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Mesquite bugs and other insects in the diet of pallid bats in southeastern Arizona

Nicholas J Czaplewski Corresp., [1] , **Katrina L Menard** [2] , **William D Peachey** [3]

[1] Section of Vertebrate Paleontology, Oklahoma Museum of Natural History, Norman, Oklahoma, United States of America
[2] Section of Recent Invertebrates, Oklahoma Museum of Natural History, Norman, Oklahoma, United States
[3] Sonoran Science Solutions, Tucson, Arizona, United States

Corresponding Author: Nicholas J Czaplewski
Email address: nczaplewski@ou.edu

The pallid bat (*Antrozous pallidus*) is a species of arid and semiarid western North America, inhabiting ecoregions ranging from desert to oak and pine forest. Considered primarily insectivorous predators on large arthropods but taking occasional small vertebrate prey, pallid bats were recently shown to be at least seasonally omnivorous; they demonstrate unusual dietary flexibility and opportunism in certain parts of their geographic range and at different times of year. In a few areas they take nectar from cactus flowers and eat cactus fruit pulp and seeds. Until recently mesquite bugs were primarily tropical-subtropical inhabitants of Mexico and Central America but have since occupied the southwestern United States where mesquite trees occur. Pallid bats regularly use night roosts as temporary shelters in which to process and consume large arthropods caught near their foraging areas. Using a noninvasive method, we investigated the bats' diet by collecting food parts discarded by the bats beneath three night roosts in soil-piping cavities at the Cienega Creek Natural Preserve, Arizona. We also made phenological and behavioral observations of the mesquite bugs, *Thasus neocalifornicus*, and their interactions with the mesquite trees. The bats discarded inedible parts of at least 36 species in 8 orders of mainly large-bodied and nocturnal insects below the night-roosts. In addition, one partial bat wing represents predation upon a phyllostomid bat, *Choeronycteris mexicana*. About 17 of the insect taxa are newly reported as prey for pallid bats, as is the bat *C. mexicana*. The large majority of culled insect parts (88.8%) were from adult mesquite bugs. As nymphs, mesquite bugs are aposematically colored and secrete noxious pheromones; nymphs did not appear in the bat-culled insect parts. Adult mesquite bugs are darkly colored and secrete different noxious pheromones than the nymphs. During daytime hours in the summer adult bugs are abundant, flying around the canopy and alighting on the edges of the trees. In late summer and early fall they breed and lay eggs that overwinter on the mesquite branches to hatch in January. Soon after breeding,

the adult bugs die. When summer heat diminishes and nighttime low temperatures drop below 21°C, the adult bugs become immobile on the periphery of the trees where they probably make easy prey for foliage-gleaning pallid bats. The historically subtropical-tropical mesquite bugs may have moved into the southwestern United States with the spread of cattle and mesquites. In this area of Arizona, pallid bats provide an important natural control on the local mesquite bug population. The high diversity of other insect remains and the remains of another species of bat provide additional supportive evidence of a diet for pallid bats that reflects their plasticity across a variety of habitats. This behavioral plasticity probably enhances the bats' survival across their range in the face of climate change.

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MESQUITE BUGS AND OTHER INSECTS IN THE DIET OF PALLID BATS IN SOUTHEASTERN ARIZONA

Nicholas J. Czaplewski,[1] Katrina L. Menard,[1] and William D. Peachey[2]

[1]Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma, United States of America
[2]Sonoran Science Solutions, Tucson, Arizona, United States of America

Corresponding author Nicholas J. Czaplewski, nczaplewski@ou.edu

ABSTRACT

The pallid bat (*Antrozous pallidus*) is a species of arid and semiarid western North America, inhabiting ecoregions ranging from desert to oak and pine forest. Considered primarily insectivorous predators on large arthropods but taking occasional small vertebrate prey, pallid bats were recently shown to be at least seasonally omnivorous; they demonstrate unusual dietary flexibility and opportunism in certain parts of their geographic range and at different times of year. In a few areas they take nectar from cactus flowers and eat cactus fruit pulp and seeds. Until recently mesquite bugs were primarily tropical-subtropical inhabitants of Mexico and Central America but have since occupied the southwestern United States where mesquite trees occur. Pallid bats regularly use night roosts as temporary shelters in which to process and consume large arthropods caught near their foraging areas. Using a noninvasive method, we investigated the bats' diet by collecting food parts discarded by the bats beneath three night roosts in soil-piping cavities at the Cienega Creek Natural Preserve, Arizona. We also made phenological and behavioral observations of the mesquite bugs, *Thasus neocalifornicus*, and their interactions with the mesquite trees. The bats discarded inedible parts of at least 36 species in 8 orders of mainly large-bodied and nocturnal insects below the night-roosts. In addition, one partial bat wing represents predation upon a phyllostomid bat, *Choeronycteris mexicana*. About 17 of the insect taxa are newly reported as prey for pallid bats, as is the bat *C. mexicana*. The large majority of culled insect parts (88.8%) were from adult mesquite bugs. As nymphs, mesquite bugs are aposematically colored and secrete noxious pheromones; nymphs did not appear in the bat-culled insect parts. Adult mesquite bugs are darkly colored and secrete different noxious pheromones than the nymphs. During daytime hours in the summer adult bugs are abundant, flying around the canopy and alighting on the edges of the trees. In late summer and early fall they breed and lay eggs that overwinter on the mesquite branches to hatch in January. Soon after breeding, the adult bugs die. When summer heat diminishes and nighttime low temperatures drop below 21°C, the adult bugs become immobile on the periphery of the trees where they probably make easy prey for foliage-gleaning pallid bats. The historically subtropical-tropical mesquite bugs may have moved into the southwestern United States with the spread of cattle and mesquites. In this area of Arizona, pallid bats provide an important natural control on the local mesquite bug population. The high diversity of other insect remains and the remains of another species of bat provide additional supportive evidence of a diet for pallid bats

that reflects their plasticity across a variety of habitats. This behavioral plasticity probably enhances the bats' survival across their range in the face of climate change.

INTRODUCTION

The pallid bat, *Antrozous pallidus*, is widespread in western North America, inhabiting a range of mostly arid to semiarid, rocky habitats at low to medium elevation (mostly <1800 m) to low, open deserts to oak and pine forest. Studies of their dietary habits have shown that this species is generally a predator on relatively large-bodied arthropods, especially insects, but also taking arachnids, centipedes, and millipedes (arthropodophagous, terminology following Segura-Trujillo, 2017). However, pallid bats are opportunistic and flexible, occasionally taking fruit from organ pipe cactus (*Stenocereus thurberi*) and cardón (*Pachycereus pringlei*) in the Southwest, and at least incidentally, they also take pollen and nectar from flowering columnar cacti (Howell, 1980; Herrera et al., 1993; Simmons & Wetterer, 2002; Frick et al., 2013; Aliperti et al., 2017) and probably agaves (Ammerman et al., 2012). Most often, pallid bats prey upon relatively large, flightless arthropods; occasionally they also eat small vertebrates (Engler, 1943; Orr, 1954; O'Shea & Vaughan, 1977; Bell, 1982; Lenhart et al., 2010; Rambaldini & Brigham, 2011). Some of these prey items are taken during a brief touchdown or are gleaned from foliage during flight. Pallid bats use a characteristic searching flight that usually involves relatively slow and maneuverable flying about 0.5-2.5 m above the ground while making rhythmic rises and dips interspersed with swoops and glides when the bat detects prey (O'Shea & Vaughan, 1977). Occasionally the bats hover near low or thorny vegetation, or land on the ground where they are quite agile at using a variety of gaits and strides to pursue prey. This foraging style carries high risks of injury and predation for the bats, whose wing membranes and bones heal but show scars and deformities (Davis, 1968). While preying upon scorpions and centipedes they also endure venomous stings to the face and other body parts (Hopp et al., 2017). Pallid bats take arthropod species that share at least two of four characteristics: (1) large size; (2) either obligatorily or primarily active on the ground surface; (3) fly weakly at low heights; or (4) fly strongly but often land on vegetation (O'Shea & Vaughan, 1977). The bats frequently retreat to a night roost to rest or manipulate and eat the prey they have caught. They alight on the ceilings of rock shelters, overhangs, or small grottos temporarily to process their prey. The bats drop undesired parts of the insects and other arthropods such as wings, elytra, and legs. The discarded items provide qualitative data on pallid bat diets (e.g., Orr, 1954; Ross, 1961, 1967; O'Shea & Vaughan, 1977; Bell, 1982; Lenhart et al., 2010), although Johnston & Fenton (2001) found that the insects represented in the culled parts were biased toward the hardest and largest prey species eaten relative to species represented in fecal pellets.

As foliage- and surface-gleaning bats that hunt arthropods moving or resting on plant or ground surfaces, pallid bats have well-developed acoustical, olfactory, and visual senses. Pallid bats mainly locate their prey by sound, either through active echolocation or passive detection of the faint sounds made by moving arthropod prey (O'Shea & Vaughan, 1977). In experiments with insects and their pheromones other than those of mesquite bugs (*Thasus* spp.), pallid bats are also quite sensitive to olfactory cues and were able to distinguish prey odors from controls and from non-prey species. The bats showed selectivity upon closely approaching certain prey insects versus a non-prey noxious insect (the Pinacate beetle or desert stink beetle *Eleodes*: Tenebrionidae) or paper balls impregnated with their odors (Johnston, 2002). The bats also have relatively large eyes and high visual acuity at low light levels (Bell & Fenton, 1986).

Leaf-footed bugs (Heteroptera: Coreidae) are a relatively small subtropical-tropical family of about 80 species in the continental United States and Canada (Froeschner, 1988). One member genus, *Thasus* (Coreidae: Coreinae: Nematopini), has eight species primarily distributed in the Neotropics (Forbes & Schaefer, 2003). Like many other Hemiptera, Coreidae are herbivores that suck the contents of plant tissues, not the sap of the plants' vascular systems. Many coreids are also host specific, feeding on one or two families of plants (Froeschner, 1988). The only species of *Thasus* in the United States is *Thasus neocalifornicus* (giant mesquite bug); the species also occurs in Baja California and Sonora and Chihuahua, Mexico (Forbes & Schaefer, 2003). The closely related species *Thasus gigas* and *Thasus acutangulus* occur further south in Mexico and Central America; these two species were once considered synonymous with *T. neocalifornicus* but have since been shown to be distinct (Brailovsky & Barrera in Brailovsky et al., 1995; Forbes & Schaefer, 2003). Schaefer & Packauskas (1998) speculated that the United States populations of *T. neocalifornicus* in Arizona might have been an accidental introduction by humans. It has been recorded in Arizona since at least 1876 (Forbes & Schaefer, 2003) and is now also known north of Mexico from California to Texas (https://bugguide.net/node/view/20163).

Thasus neocalifornicus is ecologically tied to mesquites (*Prosopis*, Fabaceae; De La Torre-Bueno, 1945; Ward et al., 1977; Schuh & Slater, 1995; Brummermann, 2010). Mesquite trees have spread widely in the United States during the last two centuries along with cattle (Turner et al., 2003); their bean pods also form an important food for cattle and a variety of other vertebrates including coyotes (*Canis latrans*), javelinas (*Pecari tajacu*), and humans (pers. observ.). As a brief synopsis of the annual phenological cycle of *T. neocalifornicus* relative to their host plant, mesquite bugs are univoltine (having one generation per year and overwintering as eggs; Jones, 1993). The adults first start to appear from the fifth nymphal instars around July-August, with the highest proportion of adults between May-September. Females start ovipositing around August and continue through October, when the mesquite trees start dropping their leaves (October-January). Eggs eclose in February, and nymphs aggregate around the eggs to use up the rest of the egg reserves and feed. Nymphs aggregate using specialized pheromones (adults do not respond to the pheromones in tests), and secrete malodorous, toxic pheromones in self-defense and possibly as alarm chemicals to alert conspecifics against predator attacks. The nymphal toxins are effective on insect predators in tests; tests do not seem to have been made on vertebrate predators (Prudic et al., 2008). Nymphs feed on mesquite leaves and pods (once available), and molt through their first-fifth instars from January-July; they often migrate to the base of their host trees in summer, probably in response to high afternoon temperatures (Jones, 1993). Mesquites flower from February-March, and bear fruits (bean pods) from July-October. As nymphs, mesquite bugs are unable to fly and are aposematically colored red, white, and brownish or blackish to advertise their noxious secretions. This coloration is almost universally a warning to vertebrate predators, advertising that these insects taste bad or are even toxic. The coloration probably deters visually oriented diurnal predators such as birds and larger invertebrate predators. Although the warning coloration might be visible to bats during twilight hours, night-active predators like bats might be repelled by the nymphs' noxious pheromones or other defenses. The nymphs often stay under the foliage on the spiny branches of the mesquite canopy; they also form defensive aggregations that secrete noxious fluid from their abdomens, similarly to a related species, *Thasus acutangulus* in the Central American tropics (Aldrich & Blum, 1978). By contrast, the adult mesquite bugs are large and dark colored (blackish brown and dark reddish) and no longer secrete the chemicals that are toxic to small insect predators. Instead, the adults secrete a different set of noxious chemicals from those of the nymphs to trigger aggregations and in response to a simulated predator disturbance. These chemicals include hexyl acetate, hexenal, and hexanol (Prudic et al., 2008; Noge, 2015). Adult pheromones are not toxic or deterrent to insect predators but might deter vertebrates such as birds, a major group of predators on adult heteropteran insects (Prudic et al., 2008). Adult mesquite bugs feed in the tissues of stems, branches, and pods of mesquite trees until late summer, then breed and lay eggs on mesquite stems and under bark in late summer-early fall. Mesquite bugs overwinter only in the egg stage, emerging from the eggs in February (Jones, 1993). Mesquite bugs (*Thasus neocalifornicus*) adults fit the characteristics of pallid bat prey noted above (following O'Shea & Vaughan, 1977) in being of large size, flying weakly, and often landing on vegetation.

During 1994-1996, in the process of studying bats roosting in soil-piping cavities in southern Arizona (Van de Water & Peachey, 1997), we observed reddish guano and culled wings of mesquite bugs beneath a pallid bat night roost. Collecting these discarded fragments eventually grew into the present contribution to knowledge of the behavior of mesquite bugs and the diet of pallid bats. With this paper we add to the long list of arthropod prey (and a smaller bat as prey) taken by pallid bats. Importantly, we document some initial observations relevant to an impressive example of these bats feeding opportunistically on large numbers of mesquite bugs in southeastern Arizona.

MATERIALS AND METHODS

In the process of observing and studying Mexican long-nosed bats at the Cienega Creek Natural Preserve under Arizona Game and Fish Commission permit I-96-024, one of us (WDP) discovered reddish guano and culled insect parts beneath a night roost of pallid bats in one of several soil-piping cavities. Realizing the potential of these discarded remains to bolster knowledge of the diet of pallid bats in this area, we searched for other such night feeding roosts in the local area and opportunistically revisited them to collect the prey remains while the bats were absent.

Study area

A small remnant mesquite bosque (bottomland forest) occurs at 1030-1060 m elevation in an abandoned meander loop of Cienega Creek, in the Cienega Creek Natural Preserve (CCNP), southeast of Tucson in Pima County, Arizona. Dominant plants in the bosque are velvet mesquite (*Prosopis velutina*) and graythorn (*Zizyphus*). Adjacent to the bosque, Cienega Creek flows above ground for parts of its reach where there are surface outcroppings of porphyritic andesite dikes at the upstream and downstream limits of the reach. There the creek forms a riverine marsh or ciénaga, one of few remaining perennial reaches of the stream, and a disappearing habitat feature in the desert southwest (Turner, 1974; Hendrickson & Minckley, 1984). The riparian area is dominated by tree species such as cottonwood (*Populus*), willow (*Salix*), ash (*Fraxinus*), mesquite, and the shrubs seepwillow (*Baccharis*) and sumac (*Rhus*). Cattails (*Typha*) grew in the water of the riverine marsh. The bosque grows on a low Quaternary terrace 2-10 m above the stream channel level and abruptly separated from it by vertical banks. On surrounding gravelly hills adjacent to the bottomland is semi-desert grassland and desert scrub with palo verde (*Cercidium*) and saguaro (*Carnegiea*), accented by species of yucca (*Yucca*), agave (*Agave*), acacia (*Acacia*), and ocotillo (*Fouquieria*) with occasional juniper (*Juniperus*). Foothills of the Rincon Mountains occur to the north of the ciénaga and bear junipers and oak woodland at higher elevations.

The relative representation of trees and many other plants in this area was strongly changed in historic times after colonization; the extensive removal in the 1800s of oaks and junipers for railroads and livestock overgrazing resulted in an increase in the density of mesquites (Bahre & Hutchinson, 1985; Turner et al., 2003). As a result, Cienega Creek became entrenched and presently flows at a lower level than it did during and prior to the 1800s. The lowering of the water table, headward erosion, and subsurface withdrawal are removing the soil beneath the mesquite trees, exposing their roots, gullying the terraces and bosque, and forming a pseudokarst terrain with natural bridges, blind and interrupted reaches, sinkholes, and underground cavities through soil-piping action (Fig. 1). In the Cienega Creek Natural Preserve, the cavities provided roosting sites for night-roosting pallid bats in the summer time, as well as refuges or nesting areas at various times of year for other species including other bats (*Choeronycteris mexicana, Corynorhinus townsendii,* and *Myotis velifer*), woodrats (*Neotoma albigula*), javelinas (*Pecari tajacu*), skunks (*Conepatus leuconotus* and *Mephitis macroura*), and a small unidentified bird (personal observations). In the immediate vicinity of the soil-piping cavities, plants included mesquite, graythorn, desert broom (*Baccharis*), cholla cactus (*Cylindropuntia*), grasses, and small herbaceous plants. The vegetation is essentially the same on top of the flat terrace as in the bottoms of the eroding gullies, except that mesquites are absent in the gully systems. As the soil continues to erode, the soil-piping cavities seem to be ephemeral and might eventually disappear as roosting areas for bats. Episodic roof collapse from the ceilings of the soil-piping cavities at unpredictable times occasionally covered the previously accumulated insect parts dropped by the bats.

In September 2002, we observed mesquite bugs on and under mesquite trees along a normally dry tributary of Cienega Creek that had flooded the previous night during a rainstorm. We also made casual observations of pallid bats in 2001 and 2002 at a day roost that was discovered in the porch of a caretaker's residence at the nearby Colossal Cave Mountain Park. This building roost was about 5 km distant from the soil-piping cavities at CCNP and at an elevation of 1095 m, about 60 m higher than the soil-piping cavities. Although this porch served mainly as a day roost, it was also sometimes used as a night roost by pallid bats.

Collecting methods

Insect parts (predominantly of mesquite bugs) were first noted by one of us (WDP) in 1994 in one of the soil-piping cavities at Cienega Creek. In 1996, WDP discovered two additional cavities with accumulations of insect fragments and made sightings of *A. pallidus*. We chose to study the culled insect parts discarded by the pallid bats as a non-intrusive method of determining the macro-arthropodophagous diet in this population of bats. Pallid bats are sensitive to disturbance at their roosts (Arroyo-Cabrales & de Grammont 2017; O'Shea & Vaughan 1977), thus we intentionally used this method and collected insect remains at a night roost not used by the pallid bats during the daytime as a way to avoid interference in their activity. The pallid bats were usually absent from the soil-piping cavities when we collected samples in the daytime except on one occasion in September 2002 when we observed two individuals. We visited the soil-piping cavities and collected insect parts once in November 1996, once in January 2001, twice, in February and September 2002, and once in September 2004. These did not represent seasonal samples but were merely times at which we were able to visit the soil-piping cavities and collect the remains that had accumulated since our previous visit. We collected all pieces from the larger concentrations of pallid bat prey that could easily be picked up by hand for later identification. We attempted to collect all of the insect parts present on a given visit in order to sample the overall diversity of species eaten but also to estimate the relative abundance in the diet of the different insect species. Although this method possibly misses some smaller insects taken in aerial hawking flight (not a preferred mode of foraging for pallid bats; O'Shea & Vaughan, 1977; Johnston & Fenton, 2001), our study reinforces previously published data about the contribution of prey brought into night roosts to the total diet of pallid bats. We identified insect parts by comparison with intact museum specimens in the Oklahoma Museum of Natural History, Section of Recent Invertebrates, with descriptions in the literature, and with digital images and relevant data archived online (e.g., www.Bugguide.net). Individual prey parts and specimens collected in this study will be accessioned into the Department of Recent Invertebrates at the Sam Noble Oklahoma Museum of Natural History, where the data will be cataloged and made freely available to the public through GBIF and iDigBio online portals.

On 11 September 2002 we made preliminary observations and photographed mesquite bug behavior in the mesquite bosque in late afternoon and early evening. We observed apparent end-of-season mating and mortality of adult insects. We also recorded air temperatures and relative humidity with a handheld electronic sensor outside one of the pallid bat night-roosting cavities during the sundown-to-dark transition period to investigate the relationship of temperature and humidity on adult activities late in the season. On the same date, we collected several of the dead and dying mesquite bugs as voucher specimens. Hind leg parts (hind femurs and hind tibias) allowed determination of the sex of the individual mesquite bugs eaten. Males have inflated hind femurs with projecting spines while those of females are not inflated and lack spines, and males have hind tibias ridged with a central bend and spur while females have a straight hind tibia without a spur (Schuh & Slater, 1995).

RESULTS

Among the insects observed at CCNP, mesquite bugs were common in the bosque, active and feeding on mesquites. They followed the typical phenological cycle for tropical areas described in the Introduction. We observed mesquite bugs as nymphs only early in the warm season (Fig. 2). By late summer and early fall, all *Thasus* observed in the ciénaga area were adults. In late summer the mesquite bugs could be seen flying all over the mesquite bosque, alighting on the trees, and mating. When summer heat slowed, evapotranspiration was high, and there was a marked diurnal-nocturnal temperature shift. Cooler air drains from the nearby mountains and foothills and a strong down-canyon breeze flows into the bosque and ciénaga. By the end of September and early October, the bugs continued mating but appeared to be succumbing to end of season mortality, possibly due to intolerance of the decreasing nighttime temperatures. At this time of year they became inactive at night and remained exposed on the periphery of the canopy of the mesquite trees. On 11 September 2002 after the first few nights during which the temperatures started to drop below about 21°C and the bugs were clustered out on the edges of the branches, we observed individuals become immobile while mating, laying eggs, dying, and falling to the ground (Fig. 2). During the sundown-to-dark transition period on this same date, air temperature decreased by 4.2°C, from 25.2° to 21.0°, while relative humidity increased by 16%, from 69% to 85%. The moribund and immobile adult mesquite bugs on the edge of the canopy probably are easy seasonal prey for foliage-gleaning pallid bats, which retreat to the local soil-piping cavities to eat them. Upon examination, the fallen bugs on the ground beneath mesquites occurred singly or sometimes in mated pairs (one male and one female in each case). We collected three pairs of the dead ones off the ground as voucher specimens.

By 29 September 2002, no live adult mesquite bugs were present in the vicinity of the roosting cavities in the bottomland of CCNP. This was probably due to cold air drainage through the bottomland, because live adults were active in nearby upland areas on the same date. On this date, pallid bats also night-roosted on the caretaker's building porch in the upland, and many moth wings but no mesquite bug parts were observed beneath the bats. On the night of 1 October 2002, the bats were again present in the porch roost but no new culled insect parts appeared, and the number of pallid bats dwindled until 7 October when only 1 or 2 were present, and no guano was present.

Pallid bats used only three of six available soil-piping cavities in the CCNP mesquite bosque as night roosts during our study, although the other three cavities were sometimes utilized by other species of bats, especially *Choeronycteris mexicana* (Mexican long-tongued bat) in the summer. The soil-piping cavities (Fig. 1) offered several characteristics that make them suitable as night roosts for pallid bats: (1) enclosed space providing protection from the weather and nocturnal flying predators; (2) easy access with from one to three entrances of relatively large dimensions; (3) relatively spacious interior (in this aspect the cavities were somewhat like the daytime roosts described by Vaughan & O'Shea, 1976) mostly unobstructed except for occasional exposed mesquite roots; (4) high ceilings and steep walls, providing safety from ground and climbing predators, respectively; (5) rough ceiling surface texture providing secure grip for the bats' thumb claws, hind claws, or both while processing insect prey; (6) proximity to at least part of the bats' foraging area, and to at least one observed day roost.

Within the soil-piping cavities the insect pieces dropped by the pallid bats were concentrated across a small area of the floor on clods of collapsed soil that had fallen from the ceiling (Fig. 1c, d). Large guano pellets, often stained red from the mesquite bugs, attributable to the pallid bats roosting there occurred within the concentrations of culled insect parts on the floor of the soil-piping crevices. Uncommon and scattered insect parts were occasionally found distant from these dense concentrations in the same soil-piping cavities, and probably represented prey remains culled by other species of bats. Three other species of bats were observed using the cavities rarely. Two of these were smaller species than *Antrozous pallidus* (which has a body weight of 20-35 g; Harvey et al., 2011). On one occasion we observed four cave myotis, *Myotis velifer* (body weight 12-15 g) clustered in a small soil pipe in the ceiling not far from one of the cavities used by *A. pallidus*. On two consecutive days in January 2001 in a different area we observed an individual of Townsend's big-eared bat, *Corynorhinus townsendii* (body weight 8-14 g), in hibernation. Because the isolated culled insect fragments could have represented feeding by these other species, they were not collected or included in our study. The guano pellets of these smaller bat species in other parts of the soil piping cavities were smaller than pallid bat guano and were never stained red like the pallid bat scats. For pallid bats, mean scat diameter = 3.065 mm, mean length = 7.783 mm (n = 23); for Townsend's big-eared bats, mean diameter = 1.929 mm, mean length = 3.786 mm (n = 7); for cave myotis, mean diameter = 2.036 mm, mean length = 4.036 mm (n = 14). The Mexican long-tongued bat, *C. mexicana* (body weight 10-25 g), also used soil-piping cavities at CCNP, but it was never found roosting in the same cavity as pallid bats. The Mexican long-tongued bat is a specialized nectar and pollen feeding bat whose guano lacks visible insect fragments, is primarily composed of pollen sometimes with bits of anthers and filaments from the stamens, and forms yellowish or reddish-brown splats beneath its roosts rather than pellets, similar to that of other nectar-and-pollen feeding bats (pers. observ.). Large, red-stained guano pellets exactly like the pallid bat scats in the soil-piping cavities accumulated on plastic sheets laid beneath the roost on the porch of the caretaker's building, indicating that at times, both groups of pallid bats were feeding on mesquite bugs.

Only one non-insect prey item was found beneath the pallid bat night roosts, a partial bat wing with metacarpals II-III-IV, accompanying phalanges, and a bit of attached membrane of the wing tip. The proximal ends of the metacarpals are morphologically distinct from those of the vespertilionid bats of the Cienega Creek area, and instead represent those of the phyllostomid, *Choeronycteris mexicana*. The distal ends of the metacarpals and the phalanges have the epiphyses completely fused, indicating an adult bat. The skin attached to the wing bones showed some signs of feeding by decomposer arthropods, indicating that the wing had been beneath the pallid bat roost for some time before it was collected in February 2004.

Pallid bats foraging in and around the Cienega Creek mesquite bosque clearly used the soil-piping cavities as a place to hang while processing the large and sometimes-armored insects they catch. Pallid bats are equipped with robust jaws and teeth for their body size, including longitudinally curved, tapered canines with four heavy crests or flanges on the anterior, lingual, posterior, and labial surfaces running from the apex to the base of the tooth crown, with deep furrows between all except the anterior and labial flanges (Fig. 3a-a'). These canines are adapted for procuring and puncturing the thick exoskeletons of hard-bodied insects. The sharp flanges of the canines act to create stress and propagate cracks in the brittle exterior surface of the chitin, making it easier to penetrate the exoskeleton (see Freeman, 1979; 1992; 1998; Freeman & Weins, 1997) and subdue an insect. The tooth marks of the bats are readily seen on many of the culled fragments (Fig. 3b-g).

At Cienega Creek, pallid bats fed on at least 36 species of large insects (approximately 25-60 mm body length) based on parts discarded beneath the night roosts (Table 1). Of these insects, 20 taxa are reported for the first time in the diet of *A. pallidus*. No arthropod groups other than insects were represented in the discarded body parts in the soil-piping cavities. All exoskeletal parts identified appeared to be those of adult insects. We found no evidence that the pallid bats fed upon the noxious nymphs of giant mesquite bugs based on our survey of discarded body parts. The insects eaten by pallid bats at the CCNP include mainly night-active forms, many of which are ground dwelling, although a few diurnal taxa including several grasshoppers, two long-horned beetles, and a dragonfly were taken.

In terms of relative abundance, the vast majority of insects consumed by pallid bats at all three cavity roosts at Cienega Creek were adult mesquite bugs. This insect also accounted for many of the bat guano pellets being reddish in color. Of 483 total identified insect parts, 429 (88.8% frequency) were of mesquite bugs. All body parts of the mesquite bugs are represented, but mostly the least nutritious and most chitinous portions (wings, legs, antennae) were discarded; relatively few abdomens were found beneath the bat roosts (Table 2). Thus, pallid bats were eating mainly the nutritious abdomens of the mesquite bugs. Interestingly, the relatively few available remains of *Thasus* abdomens showed that the softer, ventral portion was selectively eaten and the remainder of the abdomen discarded. Of the identified *Thasus* parts, 272 forewings (Table 2) indicate a minimum of 136 individual mesquite bugs eaten. In most samples there were more male than female mesquite bug hindleg elements, although in one sample there were more female than male hindleg elements. For insect species other than mesquite bugs, relative abundance was low, representing only one to four individuals of most species (ranging from 0.002-0.014% frequency). One exception to this was the gray bird grasshopper, *Schistocerca nitens*, represented in February 2002 by 19 forewings and 57 hindwings.

DISCUSSION

Ross (1967) and subsequent authors have compiled an impressively long list of arthropod prey species taken by pallid bats. Because of the relative ease with which culled insect parts can be collected beneath bat roosts and identified, the list continues to grow. Our results add 18 taxa not previously recorded as pallid bat prey to the overall list. Pallid bats are clearly important predators on a broad diversity of insects and other arthropods, as well as occasional small vertebrates, and even cactus nectar and fruit pulp and seeds in certain parts of their range (Frick et al., 2009; 2013; 2014; Aliperti et al., 2017). Pallid bats in our study fed upon large moths as well as large beetles; Freeman & Lemen (2007) indicated that beetles were about 3.2 times harder than moths of the same body size, but that body size or volume of the insect also was important in cuticle toughness. In other words, some large-bodied moths have a chitinous cuticle that is tougher than some smaller-bodied beetles. Freeman & Lemen (2007) hypothesized that as aerial feeders some bats must limit the upper size of insects they eat, because insects that are too large cannot be processed orally in flight, especially for a bat species that depends heavily on being able to continue echolocating to fly. Some of these bats might capture prey that are too tough to process orally in flight and must land to process the prey captured. These authors also hypothesized that harder insects might take longer for bats to chew and thus limit the upper size of certain taxa of insects taken, which varies among insect taxa. Borell (1942) observed a pallid bat landing and hanging head-up by its thumb claws and using its interfemoral membrane as a pouch to help while processing some insects, then dropping the unwanted remains from the membrane as it returned to foraging.

In our study, the higher numbers of large, armored, and cumbersome legs and other body parts of mesquite bugs found beneath roosts relative to other taxa of insects suggests that mesquite bugs might be more difficult for pallid bats to process than other kinds of insects. Possibly the bats preferentially or necessarily bring mesquite bugs to a night-roost for processing compared to other less-cumbersome insect taxa. Mesquite bugs have a small head, thorax, and abdomen with large legs relative to most of the beetles and moths represented in the bats' diet. Perhaps the relative ease with which mesquite bugs are located or secured in late summer or early autumn counterbalances the energy and time needed to commute to a night roost to process them. The size and hardness of many of the insects eaten by pallid bats suggests there is a large upper size limit to what insects pallid bats are capable of processing and eating. In the CCNP area, Palo Verde Root Borer Beetle (*Derobrachus germinatus*: Cerambycidae) is perhaps the largest insect in the area; adults can reach 76-89 mm in length. This large insect was not represented in the diet of pallid bats in our study, although Ross (1961) reported *Derobrachus* as food for pallid bats in southern Arizona. Mesquite bugs (*Thasus*) are among the largest terrestrial heteropterans known (Forbes & Schaefer, 2003) and are 28-43 mm in body length.

As noted above, most of the insects eaten by the pallid bats are nocturnal, although several species represented in our study are diurnal. Most day-active insects are inactive or quiet during the night. Therefore, for bats that must be able to hear prey-generated sounds of motion to find prey, the prey list largely supports the assertion of Fuzessery et al. (1993) that pallid bats are hunting primarily with sound cues and are less dependent on visual cues. Many of the large insects consumed by pallid bats in this study make noise in flight, while others have been variously described as noisy fliers (e.g., *Cotinis mutabilis* fly noisily and somewhat haphazardly; Tallamy, 2009). The noises they make likely increase their chances of being detected by a hunting pallid bat.

Furthermore, in mesquite, which is spiny, it would be better for the bats to avoid flying in the understory or within the tree canopy to hunt for prey they cannot hear. The risk of injury is too high unless they can be certain there is potential food available there, like katydids and mesquite bugs.

As adults, mesquite bugs do not secrete the same pheromones as a defense against insect predators that they do when they are nymphs. Most insect predators are not interested in the non-toxic adult mesquite bugs because the bugs are so big. For the mesquite bugs, it might not be evolutionarily worthwhile to invest energy in producing toxic pheromones against other insect predators when it is unnecessary. As adults, the bugs switch to a defense of more muted colors (and thus being more cryptic to visually-oriented aerial predators), and a physically more armored exoskeleton (spiny hind legs, tougher wings), but they produce less noxious chemicals than as nymphs. This is not necessarily a change to prevent predation as much as a trade-off of putting less investment in defense (producing energetically expensive coloration and toxins) and more investment into reproduction (wings provide mobility to find mates, less toxic chemical investment for short period of mating and death).

As noted earlier, in laboratory experiments pallid bats showed an aversion to the odor of a Pinacate beetle *Eleodes* (Johnston, 2002); however, at least one species of *Eleodes*, *E. acuticauda* (as well as several other tenebrionid genera), has been reported as a prey item for pallid bats (Orr, 1954:232), and the genus also appeared as prey in our study. Perhaps the bats are able to process and discard the noxious parts of certain insects. Although the chemicals secreted by adult mesquite bugs differ from those secreted by the nymphs (chemical components frequently change after metamorphosis; Noge, 2015), the adult pheromones have not been tested with vertebrates, so it is unknown whether the pheromones produced by the adult bugs actually deter vertebrate predators (Prudic et al., 2008). Of the secretions produced by the adult bugs (hexyl acetate, hexanal, 1-hexanol and possibly others), hexyl acetate and hexanal might be aggregational pheromones directed toward other mesquite bugs (Prudic et al., 2008; Noge, 2015). Hexyl acetate has relatively low toxicity, although hexanal vapor is irritating to the eyes and nose of humans, and is potentially mutagenic and carcinogenic (PubChem Open Chemistry Database, https://pubchem.ncbi.nlm.nih.gov/compound/Hexyl_acetate). The secretion, 1-hexanol, seems less well investigated in the insects, but 1-hexanol causes skin and eye irritation in rabbits (https://pubchem.ncbi.nlm.nih.gov/compound/8103#section=Top) and is not considered lethal to laboratory rats (MAK Collection for Occupational Health and Safety, http://onlinelibrary.wiley.com/doi/10.1002/3527600418.mb11127kske0009/full); it readily metabolizes to 2-ethyl-1-hexanol, which is a moderate skin, eye, and mucous membrane irritant in laboratory animals (Bibra Toxicology Advice and Consulting, http://www.bibra-information.co.uk/profile-129.html). Given that pallid bats in our study never ate mesquite bug nymphs, the nymphal secretions might be effective not only against insect predators but also against bats. And given the frequency with which pallid bats in our study ate the adults, either the adult bugs are non-noxious to pallid bats or else the pallid bats are not susceptible or averse to their secretions.

The only non-insect prey item found at a pallid bat night roost in this study was another bat, the flower-visiting phyllostomid *Choeronycteris mexicana*. As noted above, *C. mexicana* utilized separate but adjacent soil-piping cavities at CCNP in summers during our study. This is the first record of *C. mexicana* as prey for *A. pallidus*. There is one previous record of pallid bats eating a Mexican free-tailed bat, *Tadarida brasiliensis*, although the predation occurred while the two species were in captivity, being held together in the same cage from which the smaller free-tailed bats were unable to escape (Engler, 1943). Thus, the *C. mexicana* at CCNP is the first recorded instance in the wild of predation by *A. pallidus* on another species of bat.

Pallid bats are not known to migrate and in winter are largely inactive, although occasional winter activity has been observed (Hermanson & O'Shea, 1983). Thus the bats must forage on the invertebrates that are available in the areas they inhabit throughout their seasons of activity. Many of the insects preyed upon by pallid bats are probably variable in their seasonal availability. Some might be continuously available during the active season for the bats, while others might be available to the bats only during specific times of the year or during specific stages in the life cycle of the insect. For example, adult mesquite bugs are available only in the middle and late summer and early autumn. Seasonal availability might also require the bats to be able to move across the landscape appreciable distances. Few telemetry studies have been done on pallid bats and their nightly foraging range is poorly known. A telemetry study in California showed that pallid bats roosted 5-11 km from the areas in which they foraged (Brown et al., 1997). Miller & Jensen (2013) netted radio-tagged individuals in Kansas and Oklahoma at distances from 120 m to 1.2 km from their day roosts. In northern California foraging individuals of both sexes made nightly foraging flights over 2 km long (Baker et al., 2008). Pallid bats are extraordinarily flexible in their foraging methods and diet, using a combination of at least auditory, olfactory, and visual cues to locate prey and other foods (Aliperti et al., 2017). Their foraging behavior is in part socially learned (Gaudet & Fenton, 1984), and groups or individuals change roost sites frequently (Lewis, 1996). Their opportunism and behavioral flexibility in flight and on the ground contributes to their success as a generalist insect predator.

Relatively little information is known about the natural history of many of the other species of insects besides mesquite bugs that support pallid bats, but available information provides glimpses into the interrelationships among the insects, the habitats and vegetation in the vicinity of the Cienega Creek Natural Preserve, and the bats. Many of the less commonly eaten insects link the pallid bats ecologically to a variety of locally available habitats and plants. In the mesquite bosque, in addition to the mesquite bugs, the larvae of the mesquite moth, *Sphingicampa hubbardi*, depend on mesquite, palo verde (*Parkinsonia*), and acacias, as do mesquite girdler beetles, *Oncideres rhodosticta*. Mesquite girdlers emerge late in the summer rainy season to mate and lay eggs; they overwinter as pupae inside the mesquite or palo verde branches (Merlin, 2003), and thus adults as represented in the pallid bat diet in our study would only be available in late summer or autumn. A scarabaeid, *Dichotomius colonicus*, is a dung beetle that uses vertebrate dung (Eiseman & Charney, 2010). Because javelinas sometimes used the bosque and gully systems for shade and shelter, javelina scat was common near the soil-piping cavities and could have provided this beetle a source of food for its larvae. Interestingly, Williams et al. (2006:1149) found that in southern Nevada, mesquite bosque habitat was rarely used by pallid bats relative to other available habitats (which were: mesquite bosque, riparian woodland, riparian shrubland, and riparian marsh), and the species spent more time in riparian woodland habitat than all the other habitats combined of those studied.

Other insects eaten by CCNP pallid bats connect the bats to ecosystems outside the mesquite bosque but in the adjacent riparian gallery forest or ciénaga. One of these insects, the rhinoceros beetle *Xyloryctes thestalus*, is dependent upon the roots of velvet ash (*Fraxinus* *velutina*; Ratcliffe, 2009), which occurs as an element of the riparian vegetation along Cienega Creek. The unidentified prionin beetle (Prionini), Mexican bush katydid *Scudderia mexicana*, and differential grasshopper *Melanoplus differentialis* inhabit moist forests or deciduous woodlands, or rank growth, which in our study area are available only in the ciénaga and riparian gallery woodland. Additional ecological links to riparian woodland include the vine moth *Eumorpha vitis* and possibly the white-lined sphinx moth *Hyles lineata*, whose caterpillars feed on the foliage of grapes (*Vitis*), Virginia creeper (*Parthenocissus*), and other vines, while the adults feed on nectar of flowers possibly including datura (*Datura*). The unidentified darner (dragonfly; Aeshnidae) lays eggs on aquatic plants and the nymphs are fully aquatic, linking pallid bats to the ciénaga habitat; adults are aerial predators on flying insects and roost on vegetation at night. Similarly, the giant black water beetle (*Hydrophilus*) eaten by the bats is aquatic in larval and adult life stages, but disperses long distances at night to find alternate aquatic habitats.

Still other insects eaten by the bats inhabit the desert ecosystem outside the mesquite bosque and riparian-ciénaga habitats, or utilize a combination of habitats depending on the life-stage of the insect. The broad-tipped, or three-eyed, conehead katydid, *Neoconocephalus triops*, utilizes open grassy areas but overwinters in forests and thickets. Katydids are acoustically conspicuous to some foliage-gleaning bats in the tropics (Belwood & Morris, 1987); the song of this katydid might attract the attention of pallid bats. Blue-winged grasshoppers *Trimerotropis cyaneipennis* favor broken canyon bottoms, steep rocky slopes, and rocky ground in mountains with open scrub, juniper-piñon, or oak woodland. Gray bird grasshoppers, the second most common insect consumed by pallid bats in this study, inhabit shrubby, desert, or riparian habitats usually at lower elevations in mountains. This grasshopper feeds on a wide variety of plants and has an extensive active season through much of the year. It is said to be a strong flier and "tends to fly lower…than most other *Schistocerca* species" (BugGuide.net), apparently within range of the low-flying pallid bat. The iris-eyed silkmoth *Automeris iris* inhabits oak woodlands in low mountains and the caterpillars feed on oaks and velvet-pod mimosa (*Mimosa dysocarpa*). Larvae of many species of underwing moths, *Catocala,* feed on oaks (Tallamy, 2009). The glorious scarab *Chrysina gloriosa* occurs in lower elevations of mountains, where the adults feed on juniper foliage and the larvae are found in decaying logs including those of sycamore and willow (Young, 1957; Ritcher, 1966). Scattered junipers occur on uplands adjacent to the mesquite bosque, and occasional sycamores occur along Cienega Creek in the vicinity of the ciénaga and mesquite bosque, so the habitat and the beetles themselves are not particularly common in this area. The uncommon occurrence of *C. gloriosa* remains (one elytron) beneath the bat roosts indicates that the pallid bats move away from the mesquite bosque at times to hunt along the riparian vegetation of the creek and on adjacent uplands among the occasional junipers. The green and mirrored surface of this beetle might serve as reflective camouflage for the beetles resting on juniper foliage (Young, 1957), but the noise it produces in flight could easily attract the attention of a pallid bat despite the relative uncommonness of this scarab in the study area.

Many kinds of animals take advantage of situations arising as they acquire food (Young, 2012). Like many predators, various species of bats are opportunistic on hatches of insects (e.g., *Myotis* [Vespertilionidae], Fenton & Morris, 1976; *Lavia frons* [Megadermatidae], Vaughan & Vaughan, 1986; Dial & Vaughan, 1987; *Taphozous melanopogon* [Emballonuridae], *Hipposideros* sp. [Hipposideridae], and *Scotophilus temminckii* [Vespertilionidae], Gould, 1978; *Hipposideros gigas* [Hipposideridae], Vaughan, 1977; *Nycteris grandis* [Nycteridae], Fenton et al., 1993) and also passively use sounds produced by the insects themselves rather than actively echolocating them. Several of the large insects preyed upon are noisy fliers, and pallid bats might thus be able to detect them easily. Some, like antlions, are said to be poor fliers as adults (Merlin, 2003). At the mesquite bosque at CCNP, the mesquite bugs are available for the entire warm season, but it is only when they become adults and aggregate on the periphery of the mesquite canopy that they are preyed upon by pallid bats. In a refuging species like the pallid bat, efficient and rapid dispersal and the ability to exploit patchy food resources is probably essential. The opportunistic feeding described here was associated with high selectivity for a single prey species that could make wide searches for patches of food energetically worthwhile.

Despite their noxious secretions, mesquite bugs apparently are not sufficiently deterrent to pallid bats as adults, and the bats in our study selected mesquite bugs as prey only when the bugs were adults. We found no evidence that pallid bats ate the noxious nymphs based on discarded body parts. Thus, the nymphs appear to be effectively defended against the bats, but not the adult bugs. The body parts discarded versus those parts eaten indicates that pallid bats take the most easily digestible and probably most nutritious parts of these insects, as has previously been observed for many kinds of bats and other predators. The abdomens of gravid female bugs filled with egg masses in particular might provide additional protein to the bats. When mesquite bugs are clustered and immobile on the periphery of the mesquite canopy, bats can likely capture the bugs easily compared to within the thorny canopy. Mated females move from the periphery deeper into the mesquite tree canopy to find appropriate places to deposit their eggs, and thus be less susceptible to being located and preyed upon by the bats compared to males, which might explain the male bias in our samples. Mesquite bugs overwinter only as eggs in mesquite bark; therefore the bats can feed on mesquite bugs during the season when the adults are available. The noxious and aposematic defenses of the nymphs, which are unable to fly, render them relatively immune to attack at night by the bats perhaps due to their odor and quieter movements, and to visually-oriented predators like birds during the day (or bats during twilight). This means that the bats must wait until late summer for the adults, and must select other kinds of insects at other times of year. By becoming immobile overnight after they alight on mesquite foliage at evening twilight, the mesquite bugs might avoid detection by pallid bats. The relatively noisy flight and possibly other movements and activities of the mesquite bugs, beetles, grasshoppers, and other large insects has been little studied and could be an important aspect of the bat-insect relationship. Similarly, the influence of anthropogenic noise (e.g., automobile traffic, railroad noise, air traffic) on a passive-sound-using predator limits the pallid bats' foraging efficiency and potentially their ability to utilize certain areas for foraging (Bunkley & Barber, 2015; Bunkley et al., 2015).

Unfortunately, in this study we were unable to collect data seasonally or regularly, but a seasonal or monthly collection of dietary data would provide a good future study to pursue this ecological relationship in greater depth. Moreover, the bats might select mesquite bugs as prey when the bugs are perhaps the most vulnerable: in late summer or early autumn after the adult females laid the eggs for the overwintering generation, and when falling nighttime air temperatures, local cool air drainage from the adjacent mountains and foothills, and high evapotranspiration might slow the insect's activity or mobility. Finally, the overwhelming majority of insects consumed in the night roosts were mesquite bugs locally derived from the mesquite bosque; the bats consumed other kinds of insects almost incidentally. In addition to their ability to endure injuries and heal (Davis, 1968), the dietary plasticity shown by pallid bats across the species' broad geographic range might help to lessen their risk of extinction (Boyles & Storm, 2007) in the face of anthropogenic environmental upset and climate change.

CONCLUSIONS

The diet of pallid bats can be investigated non-intrusively by visiting their temporary-use night roosts during the day while the bats are away at separate day roosts. However, the night roosts possibly yield evidence only of those foods that are large enough to require transport to a temporary night roost for processing of edible versus inedible parts. Adult mesquite bugs formed the predominant prey for pallid bats at the CCNP. We found no evidence of pallid bats feeding on toxic, aposematically colored nymphal stages of mesquite bugs. Adult mesquite bugs are possibly non-toxic to pallid bats, or perhaps the bats are able to tolerate the less-toxic compounds of the adult bugs. Late-season breeding and postbreeding adult mesquite bugs are exposed near the edges of the mesquite canopy and provide prey for opportunistic, foliage-gleaning pallid bats. After breeding and laying eggs that overwinter in the mesquite trees, moribund adult mesquite bugs begin to become immobile in the trees or drop from the canopy when the nighttime low temperatures at CCNP fell below 21°C. Mesquite bugs are considered to be mostly subtropical-tropical insects that may have invaded the southwestern United States during historic times with the bringing of cattle and spread of mesquite trees; pallid bats at the CCNP are providing an important natural control on the local mesquite bug population. Pallid bats at the CCNP ate numerous taxa of large-bodied insects, consistent with their diet in many other portions of the bats' range. When mesquite bugs are observable in the local mesquite trees, their procurement by pallid bats can be determined by the presence of large reddish guano pellets 2.5-3.5 mm in diameter beneath local bat night roosts. Insects parts discarded beneath pallid bat roosts can be distinguished from insect parts culled by birds or other predators by distinctive tooth marks on the discarded insect parts. Bats usually ate the abdomen and thorax of mesquite bugs and most consistently discarded the wings and legs. At the CCNP, pallid bats left the remains of no arthropods other than insects. Seventeen taxa of insects were newly identified as prey for pallid bats, and reflect a diversity of local habitats of the CCNP as foraging habitat for the bats. In addition, pallid bats ate an individual of one other local species of bat, the Mexican long-nosed bat, which roosted in separate soil-piping cavities from those used by pallid bats, another first recorded instance of such predation for pallid bats.

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FIGURE LEGENDS

Figure 1 a and b, Two soil-piping cavities developed in the terrace supporting a mesquite bosque on top with mesquite roots being exposed, and grasses in the bottoms, at Cienega Creek Natural Preserve, Arizona. The cavities serve as shelters for a variety of mammals including several species of bats. Cavity in a is dark spot in center of image; cavity in b formed a temporary natural arch. c, Interior of one of the soil-piping cavities showing a scattering of culled insect parts dropped beneath a night roost of *Antrozous pallidus*. d, Close-up view of the scattering; note large numbers of reddish guano pellets (especially within the spotlight from photographer's headlight at lower left), colored by the contents of mesquite bugs, numerous mesquite bug exoskeletal parts, moth wings, and beetle elytra.

Figure 2 Mesquite bugs, *Thasus neocalifornicus*, at the Cienega Creek Natural Preserve, Arizona. a, *T. neocalifornicus* nymph (5^{th} instar), with aposematic coloration indicating its noxious nature. b, adult, not to same scale as nymph. c, adults mating on a mesquite branch at dusk (with flash). d, breeding adults clustered on the peripheral foliage of mesquite at dusk in September 2002 (with flash). e, scattered dead adults on the ground representing a <24-hour accumulation after a rainstorm had swept away other debris.

Figure 3 a and a', Stereopair photograph of the upper teeth and anterior palate of a skull of *Antrozous pallidus* (anterior is toward the top of the image) showing the robust upper canines with strong longitudinal flanges, which help to penetrate and puncture thick chitin. Incisors and premolars are also visible. b-g, Pieces of the exoskeletons of insects discarded by *A. pallidus*, showing tooth punctures caused by the bats. b, elytron of a beetle *Chrysina gloriosa* (Scarabaeidae); b', Same as b, close-up of area enclosed by red rectangle in b, rotated 90° counterclockwise and enlarged to show tooth punctures. c, elytron of a dung beetle *Dichotomius colonicus* (Scarabaeidae). d. hind leg of mesquite bug *Thasus neocalifornicus* (Coreidae). e, elytron of *Cyclocephala* (Scarabaeidae). f, elytron of *Xyloryctes thestalus* (Scarabaeidae). g, head, thorax, and partial elytra of darkling beetle *Stenomorpha marginata* (Tenebrionidae). Scale bar in each image is in mm.

Figure 1

Plate of four photos, a-d, showing soil-piping cavities, culled insect parts, and bat guano.

(a and b) Two soil-piping cavities developed in the terrace supporting a mesquite bosque on top with mesquite roots being exposed, and grasses in the bottoms, at Cienega Creek Natural Preserve, Arizona. The cavities serve as shelters for a variety of mammals including several species of bats. Cavity in a is dark spot in center of image; cavity in b formed a temporary natural arch. (c) Interior of one of the soil-piping cavities showing a scattering of culled insect parts dropped beneath a night roost of *Antrozous pallidus*. (d) Close-up view of the scattering; note large numbers of reddish guano pellets (especially within the spotlight from photographer's headlight at lower left), colored by the contents of mesquite bugs, numerous mesquite bug exoskeletal parts, moth wings, and beetle elytra.

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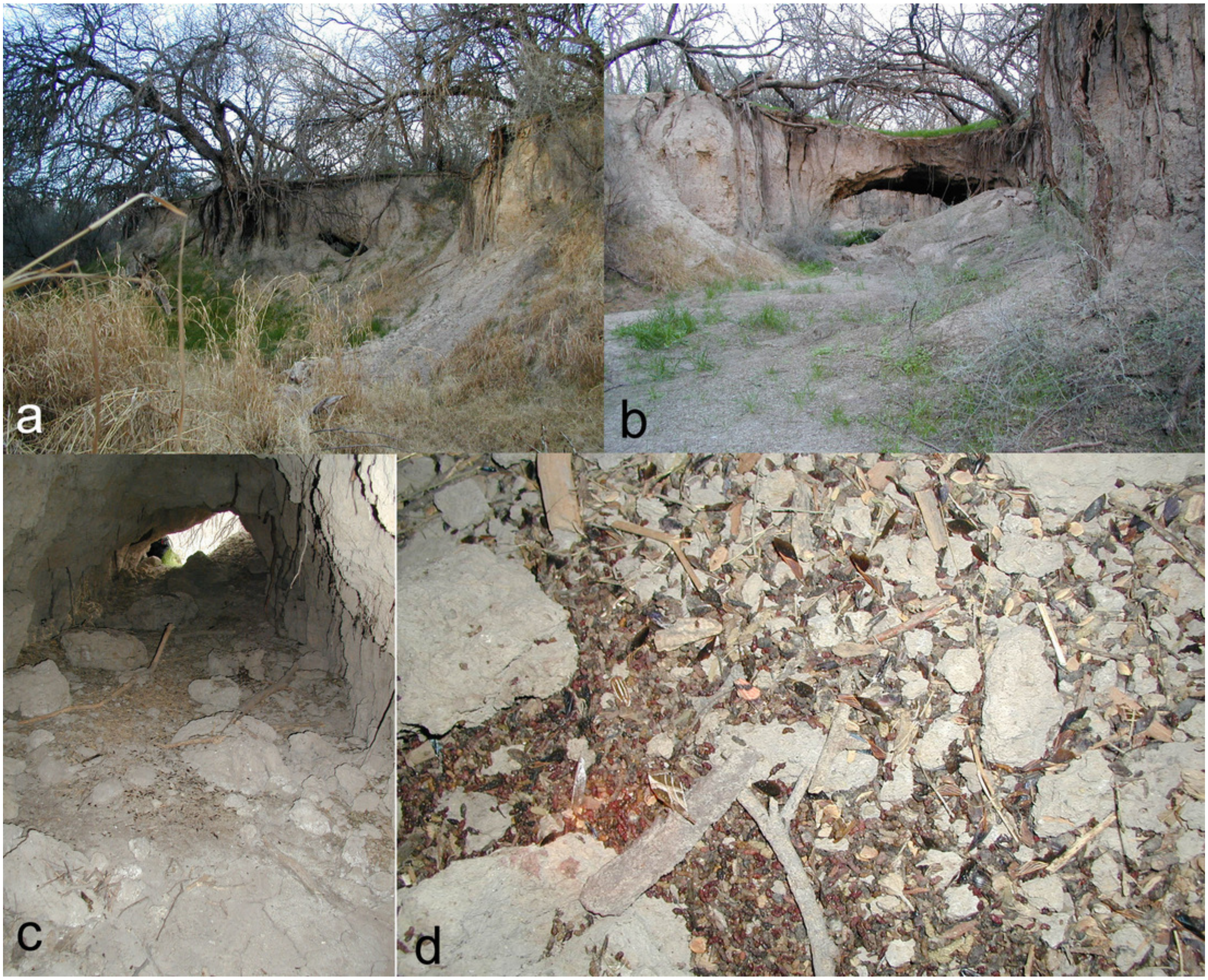
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Figure 2

Plate of several photos (a-e), showing mesquite bug nymph, adult, mating adults, clustered adults on mesquite, dead adults on the ground.

Mesquite bugs, *Thasus neocalifornicus*, at the Cienega Creek Natural Preserve, Arizona. (a) *T. neocalifornicus* nymph (5th instar), with aposematic coloration indicating its noxious nature. (b) adult, not to same scale as nymph. (c) adults mating on a mesquite branch at dusk (with flash). (d) breeding adults clustered on the peripheral foliage of mesquite at dusk in September 2002 (with flash). (e) scattered dead adults on the ground representing a <24-hour accumulation after a rainstorm had swept away other debris.

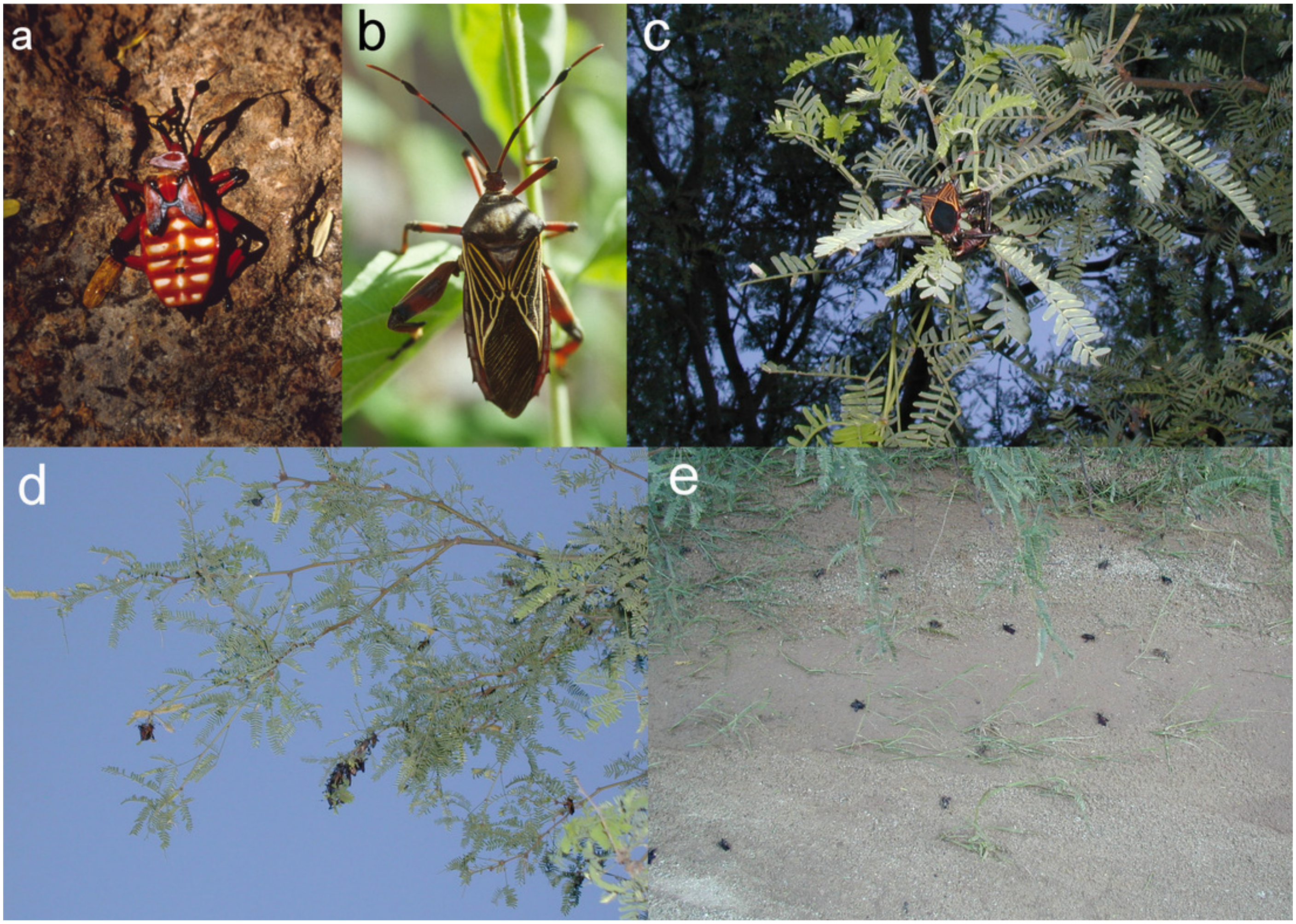

Figure 3

Plate of several photos (a-g) showing stereopair of bat teeth, pieces of the exoskeletons of insects showing bat tooth punctures.

(a and a') Stereopair photograph of the upper teeth and anterior palate of a skull of *Antrozous pallidus* (anterior is toward the top of the image) showing the robust upper canines with strong longitudinal flanges, which help to penetrate and puncture thick chitin. Incisors and premolars are also visible. (b-g) Pieces of the exoskeletons of insects discarded by *A. pallidus*, showing tooth punctures caused by the bats. (b) elytron of a beetle *Chrysina gloriosa* (Scarabaeidae); (b') Same as b, close-up of area enclosed by red rectangle in b, rotated 90° counterclockwise and enlarged to show tooth punctures. (c) elytron of a dung beetle *Dichotomius colonicus* (Scarabaeidae). (d) hind leg of mesquite bug *Thasus neocalifornicus* (Coreidae). (e) elytron of *Cyclocephala* (Scarabaeidae). (f) elytron of *Xyloryctes thestalus* (Scarabaeidae). (g) head, thorax, and partial elytra of darkling beetle *Stenomorpha marginata* (Tenebrionidae). Scale bar in each image is in mm.

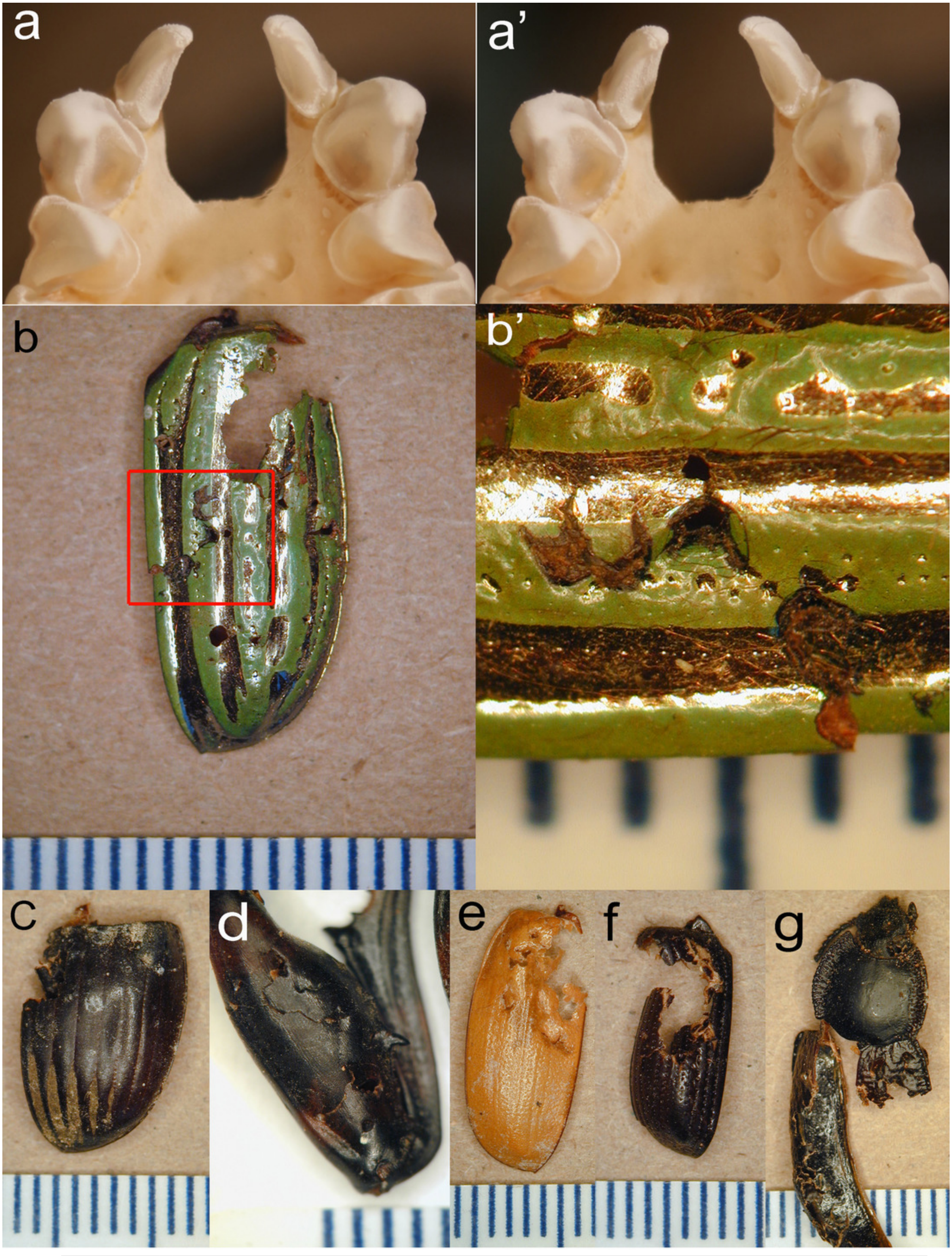
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Table 1(on next page)

List of insects and one bat identified from culled body parts deposited beneath pallid bat roosts at Cienega Creek, Arizona.

List of insects and one bat identified from culled body parts deposited beneath pallid bat roosts at Cienega Creek, Arizona. *Indicates new record of prey consumed by pallid bats.

Table 1 List of insects and one bat identified from culled body parts deposited beneath pallid bat roosts at Cienega Creek, Arizona. *Indicates new record of prey consumed by pallid bats.

Hemiptera	Coreidae	*Thasus neocalifornicus* mesquite bug
Coleoptera	Scarabaeidae	*Chrysina gloriosa* glorious scarab
		Polyphylla decemlineata ten-lined June beetle
		**Strategus aloeus* ox beetle
		Strategus sp. ox beetle
		**Xyloryctes thestalus* rhinoceros beetle
		Cyclocephala sp. masked chafer
		**Dichotomius colonicus* dung beetle
		Cotinis mutabilis green fig beetle
		Tomarus sp. carrot beetle
		Phyllophaga sp. May beetle
	Tenebrionidae	**Stenomorpha marginata* darkling beetle
		Stenomorpha sp. darkling beetle
		Eleodes sp. Pinacate or darkling beetle
	Carabidae	*Calosoma scrutator* fiery searcher
		Pasimachus sp. ground beetle
	Hydrophilidae	*Hydrophilus* sp. giant black water beetle
	Cerambycidae	*Oncideres rhodosticta* mesquite girdler
		*Prionini long-horned beetle
Orthoptera	Tettigoniidae	*Microcentrum rhombifolium* greater angle-wing katydid
		**Neoconocephalus triops* broad-tipped conehead
		**Scudderia mexicana* Mexican bush katydid
	Acrididae	*Schistocerca nitens* gray bird grasshopper
		Melanoplus differentialis differential grasshopper
		**Phlibostroma quadrimaculatum* four-spotted grasshopper
		**Trimerotropis cyaneipennis* blue-winged grasshopper
Lepidoptera	Sphingidae	*Hyles lineata* white-lined sphinx
		**Eumorpha vitis* vine sphinx
		**Sphinx* sp. sphinx moth
		Manduca sexta tobacco hornworm moth
	*Tortricidae	Indeterminate leafroller moth
	Noctuidae	*Catocala* sp. underwing moth
	Saturniidae	**Sphingicampa (=Syssphinx) hubbardi* mesquite moth
		**Automeris iris* iris-eyed silkmoth
Neuroptera	Myrmeleontidae	**Vella fallax* antlion
Odonata	*Aeshnidae	Indeterminate darner
Blattodea	Corydiidae	*Arenivaga* sp. cockroach
Diptera	Tipulidae	**Nephrotoma* sp. tiger crane fly
Chiroptera	Phyllostomidae	**Choeronycteris mexicana* Mexican long-nosed bat

Table 2 (on next page)

Body parts of adult mesquite bugs (*Thasus neocalifornicus*) discarded by night-roosting pallid bats and collected in soil-piping cavities in Cienega Creek Natural Preserve.

Table 2 Body parts of adult mesquite bugs (*Thasus neocalifornicus*) discarded by night-roosting pallid bats and collected in soil-piping cavities in Cienega Creek Natural Preserve on three visits between January 2001 and September 2002, in decreasing order of abundance. F = female, M = male.

Body Parts	Number of elements collected		
	January 2001	February 2002	September 2002
Forewings	272	213	127
Leg parts, total	183	43	99
Forelegs and midlegs	91	---	21
Hind tibias	52 (12 F, 40 M)	22 (8 F, 14 M)	57 (21 F, 36 M)
Hind femurs	40 (13 F, 27 M)	21 (7 F, 14 M)	31 (20 F, 11 M)
Hindwings	40	45	56
Isolated antennae	9	---	0
Thorax (dorsal portion)	8	0	18
Heads with attached antennae	5	1	8
Abdomens	3	8	5
Thorax with attached fore- and hindwings	1	1	0