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DISTRIBUTION OF THE SPOTTED BAT, *EUDERMA MACULATUM*, IN CALIFORNIA

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There were 14 records, including the type, for *Euderma maculatum* in California between 1891–1991. All involved salvage of single bats; most individuals were dead or moribund. In surveys from 1992 to 1997, using primarily acoustic sampling at possible foraging sites within a few kilometers of fractured resistant rock cliffs, 23 additional localities were identified, including a range extension into the Klamath Mountains of northwestern California. *E. maculatum* typically was encountered foraging in meadows on the edge of forests in mixed conifer-hardwood habitat at elevations of 800–1,500 m, but observations extend to 2,926 m in the Sierra Nevada. Usually one *E. maculatum* was observed at a foraging site, but occasionally two or three were present simultaneously. These records suggest that the species, while typically at low density within a few kilometers of geomorphically defined roosts, occurs more widely than previously realized. Although its foraging style and characteristics of its call are distinctive, *E. maculatum* overlaps extensively both in geographic range and use of roosts in rock cliffs with several other species of bat, notably *Eumops perotis*, which also has an audible echolocation call. The linked pattern of rarity, patchy distribution, and restrictive roosting requirements place this species at risk.

Key words: *Euderma maculatum*, spotted bat, distribution, habitat association, status, California

Scattered records of the spotted bat, *Euderma maculatum*, delineate a range extending from southern British Columbia to Durango, Mexico, including much of the western United States (Watkins, 1977; Woodsworth et al., 1981). Since publication of the widely used distribution map by Hall (1981), additional localities in the United States have been reported, including northwestern Colorado (Finley and Creasy, 1982; Navo et al., 1992; Storz, 1995), eastern New Mexico (Perry et al., 1997) and central Oregon (Barss and Forbes, 1984; McMahan et al., 1981). Although multiple individuals have been reported or collected at several localities (e.g., the Okanagan Valley in southern British Columbia, Fort Pierce Wash in southern Utah, and Big Bend National Park in East Texas—Easterla, 1973; Leonard and Fenton, 1983; Poché, 1975, 1981; Poché and Baillie, 1974; Ruffner et al., 1979; Wai-Ping and Fenton, 1989; Woodsworth et al., 1981), most re-

ords are of single individuals, and the species is generally regarded as rare (Fenton et al., 1987).

Euderma maculatum is one of the small number of bats in western North America whose echolocation calls are largely audible (<20 kHz). Although identification based exclusively on acoustic analysis remains problematic for many species of North American bats (Thomas et al., 1987), search-phase calls of *E. maculatum* are well characterized and generally distinctive (Leonard and Fenton, 1984; Obrist, 1995; Thomas et al., 1987; Woodsworth et al., 1981). Thus, active *E. maculatum* can be detected over short distances, with little disturbance, which allows either synoptic surveys (Fenton et al., 1987) or examination of local activity patterns and habitat use (Navo et al., 1992; Storz, 1995).

Most specimens of *E. maculatum* from California were salvaged when dead or moribund, triggering questions as to wheth-

er this sample of possible waifs or vagrants offered a meaningful basis for delineating the species' distribution and habitat associations. In extensive acoustic surveys of the western United States for *E. maculatum*, Fenton et al. (1987) monitored 10–20 sites per area in 14 areas in California (including four areas where specimens had been collected) but did not detect this species. We report multiple localities for *E. maculatum* in California, including several in which more than one individual has been encountered within a radius of a few kilometers, and observations have been repeated for ≥ 2 years. The accumulated records allow inferences about overall distribution and habitat associations of *E. maculatum* in California and provide insight into the ecology of this rare species.

MATERIALS AND METHODS

We conducted surveys from 1992 to 1997. These surveys relied largely on acoustic detection and commonly involved several observers and methods, some using unaided hearing, others using bat detectors (Model D980, Pettersson Elektronik AB, Uppsala, Sweden) coupled to stereo tape recorders. Audibility of *E. maculatum* to some observers offers major advantages for initial screening of habitats and tracking of local movements of individual bats (Navo et al., 1992; Storz, 1995). While experienced observers can make reliable species identifications, we have, in most instances, recorded and subsequently examined time-frequency-intensity plots of digitized call sequences for confirmation. That allowed quantitative comparisons of short call sequences of *E. maculatum* with sequences of co-occurring audible species, particularly *Eumops perotis*, which unaided observers may perceive as similar.

Typical bat detectors are heavily filtered below 15–20 kHz to reduce irrelevant sounds from insects, rustling vegetation, etc. (Fenton, 1988). To enhance detection of audible bats (whose calls are reduced by filtering), the low-frequency threshold in our detectors was lowered by the manufacturer to ca. 7 kHz. In field surveys, observers with the best unaided hearing detected weak signals of *E. maculatum* as effectively as the modified D980 detector, monitoring at 9–12

KHz in the heterodyne mode. When using an analog cassette recorder, we recorded comments of observers or frequency-divided (1/10) calls of bats on one track and digitally time-expanded calls on the other (input sampled at 400 kHz—Ahlén et al., 1983–1984). With a digital audio tape recorder (Sony D7 and D100 DAT) sampling at 48 kHz, we replaced the frequency-divide track with the detector's high frequency output, allowing simultaneous recording of comments and the untransformed primary harmonic of vocalizations of *E. maculatum*. Species identification, however, was based on analysis of time-expanded samples, because the inadequate anti-aliasing filters of small, consumer DAT recorders can generate spurious, and potentially confusing, audio signals from calls with frequencies greater than one-half the sampling rate (i.e., >24 kHz—G. Pavan, pers. comm.).

For unattended recording, a relay was added by the manufacturer to the trigger of the time-expansion circuit in the D980 detector. Normally when a sound exceeds the adjustable amplitude threshold, 3 s of sound (1 s pre-trigger and 2 s post-trigger) are stored in a memory buffer and output as an analog signal slowed down 10 times (i.e., over 30 s). The trigger then resets until the next triggering pulse (Ahlén et al., 1983–1984). In the modified detector, the relay actuated a tape recorder, either through a remote switch, or, more often, indirectly through a portable computer (Radio Shack 100 or 102), in which a program logged times of detection and controlled the interval between recordings.

Our data were compiled from several studies that focused on southern California and areas west of the Sierra Nevada crest. All localities treated here were either at or close to specimen localities or in proximity to cliffs that offered potential roosting habitat (i.e., >30 m high with significant exposures of near-vertical unvegetated fractured rock). Areas with extensive exposed rock were identified based on review of topographic and geologic maps and consultation with geologists and other observers. For the central Coast Range (Lake to San Luis Obispo counties) and the northern Sierran foothills (Butte and Tehama counties), overflights in a small plane quickly identified significant areas of near-vertical unvegetated rock. To generate a broad picture of the distribution of this species, a sample of the more accessible sites was then visited. Not included in the data are >100 other localities,

where the species would not be expected to roost based on topography (no exposed rock), and was not detected.

In acoustic sampling over large areas of potential roosting habitat (e.g., canyons with exposed rock), we monitored several stations (≥ 1 km apart) along a transect for ≥ 15 min/station between sunset and 4–5 h later. At some localities, acoustic monitoring in conjunction with mist netting or other activities relied on a sound-activated detector and recorder placed at one site for 6–12 h. Fenton (in litt.) noted that the first echolocation calls in the Okanagan Valley (which has a relatively high density of *E. maculatum*) were detected ≤ 20 min from the start of a sampling period in $>60\%$ of 73 1-h samples. The minimum of 15 min/station adopted in our study was a compromise, favoring wide-area reconnaissance over detection of rare events. Radiotracking data indicated that foraging *E. maculatum* either move from site to site along a regular route or occupy small feeding territories for extended periods (Wai-Ping and Fenton, 1989; Woodsworth et al., 1981). In sampling for an uncommon animal that has predictable restricted movements and is detectable to ca. 100 m (Navo et al., 1992; Storz, 1995), we found efficiency of detection improved with frequent movement among sites. Failure to detect *E. maculatum* at cliff sites was not treated in detail because sampling was inadequate to establish absence of the species from these areas.

In areas where foraging animals were detected, we generally were able to add visual confirmation of our identification using a hand-held spot-light or third-generation night-vision equipment with infrared illumination. For capture, large mist nets (3 by 18 m or 9 by 30 m, 50-denier nylon or polyester 3.8-cm mesh; Avinet, Inc., Dryden, NY) were set on poles over slowly moving water or in meadows and closely monitored while open (from sunset until at least midnight).

RESULTS AND DISCUSSION

Recent surveys for *E. maculatum* in California have nearly tripled the number of known localities and extended the known range both latitudinally and altitudinally (Fig. 1). All 14 pre-1990 locality records (Table 1) are represented by single specimens (except Yosemite Valley, where single

specimens were collected 20 years apart). Five localities are on the east side of the Sierra Nevadan crest in the Owens Valley or in deserts east of the southern Sierra Nevada. Four additional records are from southern California, the Mojave desert in the east and San Diego in the west. On the western side of the Sierra Nevadan crest, there is a cluster of records in the central Sierra Nevada between Yosemite Valley and Sequoia National Park, ranging from the margin of the Central Valley (Friant) at 104 m to Wilsonia at 2,012 m in elevation. The type specimen is isolated geographically as the only record in the southern Coast Range. There is another isolated record from Palo Cedro, 360 km N of the nearest pre-1990 locality. Most pre-1990 sites are at low elevations. All but one (Wilsonia) are $< 1,500$ m; 11 are < 500 m.

Between 1992 and early 1997, we surveyed 75 localities and detected *E. maculatum* at 24 sites (Table 1, Fig. 1). *E. maculatum* was mist netted at two sites (Yosemite Valley in Yosemite National Park and Giant Forest Village in Sequoia National Park). All other records were acoustic, generally augmented by visual observations. Although we revisited the exact locality or close vicinity of nine of the pre-1990 localities, we detected *E. maculatum* at only one of these (Yosemite Valley). We also detected the species at 23 new localities, but many of those were concentrated geographically.

New records alter the historic perspective on this species' distribution in several ways. These records document a range extension for *E. maculatum* in northern California. A single *E. maculatum* was first detected in the northern Coast Range in July 1993 at Castle Lake, followed in July 1994 by observation of a population on the south margin of nearby Castle Crags State Park. Additional localities within a 10-km radius of Castle Crags, where multiple individuals could be detected predictably, were identified in summer 1995. Although the type specimen had come from the Coast Range,

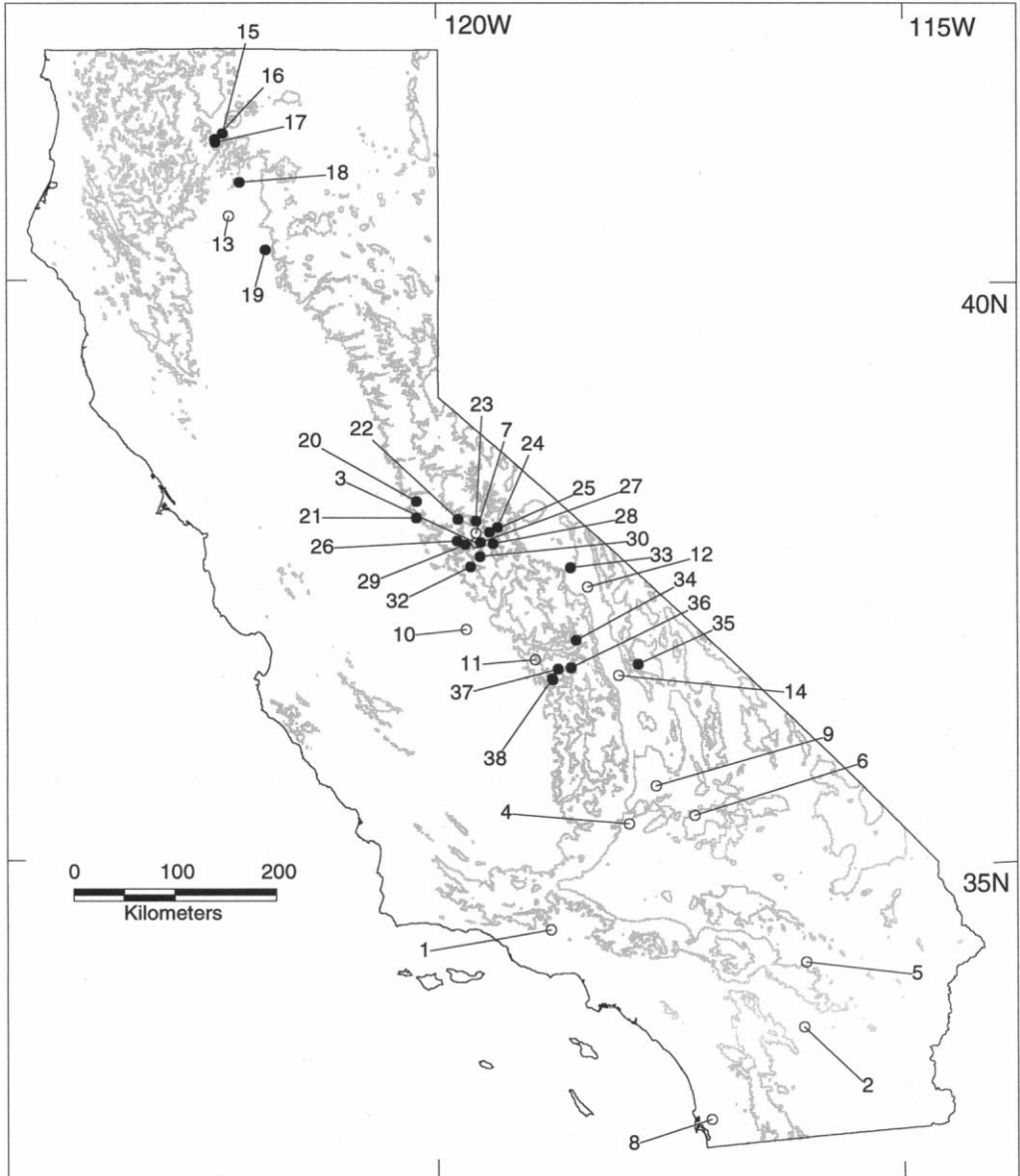


FIG. 1.—Map showing records for *E. maculatum* in California, including pre-1990 (all specimens) and post-1990 records (acoustic and capture-release) from the present study. Each number refers to a locality in Table 1. Pre-1990 records are represented by open circles and ordered chronologically. Post-1990 records are represented by closed circles and ordered latitudinally from north to south. Elevation contours are in 1,000 m intervals.

770 km to the south, we did not detect the species at that site, nor at any of nine intervening sites sampled in the Coast Range. There also have been two recent detections to the east in the foothills of the southern

Cascade-northern Sierra Nevada ranges. One is from Squaw Creek, NE of Shasta Lake, the other from Lassen National Forest, E of Red Bluff (T. Rickman, pers. comm.). These bracket the previously iso-

TABLE 1.—*Pre-1990 and post-1990 locality records for spotted bats in California. For data collected post-1990, an asterisk(*) following the locality name indicates areas in which the species was detected on multiple occasions, or at more than one local site. Date given is for the first record. A locality is defined as a 10-km radius around the site of original detection.*

Map reference	Date	County	Locality
Pre-1990			
1	April 1890	Ventura	Castaic Creek
2	1 October 1907	Riverside	Mecca
3	1 August 1931	Mariposa	Yosemite Valley
4	1 December 1933	Kern	Red Rock Canyon
5	1 May 1939	San Bernardino	Twentynine Palms
6	22 March 1948	San Bernardino	Pilot Knob
7	13 August 1951	Mariposa	Yosemite Valley
8	9 September 1955	San Diego	University of California, San Diego Campus
9	24 January 1956	San Bernardino	China Lake
10	6 June 1970	Fresno	Friant Dam
11	20 June 1975	Fresno	Wilsonia, King's Canyon National Park
12	11 May 1977	Inyo	Bishop
13	14 March 1983	Shasta	Palo Cedro
14	9 August 1985	Inyo	Lone Pine
Post-1990			
15	31 July 1993	Siskiyou	2 km S of Mt. Shasta City*
16	8 August 1993	Siskiyou	Castle Lake*
17	1 July 1994	Shasta	Castle Crags State Park*
18	23 August 1995	Shasta	Squaw Creek/Ash Creek
19	11 September 1996	Tehama	Finley Lake, Lassen National Forest
20	19 July 1995	Tuolumne	Mi Wok Ranger District, Stanislaus National Forest*
21	11 July 1995	Tuolumne	Tuolumne*
22	26 August 1992	Tuolumne	Hetch Hetchy Reservoir, Yosemite National Park*
23	10 August 1994	Mariposa	Pate Valley, Yosemite National Park
24	2 September 1995	Tuolumne	Tuolumne Meadow, Yosemite National Park
25	24 July 1996	Mariposa	Tenaya Lake, Yosemite National Park*
26	5 August 1994	Mariposa	Crane Flat, Yosemite National Park*
27	19 July 1993	Mariposa	Yosemite Valley, Yosemite National Park
27	29 August 1995	Mariposa	Yosemite Valley, Yosemite National Park
27	6 September 1995	Mariposa	Yosemite Valley, Yosemite National Park
27	1 July 1992	Mariposa	Yosemite Valley, Yosemite National Park*
28	9 October 1996	Mariposa	Merced Lake, Yosemite National Park
29	11 August 1994	Mariposa	Cascade Creek, Yosemite National Park*
30	25 August 1995	Mariposa	Ostrander Lake, Yosemite National Park
31	3 September 1996	Mariposa	Briceburg*
32	12 August 1994	Mariposa	Wawona, Yosemite National Park*
33	12 April 1997	Mono	Owens River Gorge*
34	29 August 1994	Fresno	Muro Blanco, Kings River, Sequoia National Park
35	10 April 1997	Inyo	Hunter Canyon, Saline Valley
36	10 September 1993	Tulare	Deadman Canyon, Sequoia National Park
37	3 September 1993	Tulare	Twin Lakes, Silliman Pass, Sequoia National Park
38	13 September 1995	Tulare	Giant Forest Village, Sequoia National Park
38	11 September 1995	Tulare	Giant Forest Village, Sequoia National Park*

TABLE 1.—*Extended*

Elevation (m)	Latitude and longitude	Data type	Source
296	34°24'55"N 118°47'35"W	Museum specimen	Allen, 1891
-55	33°34'18"N 116°04'35"W	Museum specimen	Grinnell, 1910
1,219	37°44'43"N 119°35'50"W	Museum specimen	Ashcraft, 1932
244	35°19'30"N 117°56'59"W	Museum specimen	Hall, 1939
183	34°08'08"N 116°03'12"W	Museum specimen	Benson, 1954
366	35°23'50"N 117°14'48"W	Visual observation	Parker, 1952
1,219	37°44'41"N 119°35'39"W	Museum specimen	Parker, 1952
15	32°46'36"N 117°04'12"W	Museum specimen	August and Dingman, 1973
213	35°39'03"N 117°39'39"W	Museum specimen	Stager, 1957
152	36°59'57"N 119°42'12"W	Museum specimen	Medeiros and Heckman, 1971
2,012	36°44'20"N 118°57'30"W	Museum specimen	California Academy of Sciences #1671
1,250	37°21'49"N 118°23'39"W	Museum specimen	Constantine et al., 1979
141	40°33'50"N 122°14'16"W	Specimen discarded	Bleich and Pauli, 1988
1,138	36°36'22"N 118°03'43"W	Museum specimen	Bleich and Pauli, 1988
1,000	41°16'42"N 122°18'04"W	Recorded calls	This study
1,657	41°13'39"N 122°22'57"W	Recorded calls	This study
646	41°12'00"N 122°22'46"W	Recorded calls	This study
411	40°51'20"N 122°07'28"W	Auditory detection	This study
856	40°16'13"N 121°51'04"W	Auditory detection	T. Rickman, pers. comm.
1,050	38°06'09"N 120°14'12"W	Auditory detection	T. Rickman, pers. comm.
823	37°57'39"N 120°14'11"W	Recorded calls	T. Rickman, pers. comm.
1,163	37°56'51"N 119°47'13"W	Recorded calls	This study
1,320	37°56'00"N 119°35'45"W	Recorded calls	This study
2,652	37°52'38"N 119°21'45"W	Recorded calls	This study
2,484	37°50'09"N 119°27'11"W	Recorded calls	This study
1,790	37°45'34"N 119°47'59"W	Recorded calls	This study
1,248	37°44'55"N 119°32'53"W	Capture/release	This study
1,248	37°44'55"N 119°32'53"W	Capture/release	This study
1,248	37°44'55"N 119°32'53"W	Capture/release	This study
1,248	37°44'55"N 119°32'53"W	Recorded calls	This study
2,199	37°44'17"N 119°24'53"W	Auditory detection	This study
1,048	37°43'38"N 119°42'43"W	Recorded calls	This study
2,592	37°37'26"N 119°33'00"W	Auditory detection	This study
439	37°36'18"N 119°57'57"W	Recorded calls	This study
1,200	37°32'13"N 119°39'19"W	Recorded calls	This study
1,828	37°31'43"N 118°34'31"W	Recorded calls	This study; P. Brown, pers comm.
2,840	36°54'34"N 118°31'16"W	Auditory detection	This study
475	36°42'08"N 117°50'55"W	Recorded calls	This study
2,926	36°40'18"N 118°42'25"W	Auditory detection	This study
2,879	36°39'30"N 118°42'54"W	Recorded calls	This study
1,940	36°34'38"N 118°46'29"W	Capture/release	This study
1,960	36°34'04"N 118°46'06"W	Auditory detection	This study

lated record from Palo Cedro (Bleich and Pauli, 1988).

Given the abundance of cliffs in the northern Coast Range, we expect that further investigations will reveal that the spotted bat is more widely distributed in northern California. The only regional surveys of mammalian distribution were conducted early in the century (Grinnell et al., 1930; Kellogg, 1916), prior to improvements in methods for surveying bats, and relatively few specimens were collected. Subsequent records for bats from the mountainous areas of northern California are limited to a few museum collections and a few published records (e.g., Marcot, 1984; Pearson et al., 1952; Pierson et al., 1996).

Euderma maculatum is distributed more widely in the Sierra Nevada than previously realized. Although *E. maculatum* had been found at high elevation in New Mexico and Arizona (Berna, 1990; Jones, 1965; Perry et al., 1997), with a record of 3,230 m (Reynolds, 1981), prior to 1992 the highest elevation locality for the species in California was Wilsonia at 2,012 m in Kings Canyon National Park. We observed *E. maculatum* at eight additional localities >2,000 m, the highest in Deadman Canyon in Sequoia National Park at 2,926 m. Multiple localities in Yosemite and Sequoia-Kings Canyon national parks also were found (Table 1, Fig. 1). Most detections at high elevation were of single individuals. Areas with the apparently largest concentrations—where multiple individuals could be repeatedly detected (e.g., Yosemite Valley, Hetch Hetchy Reservoir, and Wawona in Yosemite National Park)—were at mid-elevations (ca. 1,200–1,400 m). Multiple detections also were obtained at Giant Forest in Sequoia National Park (ca. 2,000 m) and the western Sierran foothills (ca. 800–1,100 m) in the vicinity of Sonora, where two large rivers, the Stanislaus and Tuolumne, are incised through blocks of limestone and separated by only ca. 20 km. The apparent gap in distribution in the northern Sierra

Nevada may be an artifact of lower sampling effort in this region.

The new records expand our perspective on suitable habitat for this species in California and lend definition to certain habitat constraints. Although the species in other parts of its range has been documented in a variety of habitats from desert scrub to montane coniferous forest (Best, 1988; Findley and Jones, 1965), it has been collected most often in rough desert terrain, with the majority of pre-1990 California records from low elevation xeric settings. The majority of new localities are mixed oak-conifer habitat (particularly black oak, *Quercus kelloggii*; ponderosa pine, *Pinus ponderosa*; incense cedar, *Libocedrus decurrens*). Sites at higher elevation are coniferous communities dominated by giant sequoia (*Sequoiadendron giganteum*) and red fir (*Abies magnifica*) or lodgepole pine (*P. contorta*) and white fir (*A. concolor*). A few sites at lower elevations are oak savannah (primarily *Q. lobata* and *Q. douglasii*). An association with ponderosa-pine habitat has been noted before (Berna, 1990; Findley and Jones, 1965; Handley, 1959; Navo et al., 1992; Watkins, 1977; Woodsworth et al., 1981).

Consistent with observations of Leonard and Fenton (1983) and Wai-Ping and Fenton (1989), we most commonly observed *E. maculatum* foraging over meadows (or old fields), generally in close proximity to trees. Their affinity for meadows was demonstrated by surveys we conducted in Yosemite Valley, where the species was detected at seven of 13 sites in meadows or wetlands, and at none of nine forested sites (which were sufficiently open that acoustic attenuation by the canopy was not a major bias). Our experience also indicates that the species can be easily missed if appropriate habitat is not surveyed. Mist netting over the Sacramento River near Castle Crags for 3 summers failed to detect *E. maculatum*. The species was first detected serendipitously in an old field 300 m from the river. Subsequent surveys revealed it could be predict-

ably detected at several meadows and old fields in the area but not in association with water, where other species were most readily found (Pierson et al., 1996). A single observation along the river in 1996 suggested, however, that the species may sometimes use the river as a flight corridor.

A significant constraining factor in the distribution of *E. maculatum* appears to be the availability of roosting habitat in cliffs. Wherever we found this species, there were substantial cliffs (granite, basalt, limestone, sandstone, and other sedimentary rock) within 10 km, suggesting that distribution of spotted bats is determined geomorphically. Such a constraint would help explain why the species has a patchy distribution and is relatively more common in places such as Yosemite Valley. While a number of bat species use crevices in a variety of substrates (rocks, trees, and anthropogenic structures such as buildings and bridges), spotted bats appear to be a nearly obligate cliff-roosting species. The new localities and expanded range identified in our study still suggest that distribution of this species is extremely patchy. The new records are attributable to continuing incremental improvement in survey techniques rather than a changing range in response to environmental change (Hafner and Schuster, 1996). As observed elsewhere, even with species-specific surveys, *E. maculatum* is rare relative to most co-occurring species (Fenton et al., 1987).

The linked pattern of rarity, restrictive roosting requirements, and patchy distribution raises concerns for the conservation of this species throughout its range. In mesic habitats, unvegetated cliffs are associated commonly with active stream or river channels that provide important resources and convenient corridors for people. Consequently, large-scale infrastructural development (notably highways and water impoundments) and associated alteration of the terrain often are concentrated heavily in these small areas. While *E. maculatum* may not currently face human-induced threats at

the most remote high-elevation sites, particularly within reserves, it may be affected at more accessible, moderate-elevation sites by highway construction, inundation by impoundments, rockfalls triggered by blasting for control of avalanches, intensive recreational climbing, and over-grazing of meadows. Similarly, populations in deserts may depend on production of insects in restricted relatively mesic habitats such as riparian corridors, washes, and bajadas. These areas are also foci for human development and are vulnerable to vehicular traffic, clearance of vegetation, water diversion, and dewatering by alien vegetation. Especially in arid landscapes, where surface water is limited, open waste sumps associated with oil production and cyanide-charged sources of water (process ponds and heap-leach pads) used in extraction of gold attract bats and other vertebrates and become significant causes of mortality (Clark and Hothem, 1991; Esmoil and Anderson 1995; Flickinger and Bunck, 1987).

Euderma maculatum is particularly well suited for survey by acoustic methods because its echolocation calls are relatively distinctive and its foraging patterns somewhat predictable. Additionally, the intensity and audible frequencies of its calls allow detection at distances up to 75 m (Navo et al. 1992; this study). In parts of its range, however, its echolocation call can be confused with that of other audible species (e.g., *Idionycteris phyllotis*—Simmons and O'Farrell, 1977; *Eumops perotis*—Vaughan, 1959). The primary limitations of acoustic surveys for any species are that they do not provide morphometric data or information on population parameters such as age, sex, and reproductive condition. While acoustic methods are extremely useful for many goals (e.g., assessing relative activity by site or season and species identification), considerable challenges remain in delineating the range of variation in call structure for many species from western North America.

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