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Antrozous pallidus.

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Antrozous Allen, 1862

Antrozous Allen, 1862:248. Type species *Vespertilio pallidus* by original designation. LeConte, 1856. Type locality "El Paso, El Paso Co., Texas."

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Vespertilionidae, Subfamily Nyctophilinae, Genus *Antrozous*. The genus *Antrozous* includes one Recent species, *A. pallidus*. *Antrozous* formerly included *A. dubiaquercus* from Central America (Pine et al., 1971). Engstrom and Wilson (1981) accorded this form generic rank, *Bauerus*, in support of Van Gelder (1959).

Antrozous pallidus (LeConte, 1856)

Pallid Bat

V[espertilio] pallidus LeConte, 1856:437. Type locality "El Paso, El Paso Co., Texas."

Antrozous bunkeri Hibbard, 1934:227. Type locality 7 mi S Sun City, Barber Co., Kansas.

Antrozous koopmani Orr and Silva Taboada, 1960:83. Type locality Municipio de San Juan y Martinez, Provincia de Pinar del Rio, Cuba.

Antrozous minor Miller, 1902:389. Type locality Comondu, Baja California Sur, Mexico.

CONTEXT AND CONTENT. Context given in the generic summary. Martin and Schmidly (1982) recognized six subspecies of *Antrozous pallidus*:

A. p. bunkeri Hibbard, 1934:227, see above.
A. p. koopmani Orr and Silva Taboada, 1960:83, see above.
A. p. minor Miller, 1902:389, see above.
A. p. pacificus Merriam, 1897:180. Type locality Old Fort Tejon, Kern Co., California.
A. p. packardi Martin and Schmidly, 1982:36. Type locality 12 mi W Encarnación de Diaz, Jalisco, Mexico.
A. p. pallidus (LeConte), 1856:437, see above.

DIAGNOSIS. *Antrozous pallidus* is distinguished from other North American vespertilionid bats by large ears, large eyes, and light coloration. *Plecotus townsendii* and *Plecotus phyllotis* also have large ears but, unlike *Antrozous*, these are joined basally across the midline. *Macrotus waterhousii* (Phyllostomidae) has a prominent noseleaf.

GENERAL CHARACTERS. *Antrozous pallidus* is a large, light-colored bat with large, prominent ears (Fig. 1). Measurements (in mm) are: total length, 92 to 135; length of tail, 35 to 53; length of hindfoot, 11 to 16; length of ear, 21 to 37; length of forearm, 45 to 60; length of skull, 18.6 to 24. Body mass (in g) ranges from 13.6 to 24.1 for males and 13.9 to 28.9 for females (Armstrong, 1972; Banfield, 1974; Davis, 1969*a*, 1969*b*; Hall, 1981; Hoffmeister, 1971; Ingles, 1965; Martin, 1974). Several anatomical illustrations are available of the skull (Fig. 2; Allen, 1864; Hall, 1981), postcranial skeletal elements (Martin, 1974), and myology of the shoulder and arm (Hermanson and Altenbach, 1981, 1983).

FOSSIL RECORD. *Antrozous pallidus* was identified from late Pleistocene deposits in California (Schultz, 1938; Stock, 1918), Arizona (Skinner, 1942), New Mexico (Harris and Findley, 1964), and Cuba (Orr and Silva Taboada, 1960; Silva Taboada, 1976, 1979).

DISTRIBUTION. Pallid bats are common throughout arid deserts and grasslands in the southwestern United States (Fig. 3). A few records are available indicating that the northern extent of pallid bat distribution is in southern British Columbia (Banfield, 1974). Distribution in Washington and Oregon includes Sonoran and Transitional life zones. Pallid bats in New Mexico are encountered most frequently in arid country in the vicinity of rocky outcrops, although occasional reports indicate the presence of colonies far from such locations (Findley et al., 1975). Armstrong (1974) reported pallid bats to be most numerous in the dry canyonlands of southwestern Colorado. A relatively disjunct population of *A. p. bunkeri* exists in Oklahoma and Kansas in association with karst regions (Hibbard, 1934; Morse and Glass, 1960) or gypsum outcrops (Packard and Judd, 1968). Stromberg (1982) reported an isolated colony of *A. pallidus* in eastern Wyoming, although Long (1965) did not include pallid bats in his list of Wyoming mammals. The distribution of *Antrozous* in Mexico is not known precisely. The reported southern extent of the distribution of *A. pallidus* is in the states of Jalisco (Watkins et al., 1972) and Queretaro (Schmidly and Martin, 1973). *A. p. koopmani* is known from only two Recent localities in Cuba and from four Pleistocene deposits (Silva Taboada, 1979).

FORM AND FUNCTION. The head and body of pallid bats are light brown in color, tending towards white on the ventral surface. One albinistic specimen was recorded from Nevada (Setzer, 1950). The tragus is long and lanceolate, extending more than one-half of the length of the pinna. The muzzle is squarely truncate, with a low, horseshoe-shape ridge dorsally. Several wart-like bumps (pararhinal glands) are distributed across the facial region (Walton and Siegel, 1966). These glands are modified sebaceous glands found in association with hair follicles. They are subdivided into many lobes, each lobe drained by one or more ducts that open both

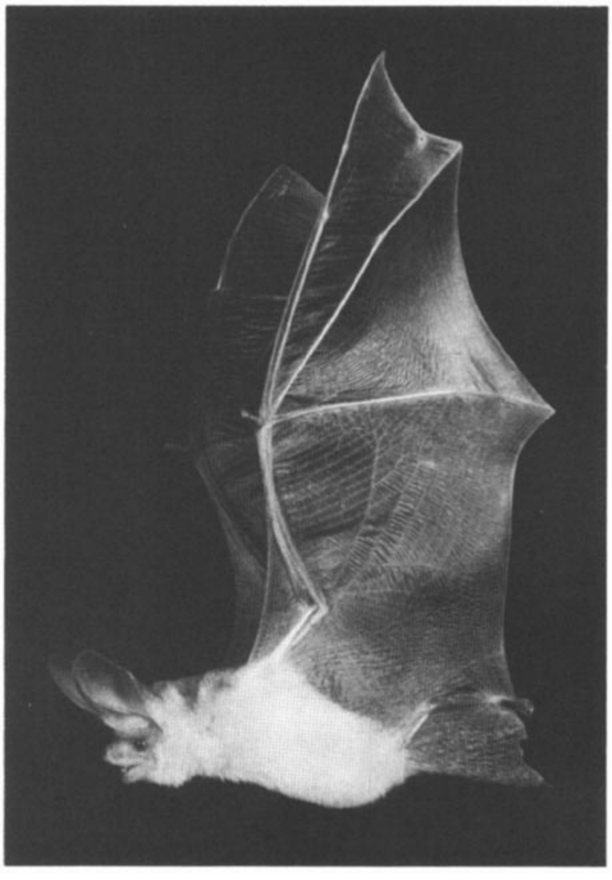

FIGURE 1. Pallid bat from New Mexico in normal flight (photo courtesy of J. S. Altenbach).

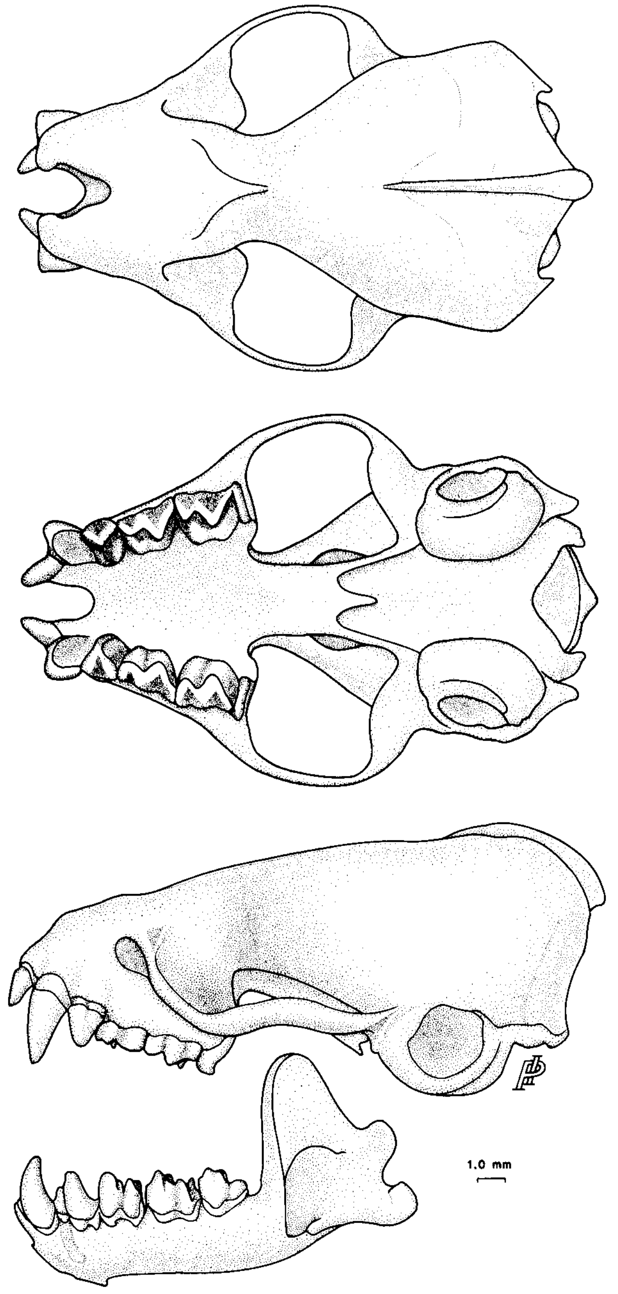

FIGURE 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Antrozous pallidus* (UF 2577) from Kern Springs, Imperial County, California (drawing by Paloma Ibarra).

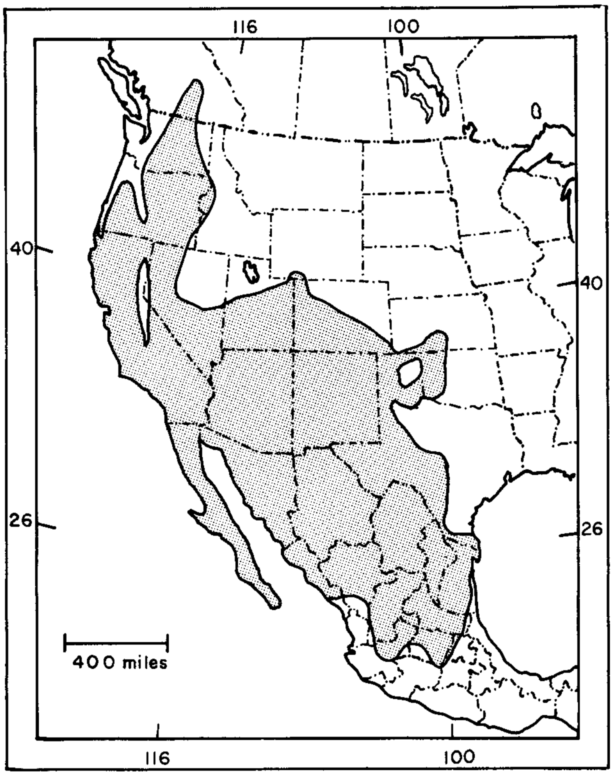

FIGURE 3. Distribution of *Antrozous pallidus* (modified from Hall, 1981). The distribution of *A. p. koopmani* on Cuba is not shown.

into hair follicles and directly onto the skin. Orr (1954) speculated that the musky odor produced by these glands served a defensive function. Walton and Siegel (1966) considered the pararhinal duct system observed in *Antrozous* to be structurally intermediate between the ducts found in *Noctula* and *Lasiurus*.

The dental formula is i 1/2, c 1/1, p 1/2, m 3/3, total 28. Upper incisors are large and simple. Lower incisors are subequal and trilobed. Cheekteeth are not particularly unique. The ectolophs of M1 and M2 are shallow; M3 is small relative to M1 and M2 and exhibits protocone, paracone, and parastyle, but lacks other distinctive features (Miller, 1907). The absence of a hypocone enhances the shearing action of the bite (Findley et al., 1975). The deciduous dental formula is i 2/3, c 1/1, p 2/2, m 0/0, total 22, replaced by permanent teeth by age 35 days (Orr, 1954).

The os penis of *A. p. pallidus*, *A. p. pacificus*, and *A. p. bunkeri* ranged from 0.98 to 1.20 mm in length, with a "saddle-like" appearance in lateral view (Krutzsch and Vaughan, 1955). The cranial tip was pointed and the caudal aspect of the bone was wide and truncated. The bacula of the three subspecies appeared sufficiently similar for Krutzsch and Vaughan to consider *A. bunkeri* (sensu Hibbard, 1934) conspecific with *A. pallidus*.

The spermatozoa of *A. pallidus* average 36 u in total length and the head is elongate and truncate posteriorly (Orr, 1954). The body extends nearly one half the total length of the spermatozoon, tapering gradually into the tail.

Male and female body masses reported by Davis (1969*a*, 1969*b*) were not significantly different in early spring (males ranged from 13.6 to 18.3 g; females, 13.9 to 20.5 g). Pregnant and lactating females weighed relatively more than males (14.3 to 28.9 g). Both sexes accumulated fat reserves in autumn but were not sexually dimorphic (males, 18.1 to 24.1 g; females, 17.9 to 25.4 g). Banfield (1974) reported male body masses from 21 to 29 g, and females from 24 to 35 g, but did not specify the season or locality. Forearm lengths and wing lengths were not significantly different for males or females of *A. p. pallidus* in Arizona (Davis, 1969*a*, 1969*b*); however, an analysis of forearm lengths of *A. p. pacificus* from northern California revealed significant sexual dimorphism (Myers, 1978).

During postnatal development, wing lengths increase relatively faster than mass and a decrease in wing loading becomes evident in juveniles before their first flights. Davis (1969*a*) observed that pregnant females had wing-loading values comparable with those of young, non-volant pallid bats. He concluded that the minimum requirements for flight were not correlated directly with attainment of "adult" wing-loading, but that ability to fly was dependent upon muscular maturity and improvement of neuromuscular coordination. Davis (1969*a*) further noted substantial variation in wing-loading estimates for individual bats (from 0.094 to 0.145 g/cm^2) and suggested that wing-loading values for pallid bats provided an adequate margin for infrequent and unpredictable stresses such as transporting young or sustaining injury. Pallid bats exhibit several healing responses to accidental damage to wings, including the ability to fuse broken phalangeal elements and to regenerate missing portions of the wing membrane (Davis, 1968).

Radiographs of the shoulder obtained during flight demonstrated clavicular adduction and abduction in synchrony with wing adduction and abduction, respectively. Clavicular movements were hypothesized to facilitate contraction of the pectoralis muscle during the downstroke (Hermanson, 1981).

The myology of *Antrozous* does not differ greatly from the descriptions of Vaughan (1959) for *Myotis*. The pectoralis and serratus ventralis are the primary muscles responsible for powering the downstroke. The subscapularis exhibits activity patterns consistent with those of a muscle responsible for fine control of wing position (Hermanson and Altenbach, 1981, 1983). Muscles generally can be described as an abductor, adductor, or bifunctional; these categories parallel the general role of the appendicular musculature of terrestrial mammals as flexors, extensors, or bifunctionals (Engberg and Lundberg, 1969).

Antrozous hearts average 0.7% of body mass, an observation that was considered low in view of the strenuous nature of flight (Herreid, 1961). The right lung is larger than the left lung, a condition typical of many mammals. The right kidney is significantly larger than and located anterior to the left kidney. Uterine horns are symmetrical and of equal size. Males in their first year have testes descended partially or completely within the tunica parietalis.

The transition between esophageal mucosa and gastric mucosa occurs 1.0 mm anterior to the esophageal-stomach junction. The stomach walls include four normal cellular layers: mucosa, submucosa, muscularis, and serosa. Four gastric glands are found in the mucosa layer, including cardiac, fundic, transitional, and pyloric glands (Rouk and Glass, 1970).

Pallid bats are heterothermic; body temperatures of inactive bats approach ambient temperatures (Licht and Leitner, 1967*a*; Orr, 1954; Trune and Slobodchikoff, 1976). With decreasing body temperature, hearing sensitivity decreases and shifts toward lower frequencies (Brown et al., 1978). Metabolic rates vary positively with ambient temperature, but show an unexpected decrease at 30°C (Trune and Slobodchikoff, 1976). This decrease at 30°C correlated with the typical warm season roost temperature for the area from which experimental animals were selected (Vaughan and O'Shea, 1976). Solitary animals have significantly higher metabolic rates than animals roosting together (Trune and Slobodchikoff, 1976).

At ambient temperatures of 35 to 36°C, Licht and Leitner (1967*a*) found that all pallid bats exhibited stable body temperatures of 36 to 38.5°C. Hyperthermia at ambient temperatures greater than 36°C conserved body water. An estimated one-half of the heat production of each animal was dissipated at these high temperatures by evaporative cooling mechanisms. Bats searched for cooler locations when ambient temperatures reached 39 to 40°C, but eventually became restful and maintained body temperatures of 40 to 41.5°C. Bats became agitated and exhibited open-mouth panting at body temperatures above 41.5°C. At these high temperatures, locomotory movements were thought to increase body heat production faster than cooling mechanisms could dissipate the heat. Prolonged exposure to heat and resultant body temperatures of 43.5°C and above were lethal.

Pallid bats lost twice as much water when wings were extended as when they were folded. This difference was correlated with higher metabolic rates in bats with extended wings but was not correlated with the difference in exposed surface area related to either posture. Resting pallid bats lost a mean of 0.44 mg H_2O/ml O_2 consumed, a relatively low value in comparison with terrestrial, desert-adapted mammals (Chew and White, 1960).

Antrozous pallidus produce a highly concentrated urine ranging from 3,150 to 4,550 mosmoles/kg body mass (Geluso, 1975). Geluso (1978) also reported that when most pallid bats were deprived of water, they maintained a positive water balance for 1 month on a mealworm diet. Pallid bats also reduced food intake in some instances of water stress, thus avoiding a potentially lethal solute load. Riedesel (1977) presented data indicating that pallid bats can suffer up to a 30% loss of body mass without exhibiting dehydration of liver tissue. In contrast, liver tissue of *Tadarida brasiliensis* exhibited significant dehydration under similar circumstances. No mechanism was presented to explain the observations.

REPRODUCTION AND ONTOGENY. Copulation generally occurs from October through December (Orr, 1954), perhaps extending through February (Barbour and Davis, 1969). Testicular length and body mass exhibit an increase from June through October (Herreid, 1961; Martin, 1974; Orr, 1954). Copulation occurs on horizontal surfaces and when bats hang upside down. Males approach females from the rear and the uropatagium of the female is pushed to one side. Neck-biting by males apparently does not occur (Orr, 1954). Sperm is stored in the reproductive tract of females, and ovulation occurs during the following spring (Orr, 1954). Concentrations of estrogen and progesterone in plasma remain relatively low during fall and winter months. Estrogen exhibits a brief high concentration in April, coincident with ovulation and blastocyst implantation and a second peak in concentration during late stages of pregnancy. Progesterone levels increase rapidly during late stages of pregnancy but remain at a low level throughout the rest of the year. Luteinizing hormone appears to initiate progesterone and estrogen synthesis and is present at a functional level only after the termination of winter torpor (Oxberry, 1979).

The time of parturition appears to be determined by local climate. Lengths of periods of embryonic development, therefore, are variable, but probably average about 9 weeks (Orr, 1954). Birth generally occurs in May and June in the southwestern United States (Barbour and Davis, 1969; Beck and Rudd, 1960; Davis, 1969*b*; Orr, 1954; O'Shea and Vaughan, 1977). Females hang upright during parturition, presentation is breech, and young are held in the curled uropatagium.

The sex ratio of newborn pallid bats is about 1:1 (Brown, 1976; Davis, 1969*b*; Herreid, 1961; Orr, 1954). Findley et al. (1975) reported an average of 1.8 newborn per litter in New Mexico, whereas Orr (1954) and Twente (1955*a*) reported two young per litter in northern California and Kansas, respectively. Three embryos were recorded occasionally (Grinnell, 1918; Hall, 1946; Orr, 1954). Single young may be larger and more precocial than twins (Brown, 1976). Fifty newborn and 18 adult females were observed in a colony in Texas indicating a ratio of 2.8 offspring per female (Herreid, 1961). Yearling females breed, but give birth to only one young (Davis, 1969*b*).

The young are born in an altricial state and in the roost stay attached to the maternal teats, enveloped in the plagiopatagium of the mother (Brown, 1976; Orr, 1954). Foraging females leave the young behind, but frequently return to attend to them (Beck and Rudd, 1960; O'Shea and Vaughan, 1977). Communal nursing does not occur (Davis, 1969*b*). Newborn pallid bats are able to crawl on their mothers and on vertical surfaces. This locomotory ability is facilitated by well-developed hindlimbs at birth. Orr (1954) reported that the hindfoot of a neonate was 71% of adult size, compared with 37% of adult size for tail length and 31% of adult size for forearm length. Forearm length was about 17 mm at birth. Forearm length increases relatively linearly to adult size in 6 to 7 weeks. Young did not fly until 4 to 5 weeks of age when forearm length reached 50 mm. Adult mass of 25 g in laboratory-reared bats was not reached until age 8 weeks (Brown, 1976). Normal flight is usually possible in wild pallid bats at 42 days of age, but flight was observed as early as 33 days (Davis, 1969*b*). Wing loading decreases with age until rudimentary flight is reached; wing growth is positively allometric with respect to body mass in prevolant pallid bats (Davis, 1969*b*).

The ears and eyes of newborn pallid bats are closed. Neonates do not respond to auditory stimuli (Brown et al., 1978). The pinna unrolls and the tragus is abducted from the external ear opening at 8 to 10 days (Orr, 1954). Auditory evoked potentials cannot be detected in bats younger than 6 days and do not begin to resemble adult patterns until 8 to 12 days of age (Brown et al., 1978). Only low frequency sounds within the range of female communication calls elicit responses in 6- to 8-day-old bats, but by 12 days of age the frequency range of responsiveness approaches that of the adult (Brown et al., 1978). Directional sensitivity and rapid temporal resolution are developed by the time of first flight (Brown et al., 1978). In the wild, short flights begin at 4 to 5 weeks of age; echolocation cries are similar to adults but with lower frequency elements. By 5 to 6 weeks young and adult echolocation pulses are indistinguishable, and by 7 weeks nocturnal activity patterns are similar (Brown and Grinnell, 1980). Eyes remain closed in the newborn for 2 to 5 days (Brown, 1976; Davis, 1969*b*) but may take longer to open under certain conditions in captivity (Orr, 1954).

Neonates are born naked. The dorsal pelage is complete by day 11, except for portions of the interscapular region. The ventral surface is fully haired at 18 days (Davis, 1969*b*; Orr, 1954). Juvenile pelage is darker than that of adults; young gradually attain lighter coloration as light-colored basal hairs grow outward during the first few months (Orr, 1954).

Deciduous upper and lower canines are the first teeth to erupt and are visible shortly before birth (Orr, 1954). The deciduous premolars erupt on days 3 to 5 and permanent teeth begin to erupt at 21 days in a sequence typical of vespertilionid bats (Fenton, 1970; Orr, 1970).

Lactation may occur from early May through mid-August (Martin, 1974; Orr, 1954). Orr (1954) noted that captive young began to accept insect food at age 6 weeks, coincident with the development of a functional permanent dentition and the ability to fly. Females wean young between 6 to 8 weeks of age (Brown, 1976; Brown and Grinnell, 1980; Orr, 1954).

ECOLOGY. Pallid bats are characteristic of desert areas and seem to be most abundant in the Sonoran life zones (Orr, 1954). They have been collected at sites ranging up to 2,440 m (Black, 1974; Martin, 1974), but are less abundant in evergreen and mixed forests than in vegetation assemblages characteristic of lower elevations (Jones, 1965). They are common in desert regions with rocky outcroppings, particularly near water (Orr, 1954), although Findley et al. (1975) reported them from arid areas devoid of these features. Pallid bats roost in small colonies in rock crevices and structures built by man but are typically not cavernicolous despite generalizations to the contrary (Dalquest and Walton, 1970). The few reports of *Antrozous* inhabiting caves or mine tunnels during the day indicate that pallid bats use crevices within these places (Hall, 1946; Orr, 1954; Twente, 1955*a*), but these reports are far outnumbered by descriptions of roosts in rock crevices (Orr, 1954; Packard and Judd, 1968; Vaughan and O'Shea, 1976) or in crevices that are artifacts of human-built structures (Dalquest, 1947*a*, 1947*b*; Davis, 1969*b*; Davis and Cockrum, 1963*a*; Hall, 1946; Herreid, 1961; Howell, 1919). Other diurnal roosting situations reported in the literature include stacks of burlap sacks (Beck and Rudd, 1960), stone piles (Racey, 1933), and hollows in trees (Bailey, 1936; Davis, 1944; Hall, 1946; Orr, 1954). Diurnal roosts may be shared with other species of bats, particularly *Tadarida brasiliensis* (Dalquest, 1947*a*, 1947*b*; Howell, 1919; Krutzsch, 1946; Licht and Leitner, 1967*a*; Orr, 1954; Vaughan, 1954; Vaughan and O'Shea, 1976). Reports of pallid bats sharing roosting places with other species of bats appear in the literature, but with the exception of *T. brasiliensis* and *Myotis yumanensis*, both of which roost among pallid bats, it is not always made clear if bat species are segregated widely within these roosts.

The seasonal selection of different rock crevices based on their thermal profiles was demonstrated for pallid bats in central Arizona, and seems to maximize the benefits of adaptive hypothermia (Vaughan and O'Shea, 1976). Horizontally-oriented crevices with stable 24-h temperatures of about 30°C are preferred diurnal roosts in summer. Vertically-oriented crevices with temperatures widely fluctuating between cool morning and warm evening extremes (that allow dormancy early in the day but passive warming before emergence) are selected at cooler seasons. The choice of horizontal crevices in summer maternity colonies also allows for ease of retrieval of fallen young.

Pallid bats also gather in night roosts that are often near, but usually distinct from, their diurnal retreats (Bell, 1982; Brown and Grinnell, 1980; Howell, 1919; Orr, 1954; O'Shea and Vaughan, 1977). Night roosting may occur in shallow caves, cliff overhangs, or shelters of structures built by man (Beck and Rudd, 1960; Bell, 1982; Brown and Grinnell, 1980; Dalquest, 1947*a*, 1947*b*; Hall, 1946; Herreid, 1961; Howell, 1919, 1980; Krutzsch, 1954; Orr, 1954; O'Shea and Vaughan, 1977; Pearson et al., 1952; Twente, 1955*a*; Vaughan, 1959). Use of tree boles also was reported (Hall, 1946). Pallid bats alight in isolation to consume prey in night roosts (Bell, 1982), but also cluster and enter a nocturnal cycle of torpor. Selection of night roosts may be based on thermal characteristics that maximize energy savings (O'Shea and Vaughan, 1977). Several other species of bats co-occur in night roosts but have not been observed in clusters with pallid bats.

Pallid bats are gregarious, with 95% of the roosting bats counted over an annual cycle in central Arizona occurring in groups larger than 20 (Vaughan and O'Shea, 1976); group size in diurnal retreats ranges from solitary individuals (Orr, 1954; Packard and Judd, 1968; Vaughan and O'Shea, 1976) to colonies of over 200 adults with additional young (Twente, 1955*a*). The largest groups consisted of summer maternity colonies composed largely of females and young (Licht and Leitner, 1967*b*; Twente, 1955*a*; Vaughan and O'Shea, 1976). Estimates of adult sex ratios are unreliable from field studies because in some areas males and females may not occur together during the summer (Beck and Rudd, 1960; Hall, 1946; O'Shea and Vaughan, 1977). Mixed-sex summer colonies, however, are well documented in other localities (Orr, 1954; Twente, 1955*a*, 1955*b*). Correlates of local variation in sex ratios are unknown, although retention of yearling males in the maternity group was demonstrated for one colony (Beck and Rudd, 1960). Males are gregarious when roosting apart from females. Up to 60 males were found in diurnal roosts (Dalquest, 1947*a*), and over 100 in night roosts (Davis and Cockrum, 1963*b*) during summer months. Colony size varies seasonally; maximum numbers coincide with presumed peaks in midsummer insect densities (O'Shea and Vaughan, 1977). Pallid bats are largely inactive in winter and are presumed to hibernate, but, with the exception of one site where two groups of about 20 and 100 were found (Twente, 1955*a*), most winter records are of small numbers (1 to 4) of individuals (Alcorn, 1944; Grinnell, 1918; Hall, 1946; Orr, 1954). Occasional winter activity of pallid bats was reported at a desert spring in Nevada. Four individuals, all males, were captured on 3 nights at ambient temperatures as low as 2°C (O'Farrell and Bradley, 1970; O'Farrell et al., 1967).

Pallid bats are chiefly insectivores and feed on large (20 to 70 mm in length) prey that are taken on the ground, or, perhaps less frequently, in flight within a few meters of the ground or from the surfaces of vegetation. Prey items include flightless arthropods such as scorpions (Vejoridae), ground crickets (Gryllacrididae), solpugids (Solpugida), and darkling ground beetles (Tenebrionidae); largely ground-roving forms, including scarab beetles (Scarabeidae), predaceous ground beetles (Carabidae), carrion beetles (Silphidae), and short-horned grasshoppers (Acrididae); and prey that are probably gleaned from vegetation, including cicadas (Cicadidae), katydids (Tettigoniidae), praying mantids (Mantidae), long-horned beetles (Cerambycidae), and sphingid moths (Sphingidae). Bell (1982) presented moths of various sizes to wild-foraging pallid bats and reported an optimum prey size class of 25 to 35 mm in body length. He suggested that such a size minimized search and handling times. Most food items reported by O'Shea and Vaughan (1977) were within 5 mm of the optimal size class.

Lists of food items of pallid bats are based largely on the analysis of fragments dropped beneath night roosts. This method could result in a bias by underestimating the dietary importance of smaller prey consumed in flight. However, analysis of stomach and fecal samples (Black, 1974; Easterla and Whittaker, 1972; Ross, 1967) agrees with reports based on fragments from night roosts. Analysis of fecal material indicated that beetles were a significant component of the diet of pallid bats but moths were not. However, Bell (1982) reported sphingid moths to be the most important dietary item collected beneath roosts in southern Arizona. The robust skull is an adaptation for *A. pallidus* to feed on large, hard-bodied prey such as ground-dwelling beetles (Freeman, 1981), and observations of these bats foraging close to the ground or other surfaces and alighting to attack and consume large prey are well documented (Bell, 1982; Easterla and Whittaker, 1972; Hall, 1946; Huey, 1936; Killpack and Goates, 1963; Nelson, 1918; O'Shea and Vaughan, 1977; Ross, 1967). In addition, pallid bats were observed to ignore swarms of small flying insects attracted to black lights (Bell, 1980). Pallid bats fare well in captivity on various diets and may consume 12 to 16% of their body mass in mealworms daily (Brown, 1976; Orr, 1954).

Although insects constitute the overwhelming proportion of the diet, pallid bats also eat lizards and smaller bats in captivity (Engler, 1943). Use of vertebrates (*Phrynosoma douglassi* and *Perognathus flavus*) as prey was confirmed in the field (Bell, 1982; O'Shea and Vaughan, 1977). In Pima County, Arizona, about 25% of the feces examined in August 1975 consisted of organ pipe cactus (*Lemaireocereus thurberi*) fruit and seeds (Howell, 1980). These are presumed to be ingested incidentally during the capture of juice-drinking noctuid moths (Noctuidae) perched on cavities in the fruit excavated during feeding by the glossophagine bat, *Leptonycteris sanborni*. Such feeding behavior can be viewed as a model for intermediate steps in the evolution of frugivory in the Chiroptera (Howell, 1980). Barbour and Davis (1969) present evidence that pallid bats also feed among the inflorescences of *Agave* in southern Arizona.

The feeding habits of pallid bats render them susceptible to injury and predation. Davis (1968) reported wing defects in 28 of 63 individuals examined in Arizona. Injuries included protruding and broken bones, membrane holes, and tears and embedded thorns and cactus spines. Most of these damages undoubtedly were incurred while they foraged on or near the ground. Pallid bats feeding on the ground were captured by humans (Nelson, 1918) and probably are taken by predators at these times; the pale coloration of pallid bats may be an adaption to provide crypsis against the desert floor (O'Shea and Vaughan, 1977). Snakes (Colubridae) (Allen, 1939) and owls (Tytonidae and Strigidae) (Baker, 1953; Glass, 1953; O'Shea and Vaughan, 1977; Twente, 1954) prey on pallid bats. Orr (1954) reported that a kestrel (*Falco sparverius*) and a sharp-shinned hawk (*Accipter striatus*) took *A. pallidus* inadvertently released during daylight. Young pallid bats first beginning to fly may be particularly vulnerable to owls; two regurgitated pellets of a great-horned owl (*Bubo virginianus*) recovered near an Arizona nursery colony contained seven skulls of immature *A. pallidus* but no adults (O'Shea and Vaughan, 1977). Other known sources of mortality include slaughter by vandals (Jones et al., 1967; O'Shea and Vaughan, 1977), extermination in buildings, and specimen collecting at roosts and watering places. In relation to certain other species of bats, *A. pallidus* collected in southern Arizona did not carry exceptional body burdens of organochlorine pesticide or mercury residues (Reidinger, 1972, 1976), and die-offs of pallid bats from exposure to environmental contaminants has not been documented (Clark, 1981). Age-specific mortality schedules and longevity records in nature are not available for this species. Individuals have survived 8 (Orr, 1958) and 9 years (Brown et al., 1978) in captivity.

Ectoparasites collected from pallid bats include bedbugs (Hemiptera), bat flies (Diptera), fleas (Siphonaptera), ticks, mites, and chiggers (Acarina) (Allred and Goates, 1964; Bradshaw and Ross, 1961; Dooley et al., 1976; Herreid, 1961; Krutzsch, 1955; Orr, 1954, 1958; Vercammen-Grandjean and Watkins, 1966). Scabies also was reported (Orr, 1958). Bat trypanosomes occurred in pallid bats in California (Mitchell, 1956). Wood (1962) detected *Borrelia*, the agent of relapsing fever, in California pallid bats. Beck et al. (1982) reported finding a bile-duct carcinoma. Constantine (1970) tabulated several reports of rabies virus in pallid bats and reviewed the relationships between bats and disease.

BEHAVIOR. Dietz (1973) observed walking behavior in 10 species of bats in three families and reported pallid bats to be the most versatile, and to use a variety of strides and gaits while locomoting on the ground. The weight is borne on the wrists and feet and the anterior part of the body is elevated (Orr, 1954). Flight of pallid bats (Fig. 1) has been described as less maneuverable than smaller vespertilionids (Orr, 1954). They may hover or glide momentarily (Orr, 1954), and, while foraging, fly in a series of dips and rises from about 0.1 to 10 m above the ground, occasionally swooping in circles and figure 8's (Bell, 1982; O'Shea and Vaughan, 1977). Pallid bats studied by Bell (1982) in New Mexico foraged in open areas most often. Pallid bats timed in flight down indoor hallways averaged 14.3 km/h (Hayward and Davis, 1964). The wingbeat cycle involves 10 to 11 strokes/s (Orr, 1954).

A head-down resting position generally is maintained throughout the day in diurnal roosts (Vaughan and O'Shea, 1976), where shifts in position and degree of dispersion are correlated with ambient thermal conditions (Licht and Leitner, 1967*b*; Vaughan and O'Shea, 1976). Pallid bats usually form clusters in diurnal roosts and in captivity (Orr, 1954; Vaughan and O'Shea, 1976). Such clustering provides distinct energetic advantages in terms of reduction of metabolic rates (Trune and Slobodchikoff, 1976). Bats that failed to join in groups in cages usually were ill or injured (Orr, 1954). Individuals are quiet during cool seasons and hours of the day, but during warmer periods pallid bats vocalize frequently and are more alert within roosts (Orr, 1954; Vaughan and O'Shea, 1976). Movements are limited, however, and behavior generally is restricted to grooming of fur and membranes by nuzzling with the snout or scratching and combing with the hindfeet (Orr, 1954). Pallid bats repeatedly circle and momentarily alight at crevice mouths at the dawn retreat, joining in swarms that circle back and forth along cliff faces near the roosts, particularly during mid-summer when "rallying" behavior may persist for up to 45 min (Vaughan and O'Shea, 1976). These behaviors are thought to advertise roost locations, a critical factor in that from 60 to 80% of the 24-h cycle is spent resting in these places. Selection of an appropriate roost has definite energetic advantages (Vaughan and O'Shea, 1976). Alternate roosts are chosen frequently during the summer when young become volant; rallying and relocation of roosts may serve to aid young in achieving skill at finding retreats (O'Shea and Vaughan, 1977). Dispersal follows the summer period of roost relocation.

Relative to other bats, pallid bats emerge from their roosts relatively late in the day (Orr, 1954), but the time of evening emergence varies seasonally. In comparison with summer, emergence is later in spring and fall, and the rates at which bats depart are slower. Some individuals may fail to emerge to particularly cool nights (O'Shea and Vaughan, 1977). Foraging is concentrated in two periods at the beginning and end of the nocturnal cycle of activity during most of the active season. Mothers and offspring may emerge and forage in unison (Brown and Grinnell, 1980; O'Shea and Vaughan, 1977). During foraging periods bats may alight at overhangs to manipulate prey, utilizing the uropatagium as an apron to contain items (Bell, 1982; Borell, 1942). Distances that bats cover during foraging are unknown, although movements of 30 km between night roosts were recorded (Davis, 1966). Bell (1982) estimated nightly movements from the day and night roosts at 3 km or less. After an initial foraging period bats with full stomachs gather at night roosts and join in clusters, and locate one another by exchanges of vocalizations (O'Shea and Vaughan, 1977). Bats in night-roosting clusters undergo torpor, especially during cool seasons. Individuals may remain torpid for over 5 h, and night roosting can occupy from 40 to 75% of the time spent away from diurnal retreats (O'Shea and Vaughan, 1977).

Homing experiments based on more than 47 trials involving release of 719 individuals at various distances and directions from points of capture indicated the maximum return distance was 174 km. Several recoveries 48 to 51 km from the release site were reported 7 to 8 h following release. Immature bats returned less commonly than adults, and females returned more often in early summer than in late summer (Davis, 1966). Most individuals failed to return from release points at distances much greater than the likely range of normal movements (Davis, 1966; Davis and Cockrum 1963*b*). No evidence for a nonrandom homing ability emerged from these studies (Davis, 1966; Wilson and Findley, 1972). One female returned to the diurnal roost after each of eight consecutive captures and releases at points ranging from 34 to 110 km away (Davis and Cockrum, 1962).

Orr (1954) recognized the presence of five audible communication signals—intimidation notes, squabble notes, directives, notes of contentment, and plaintive notes. Irritation buzzes (intimidation notes of Orr, 1954) are loud (133 db at 10 cm) trains of 5 to 10 pulses, each sweeping downward from 20 to 8 kHz and 2 ms in duration, with 12-ms intervals between sweeps (Brown, 1976). They are emitted when bats are annoyed and serve to threaten enemies and alert other pallid bats to danger; females also give them to discourage nursing during weaning. Often the teeth are bared and the wings spread in association with this sound. Squabble notes express mild irritation and can serve to space bats within roosts; the teeth also may be bared during emission of this cry (Orr, 1954). Squabble notes are variable with fundamental frequencies of 5 to 15 kHz and considerable sound energy distributed among harmonics (Brown, 1976). Directive calls consist of 1 to 6 loud (100 db at 10 cm), clear notes given in rapid succession at 35 ms intervals, sweeping down through a range of 30 to 5 kHz in 20 ms (Brown, 1976). They are used to orient bats to one another. Notes of contentment (contact notes of Brown, 1976) are given as pairs of pulses when bats are at ease in physical contact. These have not been analyzed spectrographically. Plaintive notes are loud, long-duration cries with fundamental frequencies of 10 to 15 kHz that are emitted by bats in pain (Brown, 1976). Sounds associated with courtship and mating are unknown. Squabble notes and irritation buzzes were heard in the field at diurnal roosts and night roosts (Beck and Rudd, 1960; Brown, 1976; Orr, 1954; O'Shea and Vaughan, 1977; Vaughan and O'Shea, 1976). Directive calls are given as bats emerge from diurnal retreats, as they forage, seek out night roosts, and return to diurnal roosts at dawn, with exchanges occurring between bats in roosts and bats on the wing (Orr, 1954; O'Shea and Vaughan, 1977; Vaughan and O'Shea, 1976).

Newborn pallid bats emit easily localized isolation calls (Brown, 1976; Gould, 1975) when separated from their mothers. These calls serve to direct the mother to the young; they change in spectral characteristics as the bats mature, eventually becoming the adult directive at 20 days of age. In 6-day-old bats fundamental frequencies range from about 10 to 25 kHz; durations are about 60 ms (Brown, 1976). Isolation calls show individual distinctiveness in several characteristics and females selectively respond to the cries of their own offspring, implying a vocal signature (Brown, 1976). Double-note calls recorded by Gould (1975) and Gould et al. (1973) may be individual variants of the isolation call (Brown, 1976). Captive newborn emit isolation calls continuously until rejoined by mothers. Females answer isolation calls with directive calls but young do not respond to adult sounds until 7 to 9 days old, when the auditory system becomes functional and vocalizations are first exchanged.

Echolocation is the primary means of orientation in pallid bats, but visual and olfactory sensory modalities also are involved. Orientation pulses are emitted through the mouth (Orr, 1954) during flight or when crawling or stationary (Brown, 1976). Pulses recorded in the laboratory are frequency modulated, sweeping from 70 to 25 kHz in 1 to 2 ms with an amplitude of 90 db at 10 cm and a variable repetition rate. Echolocation pulses appear in the repertoire at about 8 days of age (Brown, 1976) and become indistinguishable from those of adults in the field at about 5 to 6 weeks of age (Brown and Grinnell, 1980). Field recordings of orientation pulses of pallid bats made by Fenton and Bell (1981) show a range of 49 to 26 kHz with greatest energy at 30 kHz, two harmonics and a maximum duration of 5 ms during the search phase. Evoked potential audiograms of adults are broadly tuned from 5 to 100 kHz with maximal sensitivity from 15 to 50 kHz (Brown et al., 1978). Greater auditory sensitivity than many other bat species occurs in the 5 to 15 kHz range and correlates with both the extensive use of lower frequency communication sounds (Brown et al., 1978) and with the sound spectra of mechanical sounds produced by insects used as auditory cues in prey localization by *Antrozous* (Bell, 1982). Bell (1982) demonstrated that rustling and mechanical sounds of insects, such as wing fluttering (but not insect communication sounds), are used to locate prey on the ground. The sense of smell presumably is well developed in *A. pallidus*. Captive individuals are attracted to the urine of conspecifics (Brown, 1976).

Detailed data on the fine structure of social organization and social behavior of pallid bats are lacking, but a general outline is possible. The strongest social bonding is between the female parent and her offspring. When the young become volant they continue to roost and fly in association with adults, which are presumably their mothers (O'Shea and Vaughan, 1977). This association may continue beyond the first year (Beck and Rudd, 1960). When volant, the location of communal roosting places is well advertised and knowledge of roost locations appears to be transferred to offspring by specialized behavior and shifts in site selection (O'Shea and Vaughan, 1977). Retention of offspring in the maternity colony year after year may be matrilineal (Davis, cited in Brown, 1976). An argument based on inclusive fitness can explain some intriguing sets of observations on behavior. These include strong group cohesion (Davis, 1966), extensive rallying and vocal advertising of roost locations (O'Shea and Vaughan, 1977; Vaughan and O'Shea, 1976), the preferential positioning of immatures at the energetically most advantageous parts of roosting clusters (Trune and Slobodchikoff, 1978), attentiveness to captive females in labor by other pregnant females, the signalling to or leading of mother bats to distressed offspring by other females in captivity (Brown, 1976), and the guarding of many young bats by single adult females (Beck and Rudd, 1960). The mating system and patterns of dispersion while foraging remain to be studied for this species.

GENETICS. *Antrozous pallidus* has a diploid number of 46 and fundamental number of 50. The karyotype includes three metacentric autosomes, three submetacentric chromosomes, and 19 pairs of acrocentric chromosomes (Baker and Patton, 1967). The X chromosome is submetacentric and the Y chromosome is acrocentric. Bickham (1979) concluded that *Antrozous, Nycticeius*, and *Rhogeesa* karyotypes evolved from an all-acrocentric form, and that fusion and rearrangements created divergences from the ancestral karyotype of the "*Eptesicus*-like" group.

REMARKS. Miller (1907) assigned *Antrozous* from North America and *Nyctophilus* from the Oriental and Australian faunal regions to the vespertilionid subfamily Nyctophilinae. His decision was based upon similarities in the muzzle (Miller, 1907). Hall (1981) followed Miller in the subfamilial designation, although Koopman (1970) questioned the validity of this arrangement. Pine et al. (1971) suggested a closer relationship between *Antrozous* and the old world *Otonycteris* than between *Antrozous* and Australian nyctophilines.

The generic name *Antrozous* is formed from the Greek word *antron*, meaning cave, and *zoos*, meaning alive or living in. The species name, *pallidus*, refers to the pale coloration of this bat.

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