not likely that such a means of dispersal has played a large part in creating present distributions.

Predators.—Among the small but distinct arthropod fauna of California coastal dunes (Nagano 1981; Powell 1981), *Lutica* and *Aptostichus simus* are the only predators to occupy silk-lined burrows. The record of a male *Lutica* from an *Aptostichus* burrow is not unexpected, since their burrows are often found side by side in the dunes. While no other case of predation on *Lutica* was observed, there are a few invertebrate and vertebrate insectivores that occupy California coastal dunes and may potentially feed on *Lutica*, specifically windscorpions (Solpugida), side-blotched lizards (*Uta stansburiana*) and California legless lizards (*Anniella pulchra*) (Hayes & Guyer 1981; Nagano et al. 1981). However, such potential predators were only rarely encountered while collecting *Lutica*.

Parasites.—The record of a therevid fly larva consuming a paralyzed *Lutica* is highly unusual. Therevid larvae are predators of sand dune inhabiting insects and some may specialize on tenebrionid larvae (Doyen 1976, 1984). Their interactions with spiders have not been reported previously. Spider wasps (Pompilidae), which are abundant in southern California, are spider specialists and typically paralyze their prey (Wausbauer & Kimsey 1985), so the three paralyzed spiders found at La Jolla Beach (Ventura County) were presumably the result of pompilid activity. If these spiders were indeed attacked by pompilid wasps, the absence of wasp eggs or larvae attached to the paralyzed bodies is puzzling; perhaps they were knocked off during sifting. The presence of a therevid larva attached to one of the three paralyzed spiders was probably the result of a chance encounter with the immobile spider during the larva's movements through the sand.

Prey.—Tenebrionids (Coleoptera) and their larvae (wireworms) are among the most abundant insects in California coastal dunes (Doyen 1976, 1984) and their numbers far exceeded the numbers of other insects recovered during sifting. Both Gertsch (1961) and Thompson (1973) suspected that *Lutica* preyed on tenebrionids and my capture of many of them with wireworms in their chelicerae has proven them correct. However, save for the chance collection of *Lutica* with prey items, it will be difficult to determine whether *Lutica* prey on adult beetles (or any other organisms), given their rapid disposal of prey remains upon completion of feeding. The application of electrophoretic (Murray & Solomon 1978; Fitzgerald et al. 1986) and serological (Greenstone 1977; Southwood 1978) analyses might distinguish, from a range of possible prey items, what *Lutica* are actually eating.

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