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Biological Notes on Ground-Nesting Digger Wasps from Western Nebraska

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ABSTRACT -- Nine species of sphecid wasps nesting in sparsely vegetated sandy soils near Ogallala, Keith County, Nebraska were studied during June 2003. The first records of the nest and prey of *Cerceris clypeata gnarina* Banks and *Tachysphex williamsi* R. Bohart are presented. Two species of weevils, *Baris striata* Say and *B. subsimilis* Casey, were prey of *C. clypeata gnarina*, with 12 to 22 individuals stocked per cell. Because *B. subsimilis* is a biological control agent for thistle, this finding is a caution to researchers not to ignore the potential impact of predatory wasps on the community. The single nest of *T. williamsi* was a shallow burrow 5 cm deep; prey included grasshopper nymphs of *Melanoplus* sp. and *M. angustipennis* (Dodge). The potential of *Tachysphex* spp. predation for regulating grassland grasshopper populations deserves further study, as a nest of *T. terminatus* F. Smith contained early instar nymphs of six common grassland species, five of which constitute new prey records. A completed nest of *Oxybelus subulatus* Robertson contained a record seven cells each provisioned with four to seven male stiletto flies (*Cyclotelus rufiventris* (Loew), Therevidae). Truncated progressive provisioning with a single species of leafhopper (Cicadellidae) was practiced by *Bembicinus nanus strenuus* (Mickel), which differs from the progressive provisioning recorded for the one population previously studied. Observations of nests and prey of *Bembix sayi* Cresson, *Cerceris fumipennis* Ashmead, *Philanthus psyche* Dunning, and *Plenoculus davisi davisi* (Fox) were consistent with previous studies at other localities. Putative parasites of these nine wasp species included velvet ants (*Pseudomethoca propinqua* (Cresson), *Dasymutilla vesta* (Cresson), and *D. nigripes sparsa* Fox), cuckoo wasps (*Hedychridium fletcheri* Bodenstein and *Hedychrum violaceum* Brulle), and unidentified miltogrammine flies.

Key words: *Bembicinus*, *Bembix*, biological control, *Cerceris*, grassland grasshoppers, nest architecture, nesting behavior, *Oxybelus*, parasites, *Philanthus*, *Plenoculus*, prey records, sex-biased predation, *Sphecidae*, *Tachysphex*.

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Ground nesting digger wasps (Hymenoptera: Sphecidae) represent a conspicuous and major component of sandy soil communities everywhere (O'Neill 2001). As predators, they impact diverse members of the community of arthropods in the habitats they share. Very few data exist for digger wasps nesting in Nebraska. Because they are predators on various insects and spiders and the prevalence of intraspecific behavioral variation, data from different sphecid populations are desirable for comparative purposes.

Here we present information on the nesting behavior, prey, and parasites of nine sphecid species. For comparative information summarizing the nest architecture, biology, and behavior of the genera reported here consult the works of Evans (1966) and O'Neill (2001).

Our studies were conducted during June 2003 in Keith County, western Nebraska, about 22 km north of Ogallala along the shores of Lake McConaughy near West Arthur Bay, and along the Sutherland Canal 3 km south of Keystone (the first three species discussed). Voucher materials for all wasps, prey, and parasites were deposited in the Entomology Museum, University of Georgia, except that the bee prey were all deposited in the Snow Museum, University of Kansas, and the chrysidids are in the Bohart Museum, University of California, Davis. A subset of voucher specimens of most species was deposited in the collection of the University of Nebraska's Cedar Point Biological Station.

Cerceris clypeata gnarina Banks -- This subspecies was identified by using keys in Scullen (1965). It occurs widely in the central Great Plains, but this is the first record of its nest and prey. We found a small aggregation nesting in coarse gravely sand along the side of a farm lane that ran beside the north side of Sutherland Canal. Several nests appeared to be active on 22 June and two were excavated. Females actively provisioned during the late morning and early afternoon and left the 6 mm diameter burrow open between trips for prey. Nest entrances were surrounded by a conspicuous soil tumulus about 6 cm in diameter, as is characteristic for members of the genus *Cerceris*.

The first nest ending blindly at a depth of 22 cm, descended almost vertically. Four cells were discovered, separated from the burrow by 2 to 4 cm. Each cell contained 12 to 22 small black weevils (*Baris striata* Say and *B. subsimilis* Casey); a single beetle was found at the end of the nest tunnel. The prey appeared to be paralyzed completely or dead, as no movement could be elicited when touched with forceps. In one cell an egg was attached loosely along the lateral margin of one weevil's elytron and pronotum: it was about as long as the weevil. Another cell contained a half-grown larva; this cell, the shallowest of the four at a depth of 16 cm, appeared to be the oldest. A large mite also was observed crawling among the prey, but was lost. Because *B. subsimilis* is reported as a biological control agent for Canada thistle [*Cirsium arvense* (L.) Scop.] and bull thistle [*C. vulgare* (Savi) Tenn.] (Louda and Rand 2003) the predatory activity of a population of these wasps could impact thistle populations. Researchers interested in noxious weed

control should be alert to the fact that predatory wasps seldom are considered in the context of the total ecological community. The impact of predatory wasps on prey populations is reviewed by O'Neill (2001).

The second nest was 55 cm from the first and was closed from within the nest. The live female was found inside. The nest was also 22 cm deep and contained one completed cell with an egg and 14 weevils. A second cell at the burrow terminus contained six prey and was incomplete.

A chrysidid wasp (*Hedychrum violaceum* Brulle) and a mutillid wasp [*Pseudomethoca propinqua* (Cresson)] collected while they were searching in the nest area, were possible parasites. Other species of chrysidids and mutillids have been recorded previously as parasites of various species of *Cerceris* (O'Neill 2001).

Cerceris fumipennis Ashmead -- This widely occurring species nested in a small loose aggregation (ca. 25 nests noted) at the same locality as *C. clypeata gnarina*, but in compact sandy soil in a track about 80 m away. Externally the nests essentially were identical in appearance to those of *C. clypeata gnarina*. However, excavation of several nests between 22 and 26 June failed to find any evidence of active provisioning. Females spent much of the day resting inside their closed nests. Presumably it was early in the nesting season; supporting evidence for this came from dissecting a female, which showed no visible ovarian development.

Nest burrows descended nearly vertically for 8 to 12 cm and ended blindly. At the same depth, several old cells from previous nests were encountered. These contained numerous old elytra, head capsules, and other exoskeletal remains representing apparently two species of unidentified buprestids. According to Scullen (1965) and Scullen and Wold (1969), various species of buprestid beetles are the exclusive prey for *C. fumipennis* everywhere it has been studied. Evans (1971) provided extensive nesting details for this wasp from several localities.

Bembix sayi Cresson -- This species occasionally was encountered at the same site as the *Cerceris*, and a single freshly dug nest was found in a flat open area on the track near nests of *C. fumipennis*. Males periodically flew along the track but were extremely swift and difficult to net. The simple nest burrow was 15 cm long, sloped at about a 45° angle to the surface, and ended in a slightly enlarged cell 11 cm deep. The nest apparently was complete, but neither an inner closure nor a spur (for nest terminology see Evans (1966)) was present. The female was found resting inside, but had not yet begun provisioning. The elongate mound of sand in front of the burrow measured 15 by 10 cm and showed no evidence of being leveled. Despite extensive searching along the track, this was the only nest found.

Our limited observations agree with those of Evans (1957) in Florida and Kansas. He noted that *B. sayi* is not a gregarious nester. Nest architecture of the Nebraska nest was similar in all aspects to nests recorded by Evans and another nest from Arizona (Alcock and Gamboa 1975).

Bembicinus nanus strenuus (Mickel) -- Only a single report on the reproductive and nesting biology of this wasp exists (Evans and O'Neill 1986), based on a population in Colorado. As was true at their study site, nests of *B. nanus strenuus* were intermingled with those of *Philanthus psyche* (see below) in sandy soil sparsely vegetated with grasses and other plants, including peppergrass (*Lepidium virginicum* L.).

The first adults (both sexes) of *B. nanus strenuous* emerged on June 21, following a heavy rain the previous evening; none had been present during the previous week. Thereafter (through June 27 when observations ended), several dozen males were observed throughout most of the day (0900 to 1800 hrs) repeatedly flying irregular patterns a few centimeters above the ground along a 30 m stretch of sand. Males regularly were seen to pounce on small objects, and a few attempted matings were observed. These were brief encounters lasting 2 to 4 sec, and often were interrupted by other males pouncing on the pair. There was no evidence that males defended territories, though our impression was that individuals tended to fly fairly predictable routes. In general our observations were consistent with those of Evans and O'Neill (1986), who regarded this as a form of scramble competition.

Females nested in the same areas over which the males flew, and the first nests were completed on the first day following emergence. Nests were simple, straight, oblique burrows ending in a single cell at a depth of 6 to 7 cm. Cells measured about 9 by 10 mm. The egg (2.5 by 0.8 mm) was laid upright in the empty cell. Provisioning began the following day, being completed usually within a day, after which the nest was given a final closure.

Two nests for which detailed observations were made were dug on June 22, being completed at about 1415 hrs. The female of the first nest was observed doing a final closure on June 24 at 1215 hrs. The cell contained a single unidentified species of Cicadellidae, with two adults and 18 late instar nymphs. All prey were paralyzed profoundly and unresponsive to touch. A small larva also was present. The second nest was about 25 cm from the first and was initiated and closed at about the same times as the first. It contained 15 prey (3 adults, 12 nymphs, again all the same species as before) and a newly hatched larva. This observation differed from that of Evans and O'Neill (1986), who stated that in their population, prey were brought in progressively over several days. Evidently progressive provisioning is the rule in nearly all known *Bembicinus* (Evans, 1966, O'Neill 2001), so the apparently truncated progressive provisioning we observed merits further study (similar behavior apparently occurs in *B. neglectus* (Cresson) (Evans 1966)). It might relate to prey availability or specificity; in contrast to our small sample, Evans and O'Neill (1986) recorded a variety of Homoptera (3 families, 12 species) used as prey in their population. Evans (1966) notes that while individual nests of some species are found to contain only a single species of prey, most Bembicinus appear to attack a variety of related species.

Initial mound leveling and final closure behaviors surprisingly were elaborate in *B. nanus strenuous*. Videotapes showed that both continued over almost two hours. In initial leveling, the female periodically exits, backs over the mound, then moves forward in a zig-zag pattern, dispersing the accumulated sand. Twice, a flying male pounced on one female, and brief copulations were observed. During final closure, females moved up to 6 cm forward from the entrance, continuously scraping sand backwards toward the entrance as they walked. This behavior was repeated numerous times, each time at a slightly different angle. The result was a faintly visible series of radiating lines in front of the entrance and a slightly mounded entrance.

Philanthus psyche Dunning -- Evans and O'Neill (1988) summarized the behavior of species in this genus, commonly called beewolves. Identified by using the key presented by Ferguson (1983), *P. psyche*, one of the smaller species of *Philanthus*, is distributed widely in the western Great Plains and Great Basin, from Alberta and the Dakotas to Utah and western Texas. O'Neill (1979) studied a population of *P. psyche* in eastern Colorado, where it was active from late May to September, with more than one generation noted, and Evans and O'Neill (1988) reported on populations in New Mexico and Texas.

We observed several females and males between June 14 to 26. Nests were leveled completely such that the entrance was invisible to a human observer. Burrows were declinate, sloping at a shallow angle 25 to 35° from the surface. Prey were stored at the end of the burrow, preparatory to later removal into a cell. We excavated the nests in late afternoon but found no completed cells; instead all prey found were stored at the end of the initial oblique burrow, about 10 cm deep. According to Evans and O'Neill (1988), cells are constructed late in the day several cm vertically below the end of the oblique burrow. We observed no accessory burrow construction, and these apparently are rare in other populations studied (Evans and O'Neill 1988).

Thirteen prey, representing three species of halictids (1 female *Lasioglossum (Dialictus)* of species 1, one female and one male *Lasioglossum (Dialictus)* of species 2, three females and two males *Lasioglossum (Dialictus)* of species 3), two species of andrenid bees (one male *Perdita bishoppi* Cockerell and three males *Perdita* sp.), and a braconid, *Chelonus* sp., were recovered from the nests. These data confirmed previous findings that the predatory behavior of *P. psyche* is relatively plastic; from four localities, Evans and O'Neill (1988) reported 210 prey records that represented 54 species belonging to six families of wasps and five families of bees.

Male territoriality and marking behaviors -- casually observed on many days in small relatively bare areas of sand -- appeared essentially the same as were reported by O'Neill (1979) in a much more detailed study and summarized in Evans and O'Neill (1988). Certain patches of sand were clearly more attractive than others.

On several occasions we observed both velvet ants (Mutillidae) and cuckoo wasps (Chrysididae) parasites on the leveled mounds. Between 1650 and 1700 hrs on 18 June, two species of *Dasymutilla* were videotaped at a freshly leveled nest. First *D. vesta* (Cresson), and later *D. nigripes sparsa* Fox, discovered the same nest. *Dasymutilla vesta* rather quickly found the concealed burrow entrance and entered, staying inside for 4 min. A short while later, the female *P. psyche* returned and entered her nest; she exited after less than a minute inside and reclosed the entrance. The other mutillid, *D. nigripes sparsa*, then arrived and extensively probed the fresh sand of the nest mound, but never located the nest entrance before wandering off after about 5 min. These mutillids commonly were seen crawling actively throughout the nest site, and 38 females of *D. vesta* were collected at various times during the study. Since mutillids typically parasitize the prepupal stage of their hosts, we probably were seeing newly emerged individuals, early in the season. Other species of mutillids are known to live very long lives (Schmidt 1978).

The chrysidids collected at nests all proved to be males of *Hedychridium fletcheri* Bodenstein. L. S. Kimsey University of California, Davis (personal communication), suggested that they might have been attracted to freshly leveled mounds in order to encounter females for mating. Evans (1970) reported that females of *H. fletcheri* at Jackson Hole, Wyoming, were often seen flying from one wasp nest to another, apparently attracted by the fresh earth at the entrances. Kurczewski (1967) presented some life history information on this species as a parasite of *Tachysphex similis* Rohwer. No prior records of mutillid or chrysidid parasitism of *P. psyche* exist, but other *Philanthus* species are attacked by members of both families.

Tachysphex terminatus (F. Smith) — Pulawski (1988) summarized previous studies of the biology of *T. terminatus*, a widely distributed species east of the Rockies and south to El Salvador. Females nest in flat to slightly sloping sandy areas with sparse vegetation. Nest burrows ending usually no deeper than 4 to 6 cm below the soil surface, were oblique and up to 11 cm long. Up to five cells were constructed, but usually two or three. Prey consisted of first and second instar acridid grasshopper nymphs belonging to at least 13 species, with three to nine individuals stored per cell. Spofford et al. (1986) recorded three species of miltogrammine fly parasites of *T. terminatus*.

At 1245 hrs on 24 June, a female *T. terminatus* was observed doing a final closure. The excavated nest consisted of an oblique burrow, 6 cm long, which ended in a single cell 4 cm deep. The cell contained six acridid grasshopper nymphs, all first or second instar. The prey were paralyzed, but able to move legs and mouthparts and defecate upon being prodded with an insect pin. The wasp's egg was glued semi-erect at the base of one of the grasshopper's prothoracic legs and measured 1.5 by 0.5 mm.

Prey were identified as two Gomphocerinae, *Ageneotettix deorum* (Scudder) and *Boopedon nubilum* (Say), two Melanoplinae, *Melanoplus femurrubrum* (De Geer) (two individuals) and *Melanoplus* sp., and *Sparagemon collare* (Scudder) (Oedipodinae). Common grassland species of western Nebraska (Joern 1982), all are characterized by early hatching (Schell et al. 2004). Except for *M. femurrubrum*, all are new prey records for *T. terminatus*.

Tachysphex williamsi R. Bohart -- This red-gastered species ranges from the eastern slopes of the Rocky Mountains westward. Except for a single prey record (Elliott and Kurczewski 1985), its biology previously was unknown. A single nest was discovered on 15 June when the female returned with prey at 1405 hrs. She was pursued by two tiny unidentified miltogrammine flies and was attempting to elude them. Her evasive tactics consisted of rapid zig-zag flights to a point about 1 m from the nest, followed by straight-line flight back to her open nest. She left the prey at the entrance, entered briefly, and returned after 5 sec and dragged the grasshopper into the nest. Both flies came to the prey while it rested at the entrance and appeared to oviposit. However, no eggs or larvae were found on any prey when later checked under a microscope. Both flies remained at the nest vicinity and were captured as vouchers.

Upon excavation, the nest cell at the terminus of a nearly vertical 5 cm long burrow was found to contain three paralyzed acridid grasshopper nymphs - two second instar individuals of the narrow-winged sand grasshopper (*Melanoplus angustipennis* Dodge) and a different nymph whose identity could not be determined. No egg was present. The paralyzed prey were slightly responsive, moving legs and/or mouthparts when either their cerci or maxillary palps were touched with an insect pin. A small tumulus of soil surrounded the nest entrance.

The potential of *Tachysphex* spp. predation for regulating grassland grasshopper populations deserves further study. Several species of these wasps specialize on early instar grasshoppers. Newton (1956) recorded *T. pompiliformis* (Panzer) preying on *Oedaleonotus enigma* (Scudder), another melanopline grassland grasshopper, in Idaho. Newton credited the predatory activities of populations of at least three species of *Tachysphex* in Idaho for reducing populations of this grassland pest from 20 to 30 nymphs per square meter in early June to one in every five square meters by late June. When grasshopper populations are high the wasps might paralyze and abandon prey on the soil surface in excess of what they can use to provision their simple burrows (Newton 1956). O'Neill (1995) reported on the potential of digger wasps for regulating grasshopper populations in Montana grasslands.

Oxybelus subulatus Robertson -- A single nest of this species was found on June 24, when a female, carrying prey on her stinger, was observed at 1345 hrs returning to her open nest. She plunged into the nest and then closed the nest from within the nest. At 1530 hrs she was observed in the process of doing a final closure, quarrying sand from the lip of the nest entrance, and using it to fill the nest burrow.

Upon excavating the nest later that day, seven provisioned cells were found. Each was provisioned with four to nine stiletto flies (*Cyclotelus rufiventris* (Loew), Therevidae). All prey were paralyzed profoundly and all were males. Prey were placed head first in the cells and the wasp egg was attached obliquely to the fore coxae of the fly deepest in the pile of prey. The egg measured 2.0 by 0.5 mm. Newly hatched larvae began feeding at the neck cavity, with the flies' heads being consumed first.

Cells were clustered to one side of the burrow; all were within 2 cm of the burrow and separated by 1 to 2 cm from each other. Cells measured 8 by 10 mm. The relative ages of the larvae in the different cells suggested that the deepest cell (8 cm) was the oldest cell. The cell with the youngest larva was at a depth of 5.5 cm. This suggested that progressively newer cells were built nearer to the main burrow (which descended nearly vertically) and at progressively shallower depths. Sand excavated from a new cell probably was used to fill the short burrow (1 to 2 cm) to the previous cell.

Peckham et al. (1973) observed 36 nests of this species in central New York from mid-June until late July. Nest architecture was similar, with depths ranging from 3.1 to 6.7 cm. Peckham et al. (1973) reported two to six cells per nest, so our finding of seven cells in a single nest is unusual. They recorded over 400 prey, all Therevidae (three species), and all males. Interestingly, our prey is the same as one of the three therevid prey species that Peckham et al. (1973) recorded from New York. There were 3 to 11 prey per cell and they provided a photograph of the egg positioned across the fore coxae. Peckham et al. (1973) also reported that males guarded the nest entrances and normally were present throughout nest construction and provisioning. No male activity was noted at our single nest.

Plenoculus davisi davisi (Fox) -- A single nest of this small species was discovered in a flat bare area on the sand on June 18 when the female was observed to enter an open burrow and closed the nest from within the nest at about 1530 hrs. We excavated the nest at 0900 hrs on June 21, and found the female resting in the 2 mm diameter burrow. She was identified by using the key in Williams (1960). The short burrow descended nearly vertically and ended in a single cell 4 cm deep. The cell was 5 mm diameter and contained six small plant bugs (Miridae), four adults and two late instar nymphs. The cell apparently was incomplete, as neither egg nor larva was present, and no additional cells were located.

The widely distributed *P. davisi davisi* previously has been studied by Evans (1961, 1970), Kurczewski (1968), and Williams (1914) in diverse localities from New York to Kansas and Wyoming. Kurczewski (1968) provided extensive details on all aspects of nesting, based on more than 100 nests dug at six localities. Nest architecture and cell depth (3 to 10 cm) were quite consistent. A variety of mirid adults and nymphs were reported as prey in all previous studies (summarized in Kurczewski, 1968).

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LITERATURE CITED

Alcock, J., and G. Gamboa. 1975. The nesting behavior of some sphecid wasps of Arizona, including *Bembix*, *Microbembix*, and *Philanthus*. Arizona Academy of Sciences 10:160-165.

Elliott, N. E., and F. E. Kurczewski. 1985. Nesting and predatory behavior of some Tachysphex from the western United States (Hymenoptera: Sphecideae). Great Basin Naturalist 45:293-298.

Evans, H. E. 1957. Studies on the comparative ethology of digger wasps of the genus Bembix. Comstock Publishing Associates, Ithaca, New York.

Evans, H. E. 1961. Notes on the nesting behavior of *Plenoculus davisi* Fox (Hymenoptera: Sphecidae). Entomological News 72:225-228.

Evans, H. E. 1966. The comparative ethology and evolution of the sand wasps. Harvard University Press, Cambridge, Massachusetts.

Evans, H. E. 1970. Ecological-behavioral studies on the wasps of Jackson Hole, Wyoming. Bulletin of the Museum of Comparative Zoology 140:451-511.

Evans, H. E. 1971. Observations on the nesting behavior of wasps of the tribe Cercerini. Journal of the Kansas Entomological Society 44:500-523.

Evans, H. E., and K. M. O'Neill. 1986. Reproductive and nesting biology of *Bembecinus nanus strenuous* (Mickel) (Hymenoptera: Sphecidae). Proceedings of the Entomological Society of Washington 88:628-633.

Evans, H. E., and K. M. O'Neill. 1988. The natural history and behavior of North American beewolves. Cornell University Press, Ithaca, New York.

Ferguson, G. R. 1983. Two new species in the genus *Philanthus* and a key to the politus group (Hymenoptera: Philanthidae). Pan-Pacific Entomologist 59:55-63.

Joern, A. 1982. Distributions, densities, and relative abundances of grasshoppers (Orthoptera: Acrididae) in a Nebraska sandhills prairie. Prairie Naturalist 14:37-45.

Kurczewski, F. E. 1967. *Hedychrum fletcheri* (Hymenoptera: Chrysididae: Elampinae), a probable parasite of *Tachysphex similis* (Hymenoptera: Sphecidae: Larrinae). Journal of the Kansas Entomological Society 40:278-284.

Kurczewski, F. E. 1968. Nesting behavior of *Plenoculus davisi* (Hymenoptera: Sphecidae: Larrinae). Journal of the Kansas Entomological Society 41:179-207.

Louda, S. M., and T. A. Rand. 2003. Native thistles: expendable or integral to ecosystem resistance to invasion? Pp. 5-15 *in* The importance of species: Perspectives on expendability and triage. (P. Kareiva and S. A. Levin, editors). Princeton University Press, Princeton, New Jersey.

Newton, R. C. 1956. Digger wasps, *Tachysphex* spp., as predators of a range grasshopper in Idaho. Journal of Economic Entomology 49:615-619.

O'Neill, K. M. 1979. Territorial behavior in males of *Philanthus psyche* (Hymenoptera: Sphecidae). Psyche 86:19-43.

O'Neill, K. M. 1995. Digger wasps and robber flies as predators of grasshoppers on Montana rangeland. Pan-Pacific Entomologist 71:248-250.

O'Neill, K. M. 2001. Solitary wasps. Behavior and natural history. Cornell University Press, Ithaca, New York.

Peckham, D. J., F. E. Kurczewski, and D. B. Peckham. 1973. Nesting behavior of Nearctic species of *Oxybelus* (Hymenoptera: Sphecidae). Annals of the Entomological Society of America 66:647-661.

Pulawski, W. J. 1988. Revision of North American *Tachysphex* wasps including Central American and Caribbean species (Hymenoptera: Sphecidae). Memoirs of the California Academy of Sciences 10:1-211.

Schell, Sp., J. Lockwood, Sc. Schell, and K. Zimmerman. 2004. Grasshoppers of Wyoming and the west. http://www.sdvc.uwyo.edu/grasshopper/ghwywfrm.htm, accessed 8 April 2004.

Schmidt, J. 0. 1978. *Dasymutilla occidentalis*, a long-lived aposematic wasp (Hymenoptera: Mutillidae). Entomological News 89:135-136.

Scullen, H. A. 1965. Review of the genus *Cerceris* in America north of Mexico (Hymenoptera: Sphecidae). Proceedings of the United States National Museum 116:333-548.

Scullen, H. A., and J. L. Wold. 1969. Biology of wasps of the tribe Cercerini, with a list of the Coleoptera used as prey. Annals of the Entomological Society of America 62:209-214.

Spofford, M. G., F. E. Kurczewski , and D. J. Peckham. 1986. Cleptoparasitism of *Tachysphex terminatus* (Hymenoptera: Sphecidae) by three species of *Miltogrammini* (Diptera: Sarcophagidae). Annals of the Entomological Society of America 79: 350-358.

Williams, F. X. 1914. The Larridae of Kansas. The Kansas University Science Bulletin 18:121-213.

Williams, F. X. 1960. The wasps of the genus *Plenoculus* (Hymenoptera: Sphecidae, Larrinae). Proceedings of the California Academy of Sciences 31:1-49.

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