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Jeannel, René

René Jeannel was born in 1879. Son and grandson of medical doctors, he was interested in insects since childhood, but studied medicine in Paris. He decided to work on a degree in science followed by doctoral studies at the Sorbonne. Some invertebrates that he had collected in a cave in southwestern France (described in part in 1905 in his second entomological paper) drew the attention of Emil Racovitza, who began to include René in 1905 in a huge project to explore the zoology of the subterranean world. His doctoral thesis in medicine (surgery) was published in 1907. From 1908 to 1912 he worked alongside Racovitza at the Arago laboratory. In 1912 he moved to the entomology laboratory of the Muséum National d'Histoire Naturelle, and worked there until 1914, the outbreak of World War I. In 1919–1920 he worked in the faculty of sciences at Toulouse, France, but in 1920 was appointed professor at the university of Cluj in Romania. In 1927 he returned to France as professor at the Muséum National d'Histoire Naturelle and director of the museum's vivarium. His overseas explorations were with Charles Alluaud in 1912–1913 to eastern Africa, with Arambourg and Chappuis in 1932–1933 to eastern Africa, and on the voyage of the Bougainville to the subantarctic Kerguelen and Crozet islands in 1938. He also explored caves in the eastern USA in August–September 1928 following the International Congress of Entomology in Ithaca, New York. His interests were in systematics and speleology, with a strong component of biogeography. He quickly recognized the importance of Wegener's theory of plate tectonics. His taxonomic interests were in the families Carabidae and Catopidae (now called Leiodidae), and Pselaphidae (subsequently reclassified as subfamily Pselaphinae of Staphylinidae). A long series of publications recounted cave explorations and discoveries, and dozens of these were published in a numbered series called "Biospeologica" in the pages of the journal Archives de Zoologie

Expérimentale et Générale. His works on the taxonomic groups of his interests were of worldwide scope, including, for example, studies of all three in southern South America, published in volume 1 of "Biologie de l'Amérique australe" (1962). His huge output of publications was a model for colleagues and students alike. Married and with children and grandchildren, he died on February 20, 1965.

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Jerusalem Crickets (Orthoptera: Stenopelmatidae)

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Four extant New World genera, herein collectively referred to as Jerusalem crickets, comprise the subfamily Stenopelmatinae, family Stenopelmatidae in the order Orthoptera. These genera are *Stenopelmatus* (with 33 described species), *Ammopelmatus* (2), *Viscainopelmatus* (1), and *Stenopelmatopterus* (3). Species are frequently distinguished by a combination of subtle morphological characters present only in adults, karyotype number, geographical distribution, calling-drum patterns, and mitochondrial DNA (mtDNA) profiles.

The Entomological Society of America's common name directory lists "Jerusalem cricket" as applicable only to *Stenopelmatus fuscus*, a species restricted to northern New Mexico and adjoining northeastern Arizona. Unfortunately,

this name has been applied by various authors to many species ranging from the California Pacific coast north into Canada, east to the Great Plains, and south into Mexico. Because of such taxonomic confusion and general physical similarities between species, we have decided to call all individuals of the subfamily “Jerusalem crickets” until Weissman’s revisionary studies are completed.

Jerusalem crickets are distributed (Fig. 3a) in the western half of the U.S. and throughout Mexico and Central America. Though 17 species are described from the United States and Canada, we estimate that three times that many species are undescribed. Similarly impressive biodiversity occurs in Mexico and Central America where 19 species are named and dozens of taxa are unnamed. Two described species have no locality data. The three heaviest insect species, on average, in California are undescribed Jerusalem crickets that easily reach about 7.5 cm in length and weigh up to 13 g.

Origin of Common Name

In the United States, stenopelmatids are called sand crickets, stone crickets, potato bugs, skull insects, and most commonly Jerusalem crickets. The last name is preferred since using it would eliminate confusion with any other insect group. “Jerusalem cricket” appears to be derived from jargon of young boys of the nineteenth century. The epithet “Jerusalem” was commonly used as a swear word by any young lad who was suddenly startled or surprised by a natural phenomenon. Additionally Berrey and van den Bark’s 1953 *American Thesaurus of Slang* lists both “Jerusalem!” and “cricket!” as expletives. Thus, R. Doult envisioned a rural boy in the western United States turning over a rock and in surprise shouting, “Jerusalem! What a cricket.”

In various parts of Mexico, Jerusalem crickets are called *niña de la tierra* (child of the earth) or *cara de la niña* (face of the child). They are

universally, and mistakenly, thought to be poisonous.

Determination of the Adult Stage

Females: Adult females are distinguished by a darkened (at least at the tips and on the ventral surfaces), sclerotized ovipositor (Fig. 3b), the four components of which develop progressively with each molt.

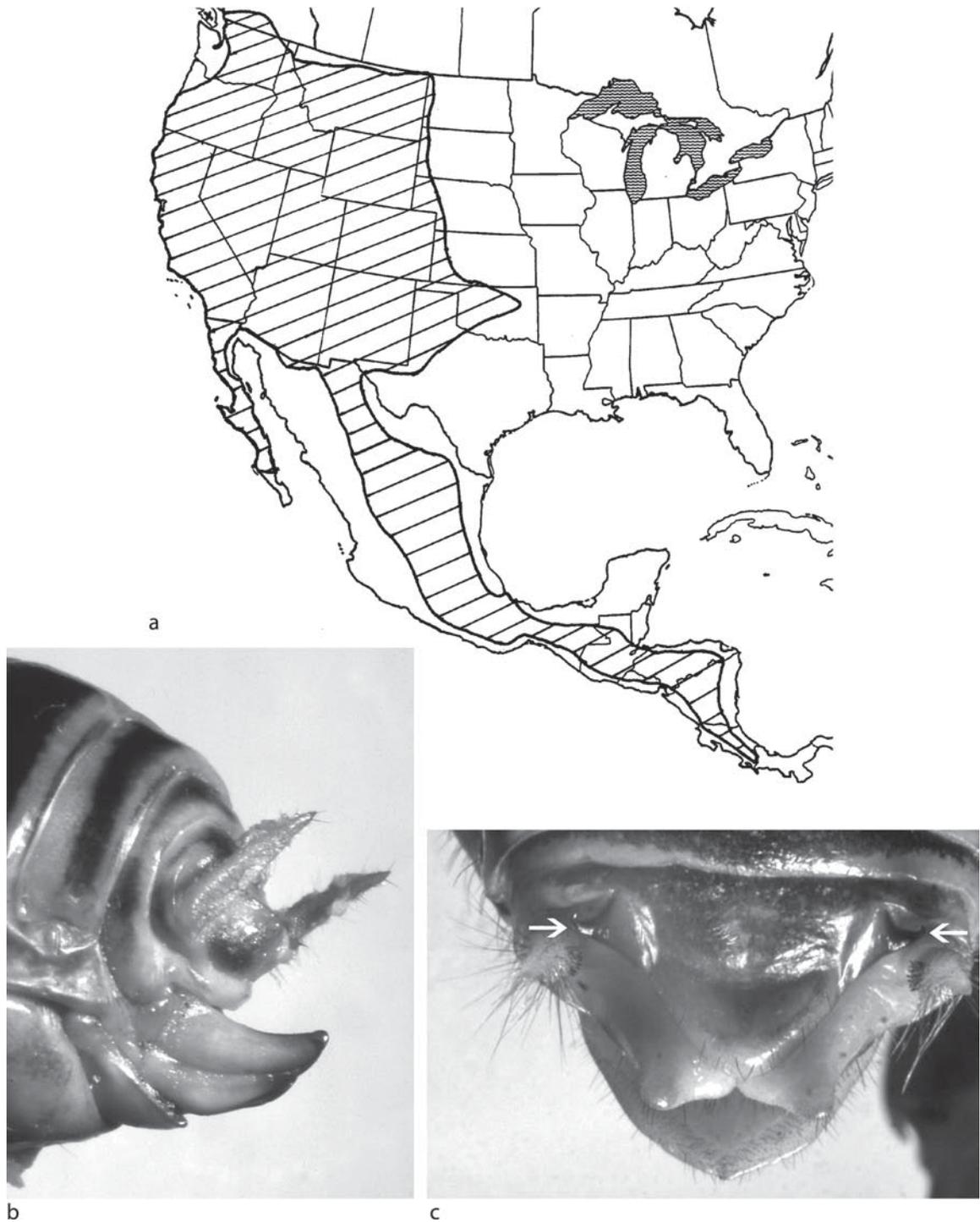
Males: Adult males have two fully developed, black, sclerotized, incurved hooks located medial to each cercus (Fig. 3c). These hooks develop gradually with each molt starting from tiny ridges barely visible in early instars. The hooks are used in mating and their importance is discussed later.

Karyotype

Jerusalem crickets have the typical orthopteran male XO/female XX sex determination system. Analysis by N. Ueshima shows that two Jerusalem cricket species have 19 chromosomes in the male and three species have 21. Another 150 individuals, probably representing some 80–90 species, have been karyotyped, and the 25 karyotype number was found twice as often as the 23 number.

Life Cycle

Most Jerusalem cricket species require 1¼ years from egg hatch to maturity (molt to adult), although some individuals in populations at high elevations and/or northern latitudes, with their shorter growing season, may require an extra year. Individuals of most species become adult in mid-summer, with members of some California species maturing a month or two later. There is no obvious protandry, wherein males mature before females. Adult males disappear in the field before adult females, apparently due to a combination of



Jerusalem Crickets (Orthoptera: Stenopelmatidae), Figure 3 Characteristics of Jerusalem crickets: (a) distribution (*stippled area*) of the Jerusalem crickets in North and Central America; (b) adult female Jerusalem crickets are characterized by a pointed, sclerotized, dark ovipositor; (c) adult male Jerusalem crickets are characterized by completely formed hooks (*arrows*).

shorter life span (as documented in laboratory specimens) and sexual cannibalism (see below). At least two southern California species have a summer adult aestivation period where they are physically active but do not drum and are sexually unreceptive.

Eggs apparently are laid underground soon after mating, as indicated by the fall appearance of tiny nymphs. It is unknown if eggs have any dormancy period since Weissman has never been able to get females to oviposit in the laboratory, nor has he collected egg clutches in the field. Jerusalem crickets probably have from 9 to 12 molts before becoming adult, but since all individuals quickly eat their cast skins, such determination is imprecise. There is no evidence of prenatal care.

Adult females live from 6 to 12 months in the laboratory. Adult males live about half as long as females.

Ecology

Within the United States, Canada, Baja California, Mexico, and northern mainland Mexico, various Jerusalem cricket species live in most available habitats from oak savannah, grassland, chaparral, coastal and inland sand dunes to above the tree line. These species are generalists and a laboratory diet of organic romaine lettuce (for water), and dry cat and rabbit food, along with uncooked old-fashioned oats, is adequate for rearing. Many sand dune inhabiting species are endemics restricted to that particular dune system. Jerusalem crickets are absent from both salt and fresh water habitats, and desert areas of high alkalinity or salinity.

Once south of the United States-mainland Mexico border, and throughout their distribution as far south as southern Costa Rica, most Jerusalem cricket species are associated with some combination of high elevation, cool and moist, cloud forest type environment. The largest group is characterized by tens of species, most undescribed, where individuals readily hop upwards to 10 cm. These fast moving, good climbing, “spiny” and thin-legged

individuals, occasionally with wing pads or completely developed wings, all appear to be active obligate predators. These species seek daytime refuge in downed forest trees (where they may eat co-inhabiting beetle larvae), possibly ascending at night into vertical trees to hunt live arthropods. They are most easily captured by tearing apart such downed, rotting trees, using a pickaxe or similar tools during daylight. The wetter and cooler the weather, the higher the rate of successful discovery.

Jerusalem crickets are large morsels of food and are eaten by many nocturnal predators, including foxes, skunks, bats, opossums, various owl species, various rodents, tropical vipers, and scorpions. Because of such risks, Jerusalem crickets employ several defensive strategies: they are largely nocturnal in activity; frequently flip on their backs with strong mandibles (which can draw human blood) agape when disturbed; employ abdominal-femoral defense stridulation; can kick with long, sharp, hind leg tibial spines; and some taxa have an offensive-smelling anal discharge. They are parasitized by tachinid flies (Diptera: Tachinidae), hairworms (Nematomorpha), and mermithid (Nematoda: Mermithidae) worms.

Different Jerusalem cricket species are rarely microsympatric, two species having been found together at only 30 localities (out of thousands) involving 20 different species-pairs. They may be commensals in *Pogonomyrmex* harvester ant nests in the southwestern United States.

Drumming and Communication

Jerusalem crickets are generally nocturnal and largely subterranean, thus limiting the effectiveness of visual and olfactory communication. They also do not fly, in spite of several species having fully developed hind wings. Jerusalem crickets have no auditory tympana to detect airborne sounds, nor does any species have wings with a sound producing apparatus. Information on location, distance, and sometimes sex, is exchanged via ground

transmission of impulses produced by the abdomen (and sometimes the thorax-abdomen unit) striking the substrate (drumming), producing a percussion wave. These ground impulses are detected by other Jerusalem crickets through their subgenual organs, which are located in the proximal tibiae of all six legs and are the most vibration-sensitive organs in any insect group. Subgenual organs also respond to high intensity airborne sounds. Both sexes of all species drum spontaneously, sometimes producing sounds audible at 20 m.

There are four types of drumming. “Calling” drums are, in many cases, species-specific and spontaneously made by isolated adult males and females. This drumming is as valuable a taxonomic character as the species-specific calling songs of field crickets and katydids because it appears to serve in uniting the sexes. These drums vary in complexity among species and range from a series of single strikes at rates of 0.5–15 drums per second, to groupings of strikes with rates approaching 40 drums per second (Fig. 4b). In several species, the male and female drum differently (Fig. 4a) thus permitting long range sex determination. Calling-song drumming rates in Jerusalem crickets vary linearly with temperature. Those species with fast rates increase their drumming speed more for a given temperature rise than does a slower drumming species. While drumming speed appears to be unrelated to body size, it may be related to substrate consistency and/or density: sand-dune-inhabiting taxa all drum relatively slowly.

Presumptive “sex clarification” drums are produced by adult males of certain species. These are a series (Fig. 4c) of fast, very loud, non-species-specific drums produced when these males detect their calling drum. Sex clarification drums occur only in species where the male and female have the same calling drum, and one sex cannot tell who they are answering. In the field, this answering strategy should enable males to conserve energy and avoid possible injury or predation by not searching for other males. Sex clarification drums are unknown from any of the eight species where

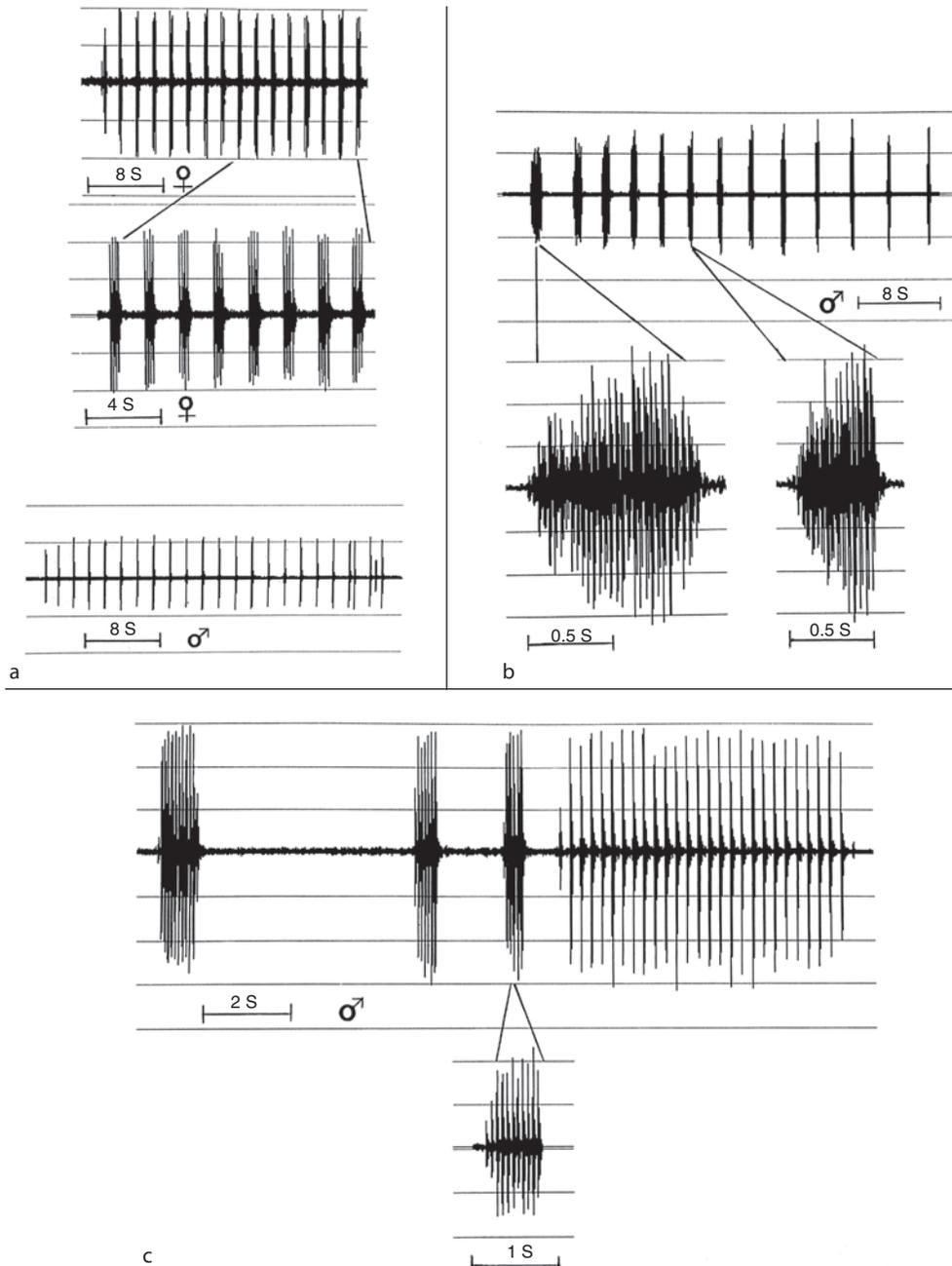
males and females drum differently, since each sex can identify the other sex by drum.

“Courtship” drums are frequently made by males (and less commonly by females) when two adults of either sex are within 6 cm of each other. This drumming consists of short series of barely audible, non-species-specific abdominal strikes or tremulations (where the abdomen does not make surface contact) at a rate of two to four per second.

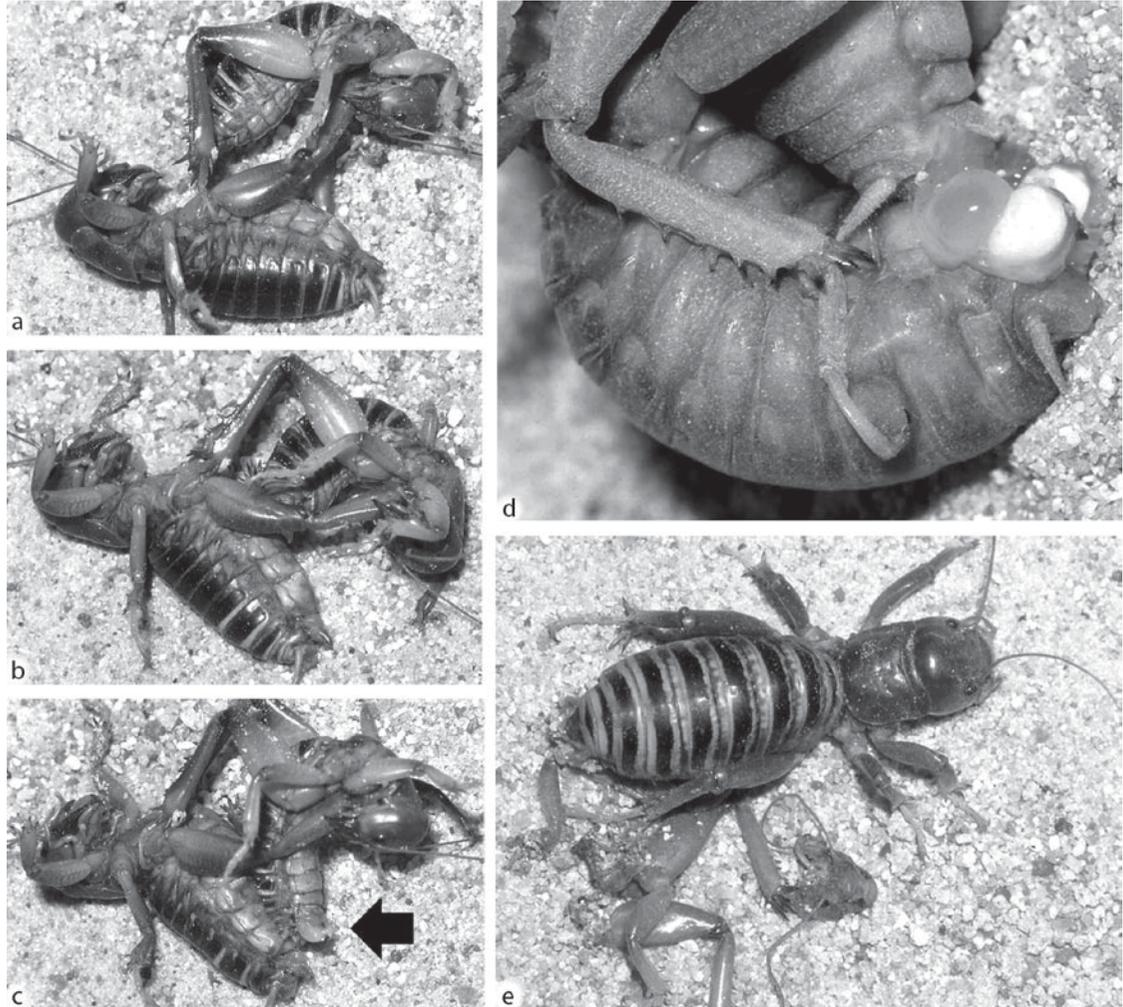
“Nymphal” drums are known from at least 25 species. They have the same pattern as the adult species-specific calling drum, but are produced less frequently, are usually of shorter duration, and are rarely heard during more than one instar. These subadult Jerusalem crickets do duet with other nymphs and adults, although the function of such drumming is unknown.

Mating

Jerusalem cricket orientation during mating appears to be unique among orthopteroid insects, if not among all insects. The male initiates the process by rolling on his side. Once the female is also on her side, the male assumes a lateral position beside her but facing in the opposite direction (Fig. 5a). He bites one of her hind tibiae (doing no damage), positions his hind tarsi near her coxae, and curls his abdomen (Fig. 5b) between his hind legs and her hind legs toward her subgenital plate, a maneuver that often requires several minutes of adjustments. As the male’s telescoping abdomen nears the female’s subgenital plate, he positions his hooks underneath a terminal ventral plate. This provides the necessary anchor as he everts his phallic lobes (Fig. 5c) and makes contact with her subgenital plate area. Immediately upon contact, a bilobed ampulla containing sperm is passed to the female and the everted phallic lobes then empty and deposit a sticky bilobed spermatophylax lateral to each ampulla lobe (Fig. 5d). The complete structure takes 10–20 s to transfer and weighs from 3 to 7.5% of the male’s body weight. The spermatophore is not eaten by the female.



Jerusalem Crickets (Orthoptera: Stenopelmatidae), Figure 4 Calling song (a) of southern California Jerusalem cricket species where female and male drum differently: female song (*top, middle*) composed of five trills (four drums per trill) in 8.5 seconds at 18°C male song (*lower*) composed of 10 single drums in 16 seconds at 20°C; (b) calling song of central California Jerusalem cricket species consists of grouping of strikes (trills), the drumming rate within a trill approaching 40 times per second at 20°C. This is the fastest drumming Jerusalem cricket; (c) three series of sex clarification drum in a Nevada Jerusalem cricket were followed by a calling song drum, all at 20°C. Sex clarification drum rate around 15 per second; calling drum rate around 4 per second.



Jerusalem Crickets (Orthoptera: Stenopelmatidae), Figure 5 The mating ritual: (a) early mating stage in central California Jerusalem cricket species. Male (*top*) is biting female's right hind tibia while facing in opposite direction; (b) male (*top*) is biting female's right hind tibia while positioning his hind legs and starting to curl his abdomen; (c) male (*top*) curling his abdomen between female's hind legs toward her subgenital plate and setting his hooks. Note his everted phallic lobes (*arrow*); (d) mating finished. Male (*top*) has passed spermatophore composed of whitish bilobed ampulla and clear bilobed spermatophylax. Note tip of ovipositor visible between ampulla lobes; (e) female has consumed male after mating.

In both nature and the laboratory, some 10% of matings end with the male permitting the female to eat him alive. In these first described cases of male-complicit postcoital sexual cannibalism, the male remained motionless while the female consumed him (Fig. 5e). As both males and females can and will mate repeatedly, the function of this behavior is unknown.

Systematics

A. Vandergast has examined the evolutionary patterns of acoustic signaling and karyotype number changes within the context of molecular phylogeny in the North American Jerusalem crickets. These phylogenies are highly concordant with major song characteristics and geographic regions. Specifically,

she found that species producing single drums group in a well supported monophyletic clade. Additionally, single drum species that produce a sex clarification drum (see Fig. 4c) also fall out together. Species with groupings of strikes are restricted to the Pacific coast states of California, Oregon and Washington, usually within 100 km of the coast. Lastly, those seven undescribed species from southern California and Baja California, Mexico, where males and females drum differently, also form a well-supported monophyletic lineage. When karyotype numbers were integrated into the molecular phylogeny, she found evidence for at least five independent fusion events leading to loss of chromosomes, and potentially one fission event ($2N = 19$ to $2N = 21$) throughout this group's evolutionary history.

Endangered Species

Because several Jerusalem cricket species have very limited geographical distributions, especially those endemic to small coastal and inland sand dune systems, coupled with all species being flightless, care will be necessary to protect these vulnerable taxa. The importance of limited Jerusalem cricket vagility is underscored by our genetic study of a widespread southern California Jerusalem cricket species. We showed that less than 100 years, or 50 generations, was sufficient to display patterns of genetic divergence between populations correlated with contemporary urbanization. In other words, urban development and roads disrupt gene flow and quickly cause isolated populations of Jerusalem crickets to genetically diverge from their neighbors.

- ▶ Grasshoppers
- ▶ Katydid and Crickets

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Jewel Beetles

Another name for metallic wood-boring beetles or buprestids (Coleoptera: Buprestidae).

- ▶ Beetles

Jewel Bugs

Another name for shield-backed bugs or scutellerids (Hemiptera: Scutelleridae).

- ▶ Bugs

Jewel Wasp, *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae)

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Nasonia (= *Mormoniella*) *vitripennis* is a gregarious, ectoparasitic wasp that attacks pupae and pharate adults from several families of the higher Diptera, particularly representatives of Calliphoridae and Sarcophagidae. Formerly a monophyletic genus, *Nasonia* is now represented by three