Mesquite bugs, other insects, and a bat 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 western North America, inhabiting ecoregions ranging from desert to oak and pine forest. They are primarily insectivorous predators on large arthropods that occasionally take small vertebrate prey, and are at least seasonally omnivorous in certain parts of their geographic range where 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. Using a noninvasive method, we investigated the bats' diet at the Cienega Creek Natural Preserve, Arizona, by collecting food parts discarded beneath three night roosts in soil-piping cavities in a mesquite bosque. We also made phenological and behavioral observations of mesquite bugs, *Thasus neocalifornicus*, and their interactions with the mesquite trees. We determined that the bats discarded inedible parts of 36 species in 8 orders of mainly large-bodied and nocturnal insects below the night-roosts. In addition, one partial bat wing represents probable 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 majority of culled insect parts (88%) were from adult mesquite bugs. Mesquite bug nymphs did not appear in the culled insect parts. After breeding in late summer, when nighttime low temperatures dropped below 21°C, the adult bugs became immobile on the periphery of trees where they probably make easy prey for opportunistic foliage-gleaning pallid bats. Proximity of night-roosts to mesquite bug habitat probably also enhances the bats' exploitation of these insects in this location.

1 MESQUITE BUGS, OTHER INSECTS, AND A BAT IN THE DIET OF PALLID BATS IN
2 SOUTHEASTERN ARIZONA
3
4
5 Nicholas J. Czaplewski,[1] Katrina L. Menard,[2] and William D. Peachey[3]
6
7 [1]Section of Vertebrate Paleontology, Oklahoma Museum of Natural History, University of
8 Oklahoma, Norman, Oklahoma, United States of America
9 [2]Section of Recent Invertebrates, Oklahoma Museum of Natural History, University of
10 Oklahoma, Norman, Oklahoma, United States of America
11 [3]Sonoran Science Solutions, Tucson, Arizona, United States of America
12
13
14 Corresponding author Nicholas J. Czaplewski, nczaplewski@ou.edu
15
16
17
18 ABSTRACT
19 The pallid bat (*Antrozous pallidus*) is a species of western North America, inhabiting ecoregions
20 ranging from desert to oak and pine forest. They are primarily insectivorous predators on large
21 arthropods that occasionally take small vertebrate prey, and are at least seasonally omnivorous in
22 certain parts of their geographic range where they take nectar from cactus flowers and eat cactus
23 fruit pulp and seeds. Until recently, mesquite bugs were primarily tropical-subtropical
24 inhabitants of Mexico and Central America but have since occupied the southwestern United
25 States where mesquite trees occur. Using a noninvasive method, we investigated the bats' diet at
26 the Cienega Creek Natural Preserve, Arizona, by collecting food parts discarded beneath three
27 night roosts in soil-piping cavities in a mesquite bosque. We also made phenological and
28 behavioral observations of mesquite bugs, *Thasus neocalifornicus*, and their interactions with the
29 mesquite trees. We determined that the bats discarded inedible parts of 36 species in 8 orders of
30 mainly large-bodied and nocturnal insects below the night-roosts. In addition, one partial bat
31 wing represents probable predation upon a phyllostomid bat, *Choeronycteris mexicana*. About
32 17 of the insect taxa are newly reported as prey for pallid bats, as is the bat *C. mexicana*. The
33 majority of culled insect parts (88%) were from adult mesquite bugs. Mesquite bug nymphs did
34 not appear in the culled insect parts. After breeding in late summer, when nighttime low
35 temperatures dropped below 21°C, the adult bugs became immobile on the periphery of trees
36 where they probably make easy prey for opportunistic foliage-gleaning pallid bats. Proximity of
37 night-roosts to mesquite bug habitat probably also enhances the bats' exploitation of these
38 insects in this location.
39
40

41   INTRODUCTION
42
43   The pallid bat, *Antrozous pallidus*, is widespread in western North America in arid to
44   semiarid, rocky habitats, open deserts, and oak and pine forest. Previous studies have shown that
45   this species is generally a predator on arthropods, especially insects. However, pallid bats are
46   opportunistic and flexible, occasionally taking fruit from organ pipe cactus (*Stenocereus*
47   *thurberi*) and cardón (*Pachycereus pringlei*) in the Southwest, and at least incidentally, they also
48   take pollen and nectar from flowering columnar cacti (Howell, 1980; Herrera et al., 1993;
49   Simmons & Wetterer, 2002; Frick et al., 2009, 2013, 2014; Aliperti et al., 2017) and probably
50   agaves (Ammerman et al., 2012). Most often, pallid bats prey upon relatively large, flightless
51   arthropods; occasionally they also eat small vertebrates (Engler, 1943; Orr, 1954; O'Shea &
52   Vaughan, 1977; Bell, 1982; Lenhart et al., 2010; Rambaldini & Brigham, 2011). Some of these
53   prey items are taken during a brief touchdown or are gleaned from foliage during flight. Pallid
54   bats use a characteristic searching flight that usually involves relatively slow and maneuverable
55   flying about 0.5-2.5 m above the ground while making rhythmic rises and dips interspersed with
56   swoops and glides when the bat detects prey (O'Shea & Vaughan, 1977). Occasionally the bats
57   hover near low or thorny vegetation, or land on the ground where they are quite agile at using a
58   variety of gaits and strides to pursue prey. This foraging style carries high risks of injury and
59   predation for the bats, whose wing membranes and bones heal but show scars and deformities
60   (Davis, 1968). While preying upon scorpions and centipedes they also endure venomous stings
61   to the face and other body parts (Hopp et al., 2017). Previous authors (O'Shea & Vaughan, 1977)
62   showed that pallid bats eat arthropods that share at least two of four characteristics: (1) large
63   size; (2) either obligatorily or primarily active on the ground surface; (3) fly weakly at low
64   heights; or (4) fly strongly but often land on vegetation. The bats frequently retreat to a night
65   roost to rest or manipulate and eat the prey they have caught. They alight on the ceilings of rock
66   shelters, overhangs, or small grottos temporarily to process their prey. The bats drop undesired
67   parts of the arthropods such as wings, elytra, and legs. The discarded items provide qualitative
68   data on pallid bat diets (e.g., Orr, 1954; Ross, 1961, 1967; O'Shea & Vaughan, 1977; Bell, 1982;
69   Lenhart et al., 2010), although Johnston & Fenton (2001) found that the insects represented in
70   the culled parts were biased toward the hardest and largest prey species eaten relative to species
71   represented in fecal pellets. In this study, we investigated food habits of pallid bats in
72   southeastern Arizona and made observations on their interactions with the predominant insect in
73   their local diet, the mesquite bug *Thasus neocalifornicus*. We add to the list of arthropod and
74   vertebrate prey known to be taken by pallid bats. Importantly, we document observations
75   relevant to an example of these bats feeding opportunistically on large numbers of mesquite
76   bugs, as well as the first record in the wild of their feeding on another species of bat in
77   southeastern Arizona. We also provide observations of certain mesquite bug behaviors that may
78   increase their susceptibility to the foraging style of pallid bats.
79   As gleaning bats that hunt arthropods moving or resting on plant or ground surfaces,
80   pallid bats have well-developed acoustical, olfactory, and visual senses. They mainly locate their
81   prey by sound, either through active echolocation or passive detection of the faint sounds made
82   by moving prey (O'Shea & Vaughan, 1977). In experiments with insects and their pheromones
83   other than those of mesquite bugs (*Thasus* spp.), pallid bats are also sensitive to olfactory cues
84   and are able to distinguish prey odors from controls and from non-prey species (Johnston, 2002).
85   The bats show selectivity upon closely approaching certain prey insects versus a non-prey
86   noxious insect (the Pinacate beetle *Eleodes*: Tenebrionidae) or paper balls impregnated with their

87   odors (Johnston, 2002). The bats also have relatively large eyes and high visual acuity at low
88   light levels (Bell & Fenton, 1986).
89   Pallid bats previously were reported to take certain leaf-footed bugs (Heteroptera:
90   Coreidae) only occasionally. Coreids are globally distributed but mostly subtropical and tropical
91   insects, with about 80 species in the continental United States and Canada (Froeschner, 1988).
92   One member genus, *Thasus* (Coreinae: Nematopini), has eight species primarily distributed in
93   the Neotropics (Forbes & Schaefer, 2003). Like many other Hemiptera, Coreidae are herbivores
94   that suck the contents of plant tissues (Froeschner, 1988). Many coreids are also host specific,
95   feeding on one or two families of plants (Froeschner, 1988). The only species of *Thasus* in the
96   United States is *Thasus neocalifornicus* (giant mesquite bug); the species also occurs in Baja
97   California and Sonora and Chihuahua, Mexico (Forbes & Schaefer, 2003). The closely related
98   species *Thasus gigas* and *Thasus acutangulus* occur further south in Mexico and Central
99   America; these two species were once considered synonymous with *T. neocalifornicus* but have
100   since been shown to be distinct (Brailovsky & Barrera in Brailovsky et al., 1995; Forbes &
101   Schaefer, 2003). *Thasus neocalifornicus* is ecologically tied to mesquites (*Prosopis*, Fabaceae;
102   De La Torre-Bueno, 1945; Ward et al., 1977; Schuh & Slater, 1995; Brummermann, 2010).
103   Mesquite trees have spread widely in the United States during the last two centuries along with
104   cattle (Turner et al., 2003), providing the potential for the bugs to expand their geographic range.
105   Schaefer & Packauskas (1998) speculated that the United States populations of *T.*
106   *neocalifornicus* in Arizona might have been an accidental introduction by humans. The species
107   has been recorded in Arizona since at least 1876 (Forbes & Schaefer, 2003) and is now also
108   known north of Mexico from California to Texas (https://bugguide.net/node/view/20163).
109   As a brief synopsis of the known ecology and annual phenological cycle of *T.*
110   *neocalifornicus* relative to their host plant, mesquite bugs are univoltine (having one generation
111   per year and overwintering as eggs; Jones, 1993). Eggs eclose in February, and nymphs
112   aggregate around the eggs to use up the rest of the egg reserves and feed. Nymphs aggregate
113   using specialized pheromones (adults do not respond to the pheromones in tests), and secrete
114   malodorous, toxic compounds in self-defense and possibly as alarm chemicals to alert
115   conspecifics against predator attacks. The nymphal toxins are effective on insect predators in
116   tests; tests do not seem to have been made on vertebrate predators (Prudic et al., 2008). Nymphs
117   feed on mesquite leaves and pods (once available), and molt through their first-fifth instars from
118   January-July; they often migrate to the base of their host trees in summer, probably in response
119   to high afternoon temperatures (Jones, 1993). Mesquites flower from February-March, and bear
120   fruits (bean pods) from July-October. As nymphs, mesquite bugs are unable to fly and are
121   aposematically colored red, white, and brownish or blackish to advertise their noxious secretions.
122   The coloration probably deters visually oriented diurnal predators such as birds and larger
123   invertebrate predators. Although the warning coloration might be visible to bats during twilight
124   hours, night-active bats might be repelled by the nymphs' noxious secretions. The nymphs often
125   stay under the foliage on the spiny branches of the mesquite canopy; they also form defensive
126   aggregations that secrete noxious fluid from their abdomens, similar to a related species, *T.*
127   *acutangulus* in Central America (Aldrich & Blum, 1978). The adults first start to appear from the
128   fifth nymphal instars around July-August, with the highest proportion of adults between May-
129   September. By contrast with the nymphs, the adult mesquite bugs are large and dark colored
130   (blackish brown and dark reddish) and no longer secrete the chemicals that are toxic to small
131   insect predators. Instead, the adults secrete a different set of noxious chemicals from those of the
132   nymphs to trigger aggregations and in response to a simulated predator disturbance. These

133   chemicals include hexyl acetate, hexenal, and hexanol (Prudic et al., 2008; Noge, 2015). Adult
134   pheromones are not toxic or deterrent to insect predators but might deter vertebrates such as
135   birds, a major group of predators on adult heteropteran insects (Prudic et al., 2008). Adult
136   mesquite bugs feed in the mesquite trees until late summer, then breed and lay eggs on mesquite
137   stems and under bark in late summer-early fall. Females start ovipositing around August and
138   continue through October, when the mesquite trees start dropping their leaves (October-January).
139   They overwinter only in the egg stage (Jones, 1993).
140   During 1994-1996, in the process of studying bats roosting in soil-piping cavities in
141   southern Arizona (Van de Water & Peachey, 1997), we observed reddish guano and culled wings
142   of mesquite bugs beneath a pallid bat night roost. Collecting these discarded fragments
143   eventually grew into the present contribution to knowledge of the behavior of mesquite bugs and
144   the diet of pallid bats.
145
146
147   MATERIALS AND METHODS
148
149   In the process of observing and studying Mexican long-nosed bats at the Cienega Creek Natural
150   Preserve under Arizona Game and Fish Commission permit I-96-024, one of us (WDP)
151   discovered guano and insect parts beneath a night roost of pallid bats in one of several soil-
152   piping cavities. Realizing the potential of these discarded remains to bolster knowledge of the
153   diet of pallid bats in this area, we searched for other such night feeding roosts in the local area
154   and opportunistically revisited them to collect the prey remains while the bats were absent.
155
156   **Study area**
157   A small remnant mesquite bosque (bottomland forest) occurs at 1030-1060 m elevation in an
158   abandoned meander of Cienega Creek, in the Cienega Creek Natural Preserve (CCNP), southeast
159   of Tucson in Pima County, Arizona. Dominant plants in the bosque are velvet mesquite
160   (*Prosopis velutina*) and graythorn (*Zizyphus*). Adjacent to the bosque, Cienega Creek flows
161   above ground for parts of its reach where there are surface outcroppings of porphyritic andesite
162   at the upstream and downstream limits of the reach. There the creek forms a riverine marsh or
163   ciénaga, one of few remaining perennial reaches of the stream, and a disappearing habitat feature
164   in the desert southwest (Turner, 1974; Hendrickson & Minckley, 1984). The riparian area is
165   dominated by tree species such as cottonwood (*Populus*), willow (*Salix*), ash (*Fraxinus*),
166   mesquite, and the shrubs seepwillow (*Baccharis*) and sumac (*Rhus*). Cattails (*Typha*) grew in the
167   water of the ciénaga. The bosque grows on a low Quaternary terrace 2-10 m above the stream
168   channel and abruptly separated from it by vertical banks. On adjacent gravelly hills is semi-
169   desert grassland and desert scrub with palo verde (*Cercidium*) and saguaro (*Carnegiea*), accented
170   by species of yucca (*Yucca*), agave (*Agave*), acacia (*Acacia*), and ocotillo (*Fouquieria*), with
171   occasional juniper (*Juniperus*). Foothills of the Rincon Mountains occur to the north and bear
172   junipers and oak woodland at higher elevations.
173   The relative representation of trees and many other plants in this area was strongly
174   changed in historic times after colonization; the extensive removal in the 1800s of oaks and
175   junipers for railroads and livestock overgrazing resulted in an increase in the density of
176   mesquites (Bahre & Hutchinson, 1985; Turner et al., 2003). As a result, Cienega Creek became
177   entrenched and presently flows at a lower level than it did during and prior to the 1800s. The
178   lowering of the water table, headward erosion, and subsurface withdrawal are removing the soil

179 beneath the mesquite trees, exposing their roots, gullying the terraces and bosque, and forming a
180 pseudokarst terrain with natural bridges, blind and interrupted reaches, sinkholes, and
181 underground cavities through soil-piping action (Fig. 1). In CCNP, the cavities provided roosting
182 sites for night-roosting pallid bats in the summer time, as well as refuges or nesting areas at
183 various times of year for other species including other bats (*Choeronycteris mexicana,*
184 *Corynorhinus townsendii,* and *Myotis velifer*), woodrats (*Neotoma albigula*), javelinas (*Pecari*
185 *tajacu*), skunks (*Conepatus leuconotus* and *Mephitis macroura*), and a small unidentified bird
186 (personal observations). In the immediate vicinity of the soil-piping cavities, plants included
187 mesquite, graythorn, desert broom (*Baccharis*), cholla cactus (*Cylindropuntia*), grasses, and
188 small herbaceous plants. The vegetation is essentially the same on top of the flat terrace as in the
189 bottoms of the eroding gullies, except that mesquites are absent in the gully systems. As the soil
190 continues to erode, the soil-piping cavities seem to be ephemeral and might eventually disappear
191 as roosting areas for bats. Episodic roof collapse from the ceilings of the soil-piping cavities
192 occasionally covered the insect parts dropped by the bats.
193   In September 2002, we observed mesquite bugs on and under mesquite trees along a
194 normally dry tributary of Cienega Creek that had flooded the previous night during a rainstorm.
195 We also made casual observations of pallid bats in 2001 and 2002 at a day roost that was
196 discovered in the porch of a caretaker's residence at the nearby Colossal Cave Mountain Park.
197 This building roost was about 5 km distant from the soil-piping cavities at CCNP and at an
198 elevation of 1095 m, about 60 m higher than the soil-piping cavities. Although this porch served
199 mainly as a day roost, it was also sometimes used as a night roost by pallid bats.
200
201 **Collecting methods**
202 Insect parts were first noted by one of us (WDP) in 1994 in one of the soil-piping cavities at
203 Cienega Creek. In 1996, WDP discovered two additional cavities with accumulations of insect
204 fragments and made sightings of *A. pallidus*. We chose to study the culled insect parts discarded
205 by the pallid bats as a non-intrusive method of determining the macro-arthropodophagous diet in
206 this bat population. Pallid bats are sensitive to disturbance at their roosts (Arroyo-Cabrales & de
207 Grammont 2017; O'Shea & Vaughan 1977), thus we collected insect remains at a night roost not
208 used by the bats during the daytime as a way to avoid interference in their activity. The pallid
209 bats were usually absent from the soil-piping cavities when we collected samples in the daytime
210 except on one occasion in September 2002 when we observed two individuals. We visited the
211 cavities and collected insect parts once in November 1996, once in January 2001, twice, in
212 February and September 2002, and once in September 2004. These did not represent seasonal
213 samples but were merely times at which we were able to visit the soil-piping cavities and collect
214 the remains that had accumulated since our previous visit. We collected all pieces from the larger
215 concentrations of pallid bat prey that could easily be picked up by hand for later identification
216 and to sample the overall diversity of species eaten, but also to estimate the relative abundance in
217 the diet of the different insect species. Although this method possibly misses some smaller
218 insects taken in aerial hawking flight (not a preferred mode of foraging for pallid bats; O'Shea &
219 Vaughan, 1977; Johnston & Fenton, 2001), our study reinforces previously published data about
220 the contribution of prey brought into night roosts to the total diet of pallid bats. We identified
221 insect parts by comparison with intact museum specimens in the Oklahoma Museum of Natural
222 History, Section of Recent Invertebrates, with descriptions in the literature, and with digital
223 images and relevant data archived online (e.g., www.Bugguide.net). Individual prey parts and
224 specimens collected in this study will be accessioned into the Department of Recent

225 Invertebrates at the Sam Noble Oklahoma Museum of Natural History, where the data will be
226 cataloged and made freely available to the public through GBIF and iDigBio online portals.
227   On 11 September 2002 we made observations and photographed mesquite bug behavior
228 in the mesquite bosque in late afternoon and early evening. We observed apparent end-of-season
229 mating and mortality of adult insects. We also recorded air temperatures and relative humidity
230 with a handheld electronic sensor outside one of the pallid bat night-roosting cavities during the
231 sundown-to-dark transition period to investigate the relationship of temperature and humidity on
232 adult activities late in the season. On the same date, we collected several of the dead and dying
233 mesquite bugs as voucher specimens. We inferred the sex of the mesquite bugs eaten using
234 sexually dimorphic hind leg parts (Schuh & Slater, 1995).
235
236
237 RESULTS
238
239 Among the insects observed at CCNP, mesquite bugs were common in the bosque, active and
240 feeding on mesquites. They followed the typical phenological cycle for tropical areas described
241 in the Introduction. We observed mesquite bugs as nymphs only early in the warm season (Fig.
242 2). By late summer and early fall, all *Thasus* observed in the ciénaga area were adults. In late
243 summer the mesquite bugs could be seen flying all over the bosque, alighting on the trees, and
244 mating. When summer heat slowed, evapotranspiration was high, and there was a marked
245 diurnal-nocturnal temperature shift. Cooler air drains from the nearby mountains and a strong
246 down-canyon breeze flows into the bosque and ciénaga. By the end of September and early
247 October, the bugs continued mating but appeared to be succumbing to end of season mortality,
248 possibly due to intolerance of the decreasing nighttime temperatures. At this time of year they
249 became inactive at night and remained exposed on the periphery of the canopy. On 11 September
250 2002, after the first few nights during which the temperatures started to drop below about 21°C
251 and the bugs were clustered out on the edges of the branches, we observed individuals become
252 immobile while mating, laying eggs, dying, and falling to the ground (Fig. 2). During the
253 sundown-to-dark transition period on this same date, air temperature decreased by 4.2°C, from
254 25.2° to 21.0°, while relative humidity increased by 16%, from 69% to 85%. Upon examination,
255 the fallen bugs on the ground beneath mesquites occurred singly or sometimes in mated pairs
256 (one male and one female in each case). We collected three pairs of the dead ones off the ground
257 as voucher specimens.
258   By 29 September 2002, no live adult mesquite bugs were present in the vicinity of the
259 roosting cavities of CCNP. This was probably due to cold air drainage through the bottomland,
260 because live adults were active in nearby upland areas on the same date. On this date, pallid bats
261 also night-roosted on the caretaker's building porch in the upland, and many moth wings but no
262 mesquite bug parts were observed beneath the bats. On the night of 1 October 2002, the bats
263 were again present in the porch roost but no new culled insect parts appeared, and the number of
264 pallid bats dwindled until 7 October when only 1 or 2 were present, and no guano was present.
265   Pallid bats used only three of six available soil-piping cavities in the CCNP mesquite
266 bosque as night roosts during our study, although the other three cavities were sometimes
267 utilized by other species of bats, especially *Choeronycteris mexicana* (Mexican long-tongued
268 bat) in the summer. The soil-piping cavities (Fig. 1) offered several characteristics that make
269 them suitable as night roosts for pallid bats: (1) enclosed space providing protection from the
270 weather and nocturnal flying predators; (2) easy access with from one to three entrances of

271   relatively large dimensions; (3) relatively spacious interior (in this aspect the cavities were
272   somewhat like the daytime roosts described by Vaughan & O'Shea, 1976) mostly unobstructed
273   except for occasional exposed mesquite roots; (4) high ceilings and steep walls, providing safety
274   from ground and climbing predators, respectively; (5) rough ceiling surface texture providing
275   secure grip for the bats' claws while processing prey; (6) proximity to the bats' foraging area, and
276   to at least one observed day roost.
277   Within the soil-piping cavities, the insect pieces dropped by the bats were concentrated
278   across a small area of the floor on clods of collapsed soil that had fallen from the ceiling (Fig. 1c,
279   d). Large guano pellets, often stained red from the mesquite bugs, attributable to the pallid bats
280   occurred within the concentrations of culled insect parts on the floor of the cavities. Uncommon
281   and scattered insect parts were occasionally found distant from these concentrations in the same
282   soil-piping cavities, and probably represented prey remains culled by other species of bats. Three
283   other species of bats were observed using the cavities rarely. Two of these were smaller species
284   than *Antrozous pallidus* (which has a body weight of 20-35 g; Harvey et al., 2011). On one
285   occasion, we observed four cave myotis, *Myotis velifer* (12-15 g) clustered in a small soil pipe in
286   the ceiling not far from one of the cavities used by *A. pallidus*. On two consecutive days in
287   January 2001 in a different area we observed an individual of Townsend's big-eared bat,
288   *Corynorhinus townsendii* (8-14 g), in hibernation. Because the isolated insect fragments could
289   have represented feeding by these other species, they were not collected or included in our study.
290   The guano pellets of these smaller bat species were smaller than pallid bat guano and were never
291   stained red like the pallid bat scats. For pallid bats, mean scat diameter = 3.1 mm, mean length =
292   7.8 mm (*n* = 23); for Townsend's big-eared bats, mean diameter = 1.9 mm, mean length = 3.8
293   mm (*n* = 7); for cave myotis, mean diameter = 2.0 mm, mean length = 4.0 mm (*n* = 14). The
294   Mexican long-tongued bat, *C. mexicana* (10-25 g), also used soil-piping cavities at CCNP, but it
295   was never found roosting in the same cavity as pallid bats. The Mexican long-tongued bat is a
296   specialized nectar and pollen feeding bat whose guano lacks visible insect fragments, is primarily
297   composed of pollen sometimes with bits of anthers and filaments from the stamens, and forms
298   yellowish or reddish-brown splats beneath its roosts rather than pellets, similar to that of other
299   nectar-and-pollen feeding bats (pers. observ.). Large, red-stained guano pellets exactly like the
300   pallid bat scats in the soil-piping cavities accumulated on plastic sheets laid beneath the roost on
301   the porch of the caretaker's building, indicating that at times, both groups of pallid bats were
302   feeding on mesquite bugs.
303   Only one non-insect prey item was found beneath the pallid bat night roosts, a partial bat
304   wing with metacarpals II-III-IV, phalanges, and a bit of attached membrane of the wing tip. The
305   proximal ends of the metacarpals are morphologically distinct from those of the vespertilionid
306   bats of the Cienega Creek area, and represent those of the phyllostomid, *Choeronycteris*
307   *mexicana*. The distal ends of the metacarpals and the phalanges have the epiphyses completely
308   fused, indicating an adult bat. The skin attached to the wing bones showed some signs of feeding
309   by decomposer arthropods, indicating that the wing had been beneath the pallid bat roost for
310   some time before it was collected in February 2004.
311   Pallid bats foraging in and around the mesquite bosque clearly used the soil-piping
312   cavities as a place to hang and process insects they catch. Pallid bats are equipped with robust
313   jaws and teeth for their body size, including longitudinally curved, tapered canines with four
314   heavy crests or flanges on the anterior, lingual, posterior, and labial surfaces running from the
315   apex to the base of the tooth crown, with deep furrows between all except the anterior and labial
316   flanges (Fig. 3a-b). These canines are adapted for procuring and puncturing the exoskeletons of

317 hard-bodied insects. The flanges of the canines create stress and propagate cracks in the chitin,
318 making it easier to penetrate the exoskeleton (see Freeman, 1979; 1992; 1998; Freeman &
319 Weins, 1997) and subdue an insect. The tooth marks of the bats are readily seen on many of the
320 culled fragments (Fig. 3c-i).
321   At Cienega Creek, pallid bats fed on at least 36 species of large insects (approximately
322 25-60 mm body length) based on parts discarded beneath the night roosts (Table 1). Of these
323 insects, 20 taxa are reported for the first time in the diet of *A. pallidus*. No arthropod groups
324 other than insects were represented. All exoskeletal parts appeared to be those of adult insects.
325 We found no evidence that the pallid bats fed upon the noxious nymphs of mesquite bugs. The
326 insects eaten include mainly night-active forms, many of which are ground dwelling, although a
327 few diurnal taxa including several grasshoppers, two long-horned beetles, and a dragonfly were
328 taken.
329   In terms of relative abundance, the vast majority of insects consumed by pallid bats at all
330 three cavity roosts were adult mesquite bugs. This insect also accounted for many of the bat
331 guano pellets being reddish. Of 483 total identified insect parts, 429 (88.8% frequency) were of
332 mesquite bugs. All body parts of the mesquite bugs are represented, but mostly the least
333 nutritious and most chitinous portions (wings, legs, antennae) were discarded; relatively few
334 abdomens were found beneath the bat roosts (Table 2). Thus, pallid bats were eating mainly the
335 abdomens of the mesquite bugs. Interestingly, the relatively few available remains of *Thasus*
336 abdomens showed that the softer, ventral portion was selectively eaten and the remainder of the
337 abdomen discarded. Of the identified *Thasus* parts, 272 forewings (Table 2) indicate a minimum
338 of 136 individual mesquite bugs eaten. In most samples there were more male than female
339 mesquite bug hindleg elements, although in one sample there were more female than male
340 hindleg elements. For insect species other than mesquite bugs, relative abundance was low,
341 representing only one to four individuals of most species. One exception to this was the gray bird
342 grasshopper, *Schistocerca nitens*, represented in February 2002 by 19 forewings and 57
343 hindwings.
344
345
346 DISCUSSION
347
348 Ross (1967) and subsequent authors have compiled a long list of arthropod prey species taken by
349 pallid bats. Our results add 18 taxa not previously recorded as pallid bat prey to the overall list.
350 Pallid bats in our study fed upon large moths as well as large beetles; Freeman & Lemen (2007)
351 indicated that beetles were about 3.2 times harder than moths of the same body size, but that
352 body size or volume of the insect also was important in cuticle toughness. Freeman & Lemen
353 (2007) hypothesized that, as aerial feeders, some bats must limit the upper size of insects they
354 eat, because insects that are too large cannot be processed orally in flight, especially for a bat
355 species that depends on being able to continue echolocating to fly. Some bats might capture prey
356 that are too tough to process in flight and must land to process them. These authors also
357 hypothesized that harder insects might take longer for bats to chew and thus limit the upper size
358 of certain taxa of insects taken, which varies among insect taxa.
359   In our study, the higher numbers of large, armored, and cumbersome legs and other body
360 parts of mesquite bugs found beneath roosts relative to other taxa of insects suggests that
361 mesquite bugs are more difficult for pallid bats to process than other kinds of insects. Mesquite
362 bugs have a small head, thorax, and abdomen with large legs relative to most of the beetles and

363 moths in the bats' diet. Perhaps the relative ease with which mesquite bugs are located or secured
364 in late summer or early autumn counterbalances the energy and time needed to commute to a
365 night roost to process them. The size and hardness of the insects eaten by pallid bats suggests
366 there is a large upper size limit to what insects pallid bats are capable of processing and eating.
367 Mesquite bugs (*Thasus*) are among the largest terrestrial heteropterans known (Forbes &
368 Schaefer, 2003) and are 28-43 mm in body length. The relative abundance of their body parts
369 recovered in the soil-piping cavities leads us to hypothesize that the availability of the cavities
370 and their proximity to the mesquite bosque enhanced their usage by pallid bats as a place to
371 process a seasonally abundant source of food.
372 As noted above, most of the insects eaten by the pallid bats are nocturnal, although
373 several species represented in our study are diurnal. Most day-active insects are inactive at night.
374 Therefore, for bats that must be able to hear prey-generated sounds of motion to find prey, our
375 prey list largely supports the assertion of Fuzessery et al. (1993) that pallid bats are hunting
376 primarily with sound cues and are less dependent on visual cues. Many of the large insects
377 consumed by pallid bats in this study make noise in flight, while others have been variously
378 described as noisy fliers (e.g., *Cotinis mutabilis*; Tallamy, 2009).
379 Furthermore, in spiny mesquite foliage, the bats probably avoid flying in the understory
380 or within the tree canopy to hunt for prey they cannot hear. The risk of injury is too high unless
381 they can be certain there is potential food available there, like katydids, mesquite moths, and
382 mesquite bugs.
383 As adults, mesquite bugs do not secrete the same compounds as a defense against insect
384 predators that they do as nymphs. Most insect predators are not interested in the non-toxic adults
385 because the bugs are so big. For the mesquite bugs, it might not be evolutionarily worthwhile to
386 invest energy in producing toxic compounds against other insect predators when it is
387 unnecessary. The adult bugs switch to a defense of muted colors (thus being more cryptic to
388 visually-oriented aerial predators), and a physically more armored exoskeleton (spiny hind legs,
389 tougher wings), but less noxious chemicals than nymphs. We hypothesize that this is not
390 necessarily a change to prevent predation as much as a trade-off of putting less investment in
391 defense (producing energetically expensive coloration and toxins) and more investment into
392 reproduction (wings provide mobility to find mates, less toxic chemical investment for short
393 period of mating and death).
394 As noted earlier, in laboratory experiments pallid bats showed an aversion to the odor of a
395 Pinacate beetle *Eleodes* (Johnston, 2002); however, at least one species of *Eleodes*, *E.*
396 *acuticauda*, has been reported as a prey item for pallid bats (Orr, 1954:232), and the genus also
397 appeared as prey in our study. Perhaps the bats are able to process and discard the noxious parts
398 of certain insects as well as the armored hard parts. Although the chemicals secreted by adult
399 mesquite bugs differ from those of nymphs (chemical components frequently change after
400 metamorphosis; Noge, 2015), the adult compounds have not been tested with vertebrates, so it is
401 unknown whether the chemicals produced by the adult bugs actually deter vertebrate predators
402 (Prudic et al., 2008). Of the secretions produced by the adult bugs (hexyl acetate, hexanal, 1-
403 hexanol and possibly others), hexyl acetate and hexanal might be aggregational pheromones
404 directed toward other mesquite bugs (Prudic et al., 2008; Noge, 2015). Given that pallid bats in
405 our study never ate nymphs, the nymphal secretions might be effective not only against insect
406 predators but also against bats. And given the frequency with which pallid bats ate the adults,
407 either the adult bugs are non-noxious to pallid bats or else the bats are not susceptible or averse
408 to their secretions.

409   The only non-insect prey item found at a pallid bat night roost in this study was another
410   bat, the flower-visiting phyllostomid *Choeronycteris mexicana*. As noted above, *C. mexicana*
411   utilized separate but adjacent soil-piping cavities at CCNP in summers during our study. There is
412   one previous record of pallid bats eating a Mexican free-tailed bat, *Tadarida brasiliensis*,
413   although the predation occurred while the two species were in captivity, being held together in
414   the same cage from which the smaller free-tailed bats were unable to escape (Engler, 1943).
415   Thus, the *C. mexicana* at CCNP is the first recorded instance in the wild of predation by *A.*
416   *pallidus* on another species of bat.
417   Many kinds of animals take advantage of situations arising as they acquire food (Young,
418   2012). Like many predators, various species of bats are opportunistic on hatches of insects (e.g.,
419   *Myotis* [Vespertilionidae], Fenton & Morris, 1976; *Lavia frons* [Megadermatidae], Vaughan &
420   Vaughan, 1986; Dial & Vaughan, 1987; *Taphozous melanopogon* [Emballonuridae],
421   *Hipposideros* sp. [Hipposideridae], and *Scotophilus temminckii* [Vespertilionidae], Gould, 1978;
422   *Hipposideros gigas* [Hipposideridae], Vaughan, 1977; *Nycteris grandis* [Nycteridae], Fenton et
423   al., 1993) and also passively use sounds produced by the insects rather than actively echolocating
424   them. Several of the large insects preyed upon are noisy fliers, and pallid bats might thus detect
425   them easily. Some, like antlions, are poor fliers as adults (Merlin, 2003). At CCNP, opportunistic
426   feeding was associated with high selectivity for a single prey species that could make wide
427   searches for patches of food energetically worthwhile.
428   The body parts discarded versus parts eaten indicates that pallid bats take the most easily
429   digestible and probably most nutritious parts of mesquite bugs. The abdomens of gravid female
430   bugs filled with egg masses in particular might provide additional protein. When mesquite bugs
431   are clustered and immobile on the periphery of the mesquite canopy, bats can likely capture the
432   bugs easily compared to within the thorny canopy. Mated females move from the periphery
433   deeper into the mesquite tree canopy to find appropriate places to deposit their eggs, and thus are
434   less susceptible to being located and preyed upon compared to males, which might explain the
435   male bias in our samples. The noxious and aposematic defenses of the nymphs, which are unable
436   to fly, render them relatively immune to attack at night by the bats perhaps due to their odor and
437   quieter movements, and to visually-oriented predators like birds during the day (or bats during
438   twilight). By becoming immobile overnight after they alight on mesquite foliage at evening
439   twilight, the bugs might avoid detection by bats. The noisy flight and possibly other movements
440   and activities of the mesquite bugs, beetles, grasshoppers, and other large insects has been little
441   studied and could be an important aspect of the bat-insect relationship. Similarly, the influence of
442   anthropogenic noise (e.g., automobile traffic, railroad noise, air traffic) on a passive-sound-using
443   predator limits the pallid bats' foraging efficiency and potentially their ability to utilize certain
444   areas for foraging (Bunkley & Barber, 2015; Bunkley et al., 2015).
445   Unfortunately, in this study we were unable to collect data seasonally or regularly, but a
446   seasonal or monthly collection of dietary data would provide a good future study to pursue this
447   ecological relationship in greater depth. Moreover, the bats might select mesquite bugs as prey
448   only when the bugs are the most vulnerable: in late summer or early autumn after the adult
449   females laid the eggs for the overwintering generation, and when falling nighttime air
450   temperatures, local cool air drainage from the adjacent mountains and foothills, and high
451   evapotranspiration might slow the insect's activity or mobility. Finally, the overwhelming
452   majority of insects consumed in the night roosts were mesquite bugs locally derived from the
453   mesquite bosque; the bats consumed other kinds of insects almost incidentally. In addition to
454   their ability to endure injuries and heal (Davis, 1968), the dietary plasticity shown by pallid bats

455   across the species' broad geographic range might help to lessen their risk of extinction (Boyles &
456   Storm, 2007) in the face of anthropogenic environmental upset and climate change.
457
458
459   CONCLUSIONS
460
461   The diet of pallid bats can be investigated non-intrusively by visiting their temporary-use night
462   roosts during the day while the bats are away at separate day roosts. However, the night roosts
463   possibly yield evidence only of those foods that are large enough to require transport to a
464   temporary night roost for processing of edible versus inedible parts. Adult mesquite bugs formed
465   the predominant prey for pallid bats at the CCNP. We found no evidence of pallid bats feeding
466   on toxic, aposematically colored nymphal stages of mesquite bugs. Adult mesquite bugs are
467   possibly non-toxic to pallid bats, or perhaps the bats are able to tolerate the less-toxic compounds
468   of the adult bugs. Late-season breeding and postbreeding adult mesquite bugs are exposed near
469   the edges of the mesquite canopy and provide prey for opportunistic, foliage-gleaning pallid bats.
470   After breeding and laying eggs that overwinter in the mesquite trees, moribund adult mesquite
471   bugs begin to become immobile in the trees or drop from the canopy when the nighttime low
472   temperatures at CCNP fell below 21°C. Mesquite bugs are considered to be mostly subtropical-
473   tropical insects that may have invaded the southwestern United States during historic times with
474   the bringing of cattle and spread of mesquite trees; pallid bats at the CCNP are providing an
475   important natural control on the local mesquite bug population. Their exploitation of mesquite
476   bugs is probably enhanced by the proximity of soil-piping caves to the mesquite bosque as a
477   place to process the insects. Pallid bats at the CCNP ate numerous taxa of large-bodied insects,
478   consistent with their diet in many other portions of the bats' range. When mesquite bugs are
479   observable in the local mesquite trees, their procurement by pallid bats can be determined by the
480   presence of large reddish guano pellets 2.5-3.5 mm in diameter beneath local bat night roosts.
481   Insects parts discarded beneath pallid bat roosts can be distinguished from insect parts culled by
482   birds or other predators by distinctive tooth marks on the discarded insect parts. Bats usually ate
483   the abdomen and thorax of mesquite bugs and most consistently discarded the wings and legs. At
484   the CCNP, pallid bats left the remains of no arthropods other than insects. Seventeen taxa of
485   insects were newly identified as prey for pallid bats, and reflect a diversity of local habitats of the
486   CCNP as foraging habitat for the bats. In addition, pallid bats ate an individual of one other local
487   species of bat, the Mexican long-nosed bat, another first recorded instance of such predation for
488   pallid bats.
489
490
491   ACKNOWLEDGMENTS
492

501 Invertebrates at the Oklahoma Museum of Natural History for accessioning and cataloging insect
502 parts. We appreciate the loan of a pallid bat specimen by Brandi S. Coyner and Janet K. Braun of
503 the Collection of Mammals at the Oklahoma Museum of Natural History. We thank Steve
504 Westrop and Roger Burkhalter for the use of their bellows camera with Stackshot rig and focus-
505 stacking software to capture and process images. We appreciate the many contributors to the
506 websites: Arizona: Beetles Bugs Birds and more (Margarethe Brummermann), BugGuide.net,
507 ButterfliesandMoths.org, The Moths of Southeastern Arizona, and Wikipedia for their time and
508 efforts in providing the ease of access and helpful information that proved highly useful in
509 researching habitat and food plants for many of the insects.
510
511
512 REFERENCES
513

514 Aldrich, JR, Blum, MS. 1978. Aposematic aggregation of a bug (Hemiptera: Coreidae): the
515   defensive display and formation of aggregations. *Biotropica* **10**:58-61.
516 Aliperti JR, Kelt DA, Heady PA, Frick WF. 2017. Using behavioral and stable isotope data to
517   quantify rare dietary plasticity in a temperate bat. *Journal of Mammalogy* **98**:340-349.
518 Ammerman LK, Hice CL, Schmidly DJ, Brown C, Altenbach JS. 2012. *Bats of Texas*. College
519   Station, Texas A&M University Press.
520 Arroyo-Cabrales J, de Grammont JC. 2017. *Antrozous pallidus*. The IUCN Red List of
521   Threatened Species 2017-3. http://www.iucnredlist.org/details/1790/0 and
522   http://dx.doi.org/10.2305/IUCN.UK.2017-2.RLTS.T1790A22129152.en
523 Bahre CJ, Hutchinson CF. 1985. The impact of historic fuelwood cutting on the semidesert
524   woodlands of southern Arizona. *Journal of Forest History* **29**:175-186.
525 Bell GP. 1982. Behavioral and ecological aspects of gleaning by a desert insectivorous bat,
526   *Antrozous pallidus* (Chiroptera: Vespertilionidae). *Behavioral Ecology and Sociobiology*
527   **10**:217-223.
528 Bell GP, Fenton MB. 1986. Visual acuity, sensitivity and binocularity in a gleaning insectivorous
529   bat, *Macrotus californicus* (Chiroptera: Phyllostomidae). *Animal Behaviour* **34**:409-414.
530 Boyles JG, Storm JJ. 2007. The perils of picky eating: dietary breadth is related to extinction risk
531   in insectivorous bats. *PLoS ONE* **2**:e672.
532 Brailovsky H, Schaefer CW, Barrera E, Packauskas RJ. 1995 (dated 1994). A revision of the
533   genus *Thasus* (Hemiptera: Coreidae: Coreinae: Nematopodini). *Journal of the New York*
534   *Entomological Society* **102**:318-343.
535 Brummermann M. 2010. Life cycle of the giant mesquite bug, *Thasus neocalifornicus*.
536   http://arizonabeetlesbugsbirdsandmore.blogspot.com/2010/06/life-cycle-of-giant-
537   mesquite-bug-thasus.html Accessed 14 September 2016.
538 Bunkley JP, Barber JR. 2015. Noise reduces foraging efficiency in pallid bats (*Antrozous*
539   *pallidus*). *Ethology* **121**:1116-1121.
540 Bunkley JP, McClure CJW, Kleist NJ, Francis CD, and Barber JR. 2015. Anthropogenic noise
541   alters bat activity levels and echolocation calls. *Global Ecology and Conservation* **3**:62-
542   71.
543 Davis R. 1968. Wing defects in a population of pallid bats. *American Midland Naturalist* **79**:388-
544   395.
545 De La Torre-Bueno JR. 1945. Random notes on *Thasus acutangulus*. *Bulletin of the Brooklyn*
546   *Entomological Society* **40**:83.

547   Dial KP, Vaughan TA. 1987. Opportunistic predation on alate termites in Kenya. *Biotropica*
548   **19**:185-187.
549   Engler CH. 1943. Carnivorous activities of big brown and pallid bat. Journal of Mammalogy
550   **24**:96-97.
551   Fenton MB, Morris GK. 1976. Opportunistic feeding by desert bats (*Myotis* spp.). *Canadian*
552   *Journal of Zoology* **54**:526-530.
553   Fenton MB, Rautenbach IL, Chipese D, Cumming MB, Musgrave MK, Taylor JS, Volpers T.
554   1993. Variation in foraging behavior, habitat use and diet of large slit-faced bats
555   (*Nycteris grandis*). *Zeitschrift für Säugetierkunde* **58**:65-74.
556   Forbes G, Schaefer CW. 2003. Further notes on the genus *Thasus* (Hemiptera: Heteroptera:
557   Coreidae). *Journal of the New York Entomological Society* **111**:235-241.
558   Freeman PW. 1979. Specialized insectivory: beetle-eating and moth-eating molossid bats.
559   *Journal of Mammalogy* **60**:467-479.
560   Freeman PW. 1992. Canine teeth of bats (Microchiroptera): size, shape and role in crack
561   propagation. *Biological Journal of the Linnean Society* **45**:97-115.
562   Freeman PW. 1998. Form, function, and evolution in skulls and teeth of bats. In: Kunz TH,
563   Racey PA, eds. *Bat biology and conservation*. Washington, D.C.: Smithsonian Institution
564   Press 140-156.
565   Freeman PW, Lemen CA. 2007. Using scissors to quantify hardness of insects: do bats select for
566   size or hardness? *Journal of Zoology* **271**:469-476.
567   Freeman PW, Weins WN. 1997. Puncturing ability of bat canine teeth: the tip. In: Yates TL,
568   Gannon WL, Wilson DE, eds. *Life among the muses: papers in honor of James S. Findley*.
569   Albuquerque: University of New Mexico Press 225-232.
570   Frick WF, Heady PA, Hayes JP. 2009. Facultative nectar-feeding behavior in a gleaning
571   insectivorous bat (*Antrozous pallidus*). *Journal of Mammalogy* **90**:1157-1164.
572   Frick WF, Price RD, Heady PA, Kay KM. 2013. Insectivorous bat pollinates columnar cactus more
573   effectively per visit than specialized nectar bat. *American Naturalist* **181**:137-144.
574   Frick WF, Shipley JR, Kelly JF, Heady PA, Kay KM. 2014. Seasonal reliance on nectar by an
575   insectivorous bat revealed by stable isotopes. *Oecologia* **174**:55-65.
576   Froeschner RC. 1988. Family Coreidae; Leach, 1915. In: Henry TJ, Froeschner RC, eds. *Catalog*
577   *of the Heteroptera, or true bugs, of Canada and the continental United States*. New
578   York: E.J. Brill 69-92.
579   Fuzessery ZM, Buttenhoff P, Andrews B, Kennedy JM. 1993. Passive sound localization of prey
580   by the pallid bat (*Antrozous p. pallidus*). *Journal of Comparative Physiology A* **171**:767-
581   777.
582   Gould E. 1978. Opportunistic feeding by tropical bats. *Biotropica* 10:75-76.
583   Harvey MJ, Altenbach JS, Best TL. 2011. *Bats of the United States and Canada*. Baltimore:
584   Johns Hopkins University Press.
585   Hendrickson DA, Minckley WL. 1984. Ciénegas--vanishing climax communities of the
586   American Southwest. *Desert Plants* **6**:130-175.
587   Hermanson JW, O'Shea TJ. 1983. *Antrozous pallidus*. *Mammalian Species* **213**:1-8.
588   Herrera M, Fleming LG, Findley JS. 1993. Geographic variation in carbon composition of the
589   pallid bat, *Antrozous pallidus*, and its dietary implications. *Journal of Mammalogy*
590   **74**:601-606.
591   Hopp BH, Arvidson RS, Adams ME, Razak KA. 2017. Arizona bark scorpion venom resistance
592   in the pallid bat, Antrozous pallidus. *PLoS ONE* **12**:e0183215.

593 Howell DJ. 1980. Adaptive variation in diets of desert bats has implications for evolution of
594   feeding strategies. *Journal of Mammalogy* **61**:730-733.
595 Johnston DS. 2002. Prey discrimination by olfactory cues in the pallid bat (*Antrozous pallidus*).
596   *Bat Research News* **42**:162.
597 Johnston DS, Fenton MB. 2001. Individual and population-level variability in diets of pallid bats
598   (*Antrozous pallidus*). *Journal of Mammalogy* **82**:362-373.
599 Jones WA. 1993. New host and habitat associations for some Arizona Pentatomoidea and
600   Coreidae. *Southwestern Entomologist, Supplement no.* **16**:1-29.
601 Lenhart PA, Mata-Silva V, Johnson JD. 2010. Foods of the pallid bat, *Antrozous pallidus*
602   (Chiroptera: Vespertilionidae), in the Chihuahuan Desert of western Texas. *Southwestern
603   Naturalist* **55**:110-117.
604 Merlin P. 2003. *A field guide to desert holes*. Tucson: Arizona-Sonora Desert Museum Press.
605 Noge K. 2015. Studies on chemical ecology of the heteropteran scent gland components. Journal
606   of Pesticide Science DOI: 10.1584/jpestics.J15-03
607 Orr RT. 1954. Natural history of the pallid bat, *Antrozous pallidus* (LeConte). *Proceedings of the
608   California Academy of Sciences* **28**:165-246.
609 O'Shea TJ, Vaughan TA. 1977. Nocturnal and seasonal activities of the pallid bat, *Antrozous
610   pallidus*. *Journal of Mammalogy* **58**:269-284.
611 Prudic KL, Noge K, Becerra JX. 2008. Adults and nymphs do not smell the same: the different
612   defensive compounds of the giant mesquite bug (*Thasus neocalifornicus*: Coreidae).
613   *Journal of Chemical Ecology* **34**:734-741.
614 Rambaldini DA, Brigham RM. 2011. Pallid bat (*Antrozous pallidus*) foraging over native and
615   vineyard habitats in British Colombia, Canada. *Canadian Journal of Zoology* **89**:816-
616   822.
617 Ross A. 1961. Notes on food habits of bats. *Journal of Mammalogy* **42**:66-71.
618 Ross A. 1967. Ecological aspects of the food habits of insectivorous bats. *Proceedings Western
619   Foundation of Vertebrate Zoology* **1**:205-263.
620 Schaefer CW, Packauskas RJ. 1997. Notes on the genus *Thasus* (Hemiptera: Coreidae). *Journal
621   of the New York Entomological Society* **105**:206-214.
622 Schuh RT, Slater JA. 1995. *True bugs of the world (Hemiptera: Heteroptera): classification and
623   natural history*. Ithaca, New York: Cornell University Press.
624 Simmons NB, Wetterer AL. 2002. Phylogeny and convergence in cactophilic bats. Pages 87-121 In:
625   Fleming TH, Valiente-Banuet A, eds. *Columnar cacti and their mutualists: evolution,
626   ecology, and conservation*. Tucson: University of Arizona Press 87-121.
627 Tallamy DW. 2009. *Bringing nature home: how you can sustain wildlife with native plants*.
628   Portland, Oregon: Timber Press.
629 Turner RM. 1974. Map showing vegetation in the Tucson area, Arizona. *United States
630   Geological Survey, Miscellaneous Investigations Series* MAP I-844-H; scale 1:250000.
631 Turner RM, Webb RH, Bowers JE, Hastings JR. 2003. *The changing mile revisited: an
632   ecological study of changes with time in the lower mile of an arid and semiarid region*.
633   Tucson: University of Arizona Press.
634 Van de Water PK, Peachey WD. 1997. Dietary analysis of the Mexican long tongued bat
635   *Choeronycteris mexicana* using pollen analysis of guano collected in Cienega Creek
636   Natural Preserve. Abstracts of Presentations at the 27th Annual North American
637   Symposium on Bat Research, October 8-11, Tucson, Arizona. *Bat Research News*
638   38:133.

639   Vaughan TA. 1977. Foraging behaviour of the giant leaf-nosed bat (*Hipposideros commersoni*).
640   *East African Wildlife Journal* **15**:237-249.
641   Vaughan TA, O'Shea TJ. 1976. Roosting ecology of the pallid bat, *Antrozous pallidus. Journal*
642   *of Mammalogy* **57**:19-42.
643   Vaughan TA, Vaughan RP. 1986. Seasonality and the behavior of the African yellow-winged
644   bat. *Journal of Mammalogy* **67**:91-102.
645   Ward CR, O'Brien CW, O'Brien LB, Foster DE, Huddleston EW. 1977. *Annotated checklist of*
646   *New World insects associated with Prosopis (mesquite)*. Washington, D.C.: United States
647   Department of Agriculture, Agricultural Research Service, Technical Bulletin no. 1557.
648   Young J. 2012. *What the robin knows: how birds reveal the secrets of the natural world*. Boston:
649   Houghton Mifflin Harcourt.

650   FIGURE LEGENDS
651
652
653   Figure 1 a and b, Two soil-piping cavities developed in the terrace supporting a mesquite
654   bosque on top with mesquite roots being exposed, and grasses in the bottoms, at Cienega Creek
655   Natural Preserve, Arizona. The cavities serve as shelters for a variety of mammals including
656   several species of bats. Cavity in a is dark spot in center of image; cavity in b formed a
657   temporary natural arch. c, Interior of one of the soil-piping cavities showing a scattering of
658   culled insect parts dropped beneath a night roost of *Antrozous pallidus*. d, Close-up view of the
659   scattering; note large numbers of reddish guano pellets (especially within the spotlight from
660   photographer's headlight at lower left), colored by the contents of mesquite bugs, numerous
661   mesquite bug exoskeletal parts, moth wings, and beetle elytra. Photos 1a and 1b by W. D.
662   Peachey; photos 1c-1e by N. J. Czaplewski.
663
664
665   Figure 2 Mesquite bugs, *Thasus neocalifornicus*, at the Cienega Creek Natural Preserve,
666   Arizona. a, *T. neocalifornicus* nymph (5th instar), with aposematic coloration indicating its
667   noxious nature. b, adult, not to same scale as nymph. c, adults mating on a mesquite branch at
668   dusk (with flash). d, breeding adults clustered on the peripheral foliage of mesquite at dusk in
669   September 2002 (with flash). e, scattered dead adults on the ground representing a <24-hour
670   accumulation after a rainstorm had swept away other debris. Photos by N. J. Czaplewski.
671
672
673   Figure 3 a and b, Stereopair photograph of the upper teeth and anterior palate of a skull
674   of *Antrozous pallidus* (anterior is toward the top of the image) showing the robust upper canines
675   with strong longitudinal flanges, which help to penetrate and puncture thick chitin. Incisors and
676   premolars are also visible. c-i, Pieces of the exoskeletons of insects discarded by *A. pallidus*,
677   showing tooth punctures caused by the bats. c, elytron of a beetle *Chrysina gloriosa*
678   (Scarabaeidae); d, Same as c, close-up of area enclosed by red rectangle in c, rotated 90°
679   counterclockwise and enlarged to show tooth punctures. e, elytron of a dung beetle *Dichotomius*
680   *colonicus* (Scarabaeidae). f, hind leg of mesquite bug *Thasus neocalifornicus* (Coreidae). g,
681   elytron of *Cyclocephala* (Scarabaeidae). h, elytron of *Xyloryctes thestalus* (Scarabaeidae). i,
682   head, thorax, and partial elytra of darkling beetle *Stenomorpha marginata* (Tenebrionidae).
683   Scale bar in each image is in mm. Photos by N. J. Czaplewski.
684
685

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. Photos 1a and 1b by W. D. Peachey; photos 1c-1e by N. J. Czaplewski.
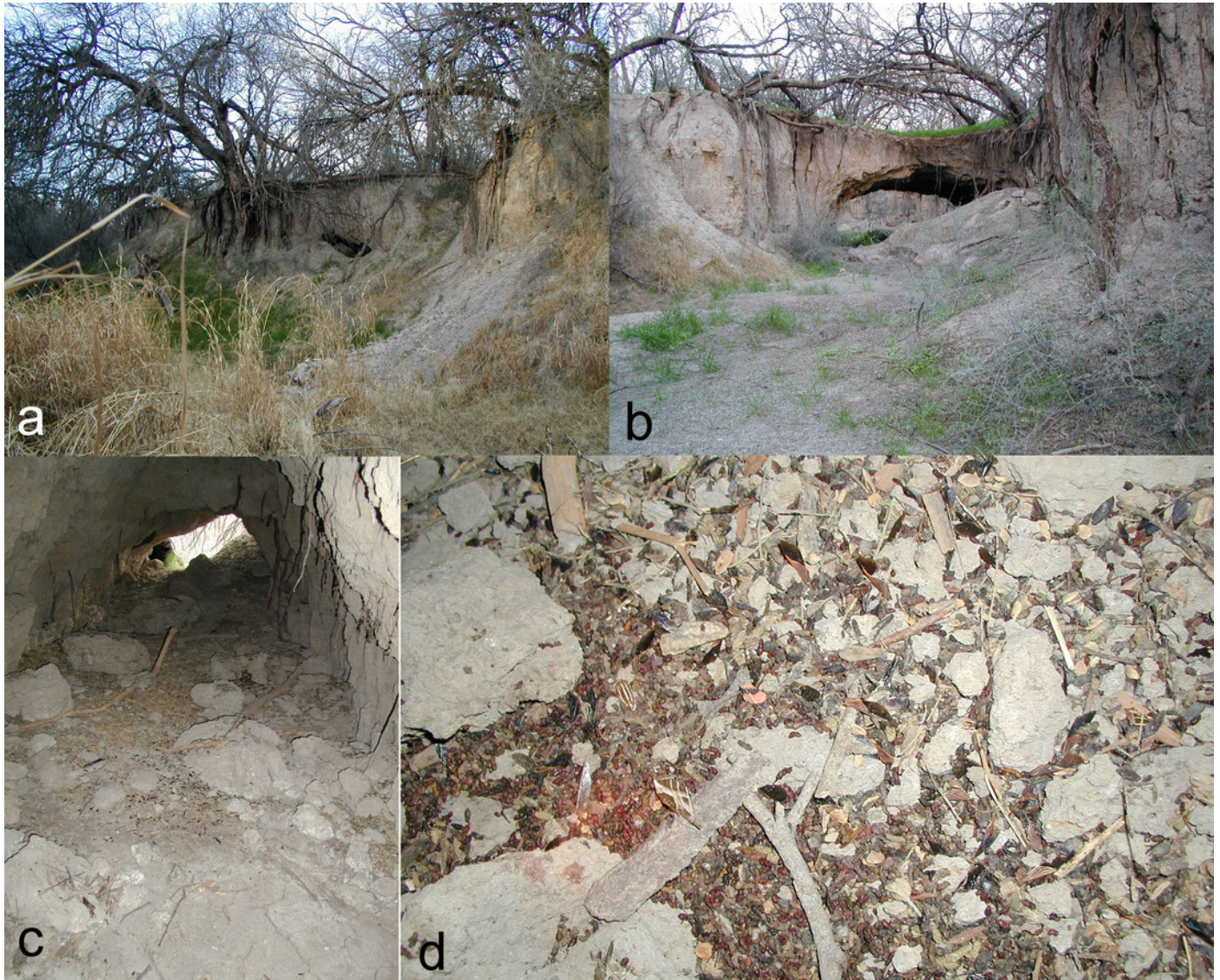
Figure 2

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. Photos by N. J. Czaplewski.
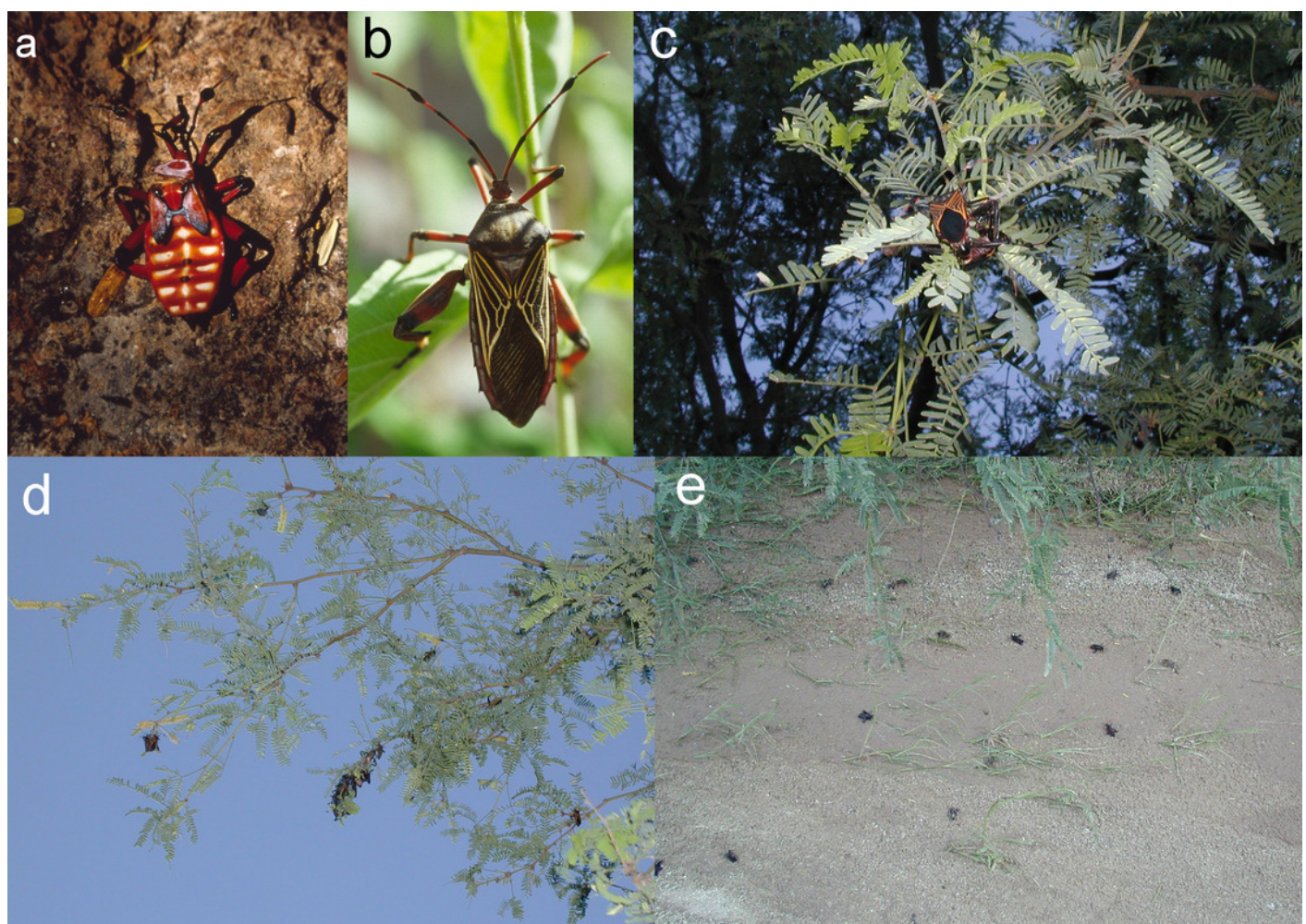
Figure 3

Stereopair of bat teeth and insect fragments.

a and b, 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. c-i, Pieces of the exoskeletons of insects discarded by *A. pallidus*, showing tooth punctures caused by the bats. c, elytron of a beetle *Chrysina gloriosa* (Scarabaeidae); d, Same as c, close-up of area enclosed by red rectangle in c, rotated 90° counterclockwise and enlarged to show tooth punctures. e, elytron of a dung beetle *Dichotomius colonicus* (Scarabaeidae). f, hind leg of mesquite bug *Thasus neocalifornicus* (Coreidae). g, elytron of *Cyclocephala* (Scarabaeidae). h, elytron of *Xyloryctes thestalus* (Scarabaeidae). i, head, thorax, and partial elytra of darkling beetle *Stenomorpha marginata* (Tenebrionidae). Scale bar in each image is in mm. Photos by N. J. Czaplewski.
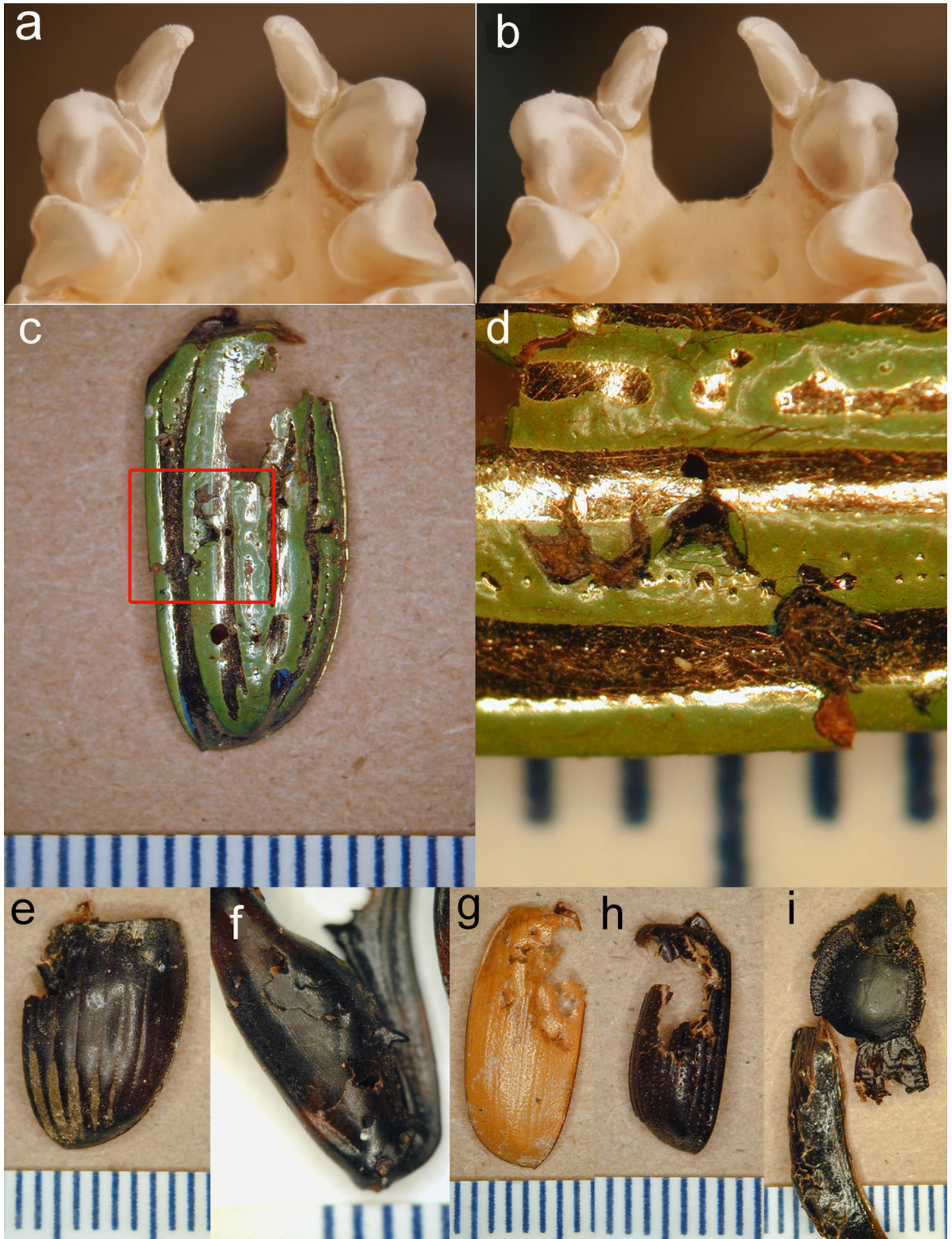
Table 1(on next page)

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

*Indicates new record of prey consumed by pallid bats.

1   Table 1 List of insects and one bat identified from culled body parts deposited beneath
2 pallid bat roosts at Cienega Creek, Arizona. *Indicates new record of prey consumed by pallid
3 bats. Fourth column shows number of identified body parts and percentage of total when over
4 1%.

Hemiptera	Coreidae	*Thasus neocalifornicus* mesquite bug	1303 (88%)
Coleoptera	Scarabaeidae	*Chrysina gloriosa* glorious scarab	1
		Polyphylla decemlineata ten-lined June beetle	4
		Strategus aloeus ox beetle	1
		Strategus sp. ox beetle	12
		Xyloryctes thestalus rhinoceros beetle	1
		Cyclocephala sp. masked chafer	1
		Dichotomius colonicus dung beetle	1
		Cotinis mutabilis green fig beetle	2
		Tomarus sp. carrot beetle	1
		Phyllophaga sp. May beetle	1
	Tenebrionidae	*Stenomorpha marginata* darkling beetle	2
		Stenomorpha sp. darkling beetle	1
		Eleodes sp. Pinacate or darkling beetle	2
	Carabidae	*Calosoma scrutator* fiery searcher	4
		Pasimachus sp. ground beetle	1
	Hydrophilidae	*Hydrophilus* sp. giant black water beetle	1
	Cerambycidae	*Oncideres rhodosticta* mesquite girdler	1
		*Prionini long-horned beetle	1
Orthoptera	Tettigoniidae	*Microcentrum rhombifolium* greater angle-wing katydid	2
		Neoconocephalus triops broad-tipped conehead	17 (1.1%)
		Scudderia mexicana Mexican bush katydid	6
	Acrididae	*Schistocerca nitens* gray bird grasshopper	76 (5%)
		Melanoplus differentialis differential grasshopper	4
		Phlibostroma quadrimaculatum four-spotted grasshopper	1
		Trimerotropis cyaneipennis blue-winged grasshopper	1
Lepidoptera	Sphingidae	*Hyles lineata* white-lined sphinx	6
		Eumorpha vitis vine sphinx	11
		Sphinx sp. sphinx moth	4
		Manduca sexta tobacco hornworm moth	1
	*Tortricidae	Indeterminate leafroller moth	1
	Noctuidae	*Catocala* sp. underwing moth	1
	Saturniidae	*Sphingicampa (=Syssphinx) hubbardi* mesquite moth	1
		Automeris iris iris-eyed silkmoth	1
Neuroptera	Myrmeleontidae	*Vella fallax* antlion	2
Odonata	*Aeshnidae	Indeterminate darner	1
Blattodea	Corydiidae	*Arenivaga* sp. cockroach	1
Diptera	Tipulidae	*Nephrotoma* sp. tiger crane fly	1
Chiroptera	Phyllostomidae	*Choeronycteris mexicana* Mexican long-nosed bat	1

5
6

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.

1   Table 2 Body parts of adult mesquite bugs (*Thasus neocalifornicus*) discarded by night-
2   roosting pallid bats and collected in soil-piping cavities in Cienega Creek Natural Preserve on
3   three visits between January 2001 and September 2002, in decreasing order of abundance. F =
4   female, M = male.
5

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

6