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Habitat use by *Myotis yumanensis* and *Tadarida brasiliensis mexicana* in South San Francisco Bay wetlands: An Acoustic Study

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HABITAT USE BY *Myotis yumanensis* AND *Tadarida brasiliensis mexicana* IN SOUTH SAN FRANCISCO BAY WETLANDS: AN ACOUSTIC STUDY

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Master of Science

by
Theresa Marie Brickley
May 2012

The Designated Thesis Committee Approves the Thesis Titled

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by

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APPROVED FOR THE DEPARTMENT OF BIOLOGICAL SCIENCES

SAN JOSÉ STATE UNIVERSITY

May 2012

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ABSTRACT

HABITAT USE BY *Myotis yumanensis* AND *Tadarida brasiliensis mexicana* IN SOUTH SAN FRANCISCO BAY WETLANDS: AN ACOUSTIC STUDY

By Theresa Marie Brickley

Research on bat habitat use within coastal estuaries is limited. The purposes of my study were to determine whether Yuma myotis (*Myotis yumanensis*) and Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) differentiate between open water and marsh within saline and brackish habitats and to examine whether climatic factors are correlated with general activity and tidal height with foraging of the two species.
I recorded echolocation sequences over 30 survey nights in Alviso, California. Two Anabat II® detectors were randomly deployed each survey night in open salt water and salt marsh or open brackish water and brackish marsh. I identified *M. yumanensis* and *T. b. mexicana* sequences within each of the four habitats and feeding buzzes in open brackish water and brackish marsh. Additionally, I logged air temperature and wind speed per hour, percent moonlight visibility per survey night, and tidal height at 15-min intervals. I recorded 1,896 sequences, 845 from *M. yumanensis* and 983 from *T. b. mexicana*. For both species, there was a significant difference in frequency of occurrence and mean number of echolocation sequences per survey night in open water versus marsh for saline but not for brackish habitats. Furthermore, *T. b. mexicana* demonstrated greater preference than *M. yumanensis* for open salt water. Although the call frequency of *T. b. mexicana* increased with higher air temperature and lower moonlight visibility, the presence/absence of echolocation calls from the two species could not be predicted from the three climatic variables. Mean tidal height did not differ between *M. yumanensis* and *T. b. mexicana* sequences with feeding buzzes and sequences without buzzes in open brackish water and brackish marsh. The results increase our knowledge about bat habitat use in estuaries and provide important information to enhance bat conservation in coastal wetlands.

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Lastly, my parents supported me emotionally and financially throughout this journey. They supported my decision to study wildlife, encouraged me not to give up on my thesis, and helped me in every way they could. My mother’s strong grammatical and editing skills helped improve this manuscript and make important formatting changes. She worked with me for hours in front of the computer and even took time off work, while my father fulfilled helpful tasks such as preparing dinner, walking my dog, and finding books at the library. My parents have always been interested and involved in all aspects of my life be it school, sports, medical challenges, work, or personal problems. They instilled in me a strong academic work ethic and a love for nature with our annual camping trips. They taught me to be genuine and hard-working while always making me feel loved. Thank you Mom and Dad, this one’s for you.

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ABBREVIATIONS

▪ CF	Constant frequency echolocation calls
▪ FM	Frequency modulated echolocation calls
▪ WPCP	San José/Santa Clara Water Pollution Control Plant
▪ EEC	Environmental Education Center, Don Edwards San Francisco Bay National Wildlife Refuge
▪ CC	Coyote Creek mitigation area
▪ AS	Artesian Slough
▪ SBSPRP	South Bay Salt Pond Restoration Project
▪ Z-CAIM	Zero-crossings Analysis Interface Module (Anabat II$^{\circledR}$ recorder)
▪ RCB MANOVA	Randomized Complete Block Multivariate Analysis of Variance
▪ RCB ANOVA	Randomized Complete Block Analysis of Variance

INTRODUCTION

Background

Bats (order Chiroptera) are a unique and diverse taxonomic group and can serve as excellent animals for ecological research (Fenton 2003). In regards to feeding, reproduction, behavior, and morphology, they are more specialized than any other mammalian group (Feldhamer et al. 2007). Furthermore, their diet, reproduction, and habitat use have been researched in riparian, forested, woodland, tropical, agricultural, and suburban landscapes. My study aims to examine use of saline and brackish habitats by Yuma myotis (*Myotis yumanensis*) and Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) in the South San Francisco Bay. These two species forage over estuaries and salt marshes at the edge of the Bay (Johnston 2007). By studying multiple bat species that occur within the study locale, I can determine whether they differentiate between open water and marsh within saline and brackish habitats.

Description of Myotis yumanensis.—The Yuma myotis (*Myotis yumanensis*; Vespertilionidae) is a small (4.0−8.5 g) bat distributed in western North America from southern British Columbia to Mexico (Nagorsen and Brigham 1995). Estuarine and saline wetlands found in narrow belts on the West Coast of the United States (Mitsch and Gosselink 1986) including the San Francisco Bay, California (Carpelan 1957; Thébault et al. 2008), overlap with this species' range. Indeed, it is one of the few bats that has been observed flying over salt water in the Pacific Northwest (Nagorsen and Brigham 1995). Structures used as roosts include buildings, bridges, caves, mines, and large, live trees in close proximity to water (Barbour and Davis 1969; Evelyn et al. 2004; Nagorsen and Brigham 1995). Yuma myotis is a wetland obligate (Johnston 2007) and is more closely associated with water than any other North American bat species (Barbour and Davis 1969). It may even be restricted to foraging and roosting along linear stream systems (Evelyn et al. 2004). Foraging flights are within only 2 km (Evelyn et al. 2004) to 4 km (Nagorsen and Brigham 1995) of the roost. *M. yumanensis* forages low over permanent streams, rivers, ponds, and other aquatic habitats (Barbour and Davis 1969; Williams et al. 2006) where it gleans emerging adult aquatic insects off the water surface (Johnston 2002). Small-bodied insects of aquatic origin (Diptera and Trichoptera) are preferred as prey (Ober and Hayes 2008a). Occurrence near open water and dependence on small insects characterize this vespertilionid.

Description of Tadarida brasiliensis mexicana.—The Mexican free-tailed bat (*Tadarida brasiliensis mexicana*; Molossidae) is a 12.0−15.0 g bat in which the lower half of the tail extends beyond the interfemoral membrane (Barbour and Davis 1969; Fenton 2001). It is found throughout California (Freeman Long et al. 1998; Johnston 2007) and across the southern United States into Central and South America (Fenton 2001). This species is a habitat generalist and forages over estuaries, oak woodland, oak savannah, and agricultural lands (Johnston 2007). Foraging has also been documented along forest edges and over fields, ponds, and parking lots (Schwartz et al. 2007). *T. b. mexicana* is gregarious and often forms large nursery colonies, such as the 20 million bats in Bracken Cave, Texas (Freeman Long et al. 1998). It can fly at speeds averaging 40 km/h and at altitudes greater than 3,000 m above ground level (Williams et al. 1973). Moreover, it may fly 100 km or more in nightly feeding flights (Davis et al. 1962) that extend from soon after sunset until just before dawn (Krutzsch 1955). High, fast flight and an extensive foraging range result in the Mexican free-tailed bat consuming a variety of insects as prey (Lee and McCracken 2005; McWilliams 2005). Flexibility in habitat use and diet reflect the generalist tendencies of this common molossid bat.

Echolocation.—Bats are known for their ability to echolocate, which they use for orientation in space and finding of prey (Broders et al. 2004; Parsons 2002; Rankin and Lewis 2002). They emit high-frequency signals from the larynx and discern the returning echoes to detect, identify, and pinpoint the location of reflected objects (Schnitzler and Kalko 2001). Although echolocation is a relatively short-range mechanism (Fenton 1985), bats can identify the basic texture, shape, size, movement, and distance of objects (Feldhamer et al. 2007). Because different bats emit signals with particular characteristics, many species are acoustically distinguishable (Rydell et al. 2002). Constant frequency (CF) search calls are longer duration narrowband signals appropriate for detecting targets (Schnitzler and Kalko 2001) and differentiating between moving and stationary objects (Feldhamer et al. 2007). CF components are typical of *Tadarida* spp. (Schnitzler and Kalko 2001; Schwartz et al. 2007). Alternatively, frequency modulated (FM) calls are shorter duration broadband signals sweeping from high to low frequencies (Fenton 1985). Bats use FM components and often add harmonics to classify and localize targets (Feldhamer et al. 2007). High levels of frequency modulation ranging from steep to shallow slope are utilized by *Myotis* spp. (Rogers et al. 2006; Schnitzler and Kalko 2001). In addition to species identification, echolocation can provide details about bat foraging behavior. A "feeding buzz" is a portion of an echolocation sequence consisting of a burst of pulses with gradually decreasing duration, decreasing amplitude, and increasing frequency (McCracken et al. 2008). While general echolocation calls indicate that a bat is searching for prey or navigating from one place to another, a feeding buzz signifies that it is attempting to capture an insect (Fenton 1985; Gillam and McCracken 2007; Schnitzler and Kalko 2001). Producing many short pulses allows the bat to accurately pinpoint prey as the range decreases (Fenton 1985).

Individual bats can exhibit some flexibility in their use of echolocation calls (Parsons 2002). They may combine CF and FM signal elements to resolve the trade-off between target detection and localization (Schnitzler and Kalko 2001) or utilize one over the other depending on the degree of clutter in the environment (Broders et al. 2004; Wund 2006). *T. b. mexicana* is capable of adjusting its call frequency to decrease overlap with an interfering acoustic signal such as calling insects (Gillam and McCracken 2007). However, there are limits to acoustic flexibility (Schnitzler and Kalko 2001). Many species use a particular type of echolocation that, combined with their morphology, results in adaptation to and exploitation of specific habitat conditions (Aldridge and Rautenbach 1987; Avila-Flores and Fenton 2005; Limpens 2002; Rogers et al. 2006). Species with a lower body mass, low wing loading and aspect ratio (short, rounded wings), and high frequency FM calls are adapted for slower, more maneuverable flight in cluttered habitats (Aldridge and Rautenbach 1987), as observed in *M. yumanensis* (Brigham et al. 1992). Alternatively, a higher body mass, high wing loading and aspect ratio (long, narrow wings), and low frequency calls with CF or shallow FM components adapt a species for faster, less maneuverable flight at high heights and in relatively open habitats (Aldridge and Rautenbach 1987; Menzel et al. 2005b). This type of echolocation and flight is representative of *Tadarida* spp. (Aldridge and Rautenbach 1987).

I predicted that the different echolocation and morphology of *M. yumanensis* and *T. b. mexicana* would influence their habitat use within the Alviso wetlands.

Acoustic Monitoring.—Bat habitat use is challenging to study directly as bats are nocturnal, usually in flight when foraging, and emit high-intensity echolocation calls that are inaudible to humans (Vaughan et al. 1997). However, bats can be monitored with relative efficiency and minimal effort through acoustic monitoring (Rydell et al. 2002; Williams et al. 2006). For more than two decades, detectors have served as a non-invasive tool to research basic aspects of bat ecology (Broders et al. 2004). Bat detectors are receivers that transform ultrasonic echolocation calls into the human hearing range and allow the physical content of recorded signals to be viewed and analyzed (Parsons et al. 2000). Detectors are objective, repeatable, and do not interfere in bats' normal activities (Johnston 2002). Researchers can record throughout the night and sample multiple locations concurrently without being present (Williams et al. 2006). More importantly, distribution and habitat associations of many bat species can be determined (Broders et al. 2004; Vaughan et al. 1997).

Despite the benefits, there are inherent limitations associated with bat detectors (Gannon et al. 2003). The Anabat system uses analysis by zero-crossing period meters, which do not show the original time-amplitude versions of calls (Fenton et al. 2001; Parsons et al. 2000). Furthermore, some of the physical details in the call such as harmonic information are lost in the transformation process and only the strongest signal received at any one time is displayed (Limpens and McCracken 2002; Rydell et al. 2002). Acoustic sampling does not provide gender, age, or reproductive information (Williams et al. 2006), and unless feeding-specific calls are recorded, a researcher does not know if a bat was navigating through an area or foraging there (Johnston 2007). The number of bats present in an area cannot be deduced from the number of sequences recorded (Johnston 2002). Lastly, some species are more difficult to detect acoustically (Parsons 2002). Based on these limitations, it is important to identify what type of biological information will be inferred from recorded calls (Gannon et al. 2003). If a researcher is mainly interested in spatial information and species of interest can be recorded and distinguished from other local species, any ultrasonic recording system is suitable (Broders et al. 2004). Furthermore, the Anabat system is well suited for multi-species studies because it can simultaneously detect all bat frequencies (Limpens and McCracken 2002; Walsh et al. 2002). I examined spatial distribution of *M. yumanensis* and *T. b. mexicana*, two species that could be detected in the Alviso estuary and acoustically differentiated. Therefore, acoustic monitoring was an appropriate tool for my study.

San Francisco Bay Wetlands.—Since the early 20th century, the San Francisco Bay has lost more than 85% of historic tidal wetlands due to draining and diking for agriculture, urban development, and salt production (Swanson et al. 2004). Native salt marsh has been converted into large, shallow, hypersaline ponds managed for solar evaporation salt production (Thébault et al. 2008), resulting in a significant loss of habitat. In 2003, the United States Fish and Wildlife Service and California Department of Fish and Game purchased 6,110 hectares of former commercial salt ponds from Cargill Salt, which were then decommissioned and opened to exchange with the Bay or adjacent sloughs. The ponds are intermittently flooded with Bay water (Goals Project 2000), and most are part of the South Bay Salt Pond Restoration Project (SBSPRP), the largest wetlands restoration program in the western United States (Thébault et al. 2008). The SBSPRP aims to restore thousands of acres of lost tidal wetlands in Alameda, Santa Clara, and San Mateo counties, California, that will provide for flood management and create a mix of habitats (Swanson et al. 2004). Alviso, a small community in San José, Santa Clara County, California, comprises one segment of these managed wetlands. It meets the southern tip of the San Francisco Bay and was the study locale for fieldwork in my thesis.

Habitat Use

Few studies have examined how individual bat species are spatially distributed among the different habitats that intermingle within a coastal wetland ecosystem. Estuarine habitats vary in degree of salinity (brackish to saline) and degree of vegetation (open water to marsh). Whether foraging bats use particular habitats more than others is poorly understood. I hypothesized that *Myotis yumanensis* and *Tadarida brasiliensis mexicana* spend more time in saline and brackish open water habitats than in marsh habitats. Menzel et al. (2005a) found that bat activity is concentrated over Carolina bays within the Atlantic Coastal Plain of the southeastern United States. This highlights the importance of wetlands to foraging bats, but information is needed in other coastal areas and for other types of wetlands. *M. yumanensis* forages over tidal sloughs, associated brackish marshes, and salt marshes along the lower watershed of the Guadalupe River in the South San Francisco Bay (Johnston et al. 2003). I wanted to expand upon these observations by comparing bat use of open water and marsh habitats within a Pacific Coast estuary.

Due to challenges in researching highly mobile, nocturnal organisms, basic aspects of ecology remain unknown for most bat species including the relative importance of different habitats (Walsh and Harris 1996). Lack of knowledge about habitat use in estuaries makes it difficult for land managers to include bats in the decision-making process of restoration efforts. The SBSPRP is a complex, long-term project resulting in significant changes in the landscape. Managers struggle to determine the appropriate balance between maintaining salt ponds versus conversion to tidal salt marsh (Thébault et al. 2008). To maximize ecological benefits of restored areas, concrete biological data is needed (Swanson et al. 2004) including the value of different habitats to wildlife species and habitat features that are important to preserve. My study will provide insight into how two local bat species, one being a wetland-obligate, utilize open water and marsh habitats within the Alviso estuary.

Air Temperature, Wind Speed, and Moonlight Visibility

Bat activity is influenced by existing weather conditions (e.g., Erkert 1982; Vaughan et al. 1997). However, most research examining the impact of climatic variables on bat activity levels has been conducted in forested, riparian, and woodland habitats where canopy coverage, windbreaks, and varying degrees of light penetration exist (e.g., Fenton et al. 1977; Hecker and Brigham 1999; Lang et al. 2006; Seidman and Zabel 2001). In contrast, the South San Francisco Bay is mostly composed of open habitats with greater exposure to abiotic elements. I hypothesized that *Myotis yumanensis* and *Tadarida brasiliensis mexicana* activity in the Alviso wetlands covaries with air temperature, wind speed, and moonlight visibility. Vaughan et al. (1997) found that total bat activity was positively correlated with air temperature, whereas other authors found no effect of temperature (Hecker and Brigham 1999; Rogers et al. 2006; Seidman and Zabel 2001). Wind speed is occasionally omitted in analyses of environmental factors (Rogers et al. 2006) or found to be insignificant (Hecker and Brigham 1999; Vaughan et al. 1997). Some studies found no direct connection between moonlight visibility and bat activity (Anthony et al. 1981; Rogers et al. 2006; Vaughan et al. 1997), while others reported that bats adjusted when they foraged (Lang et al. 2006) and where they foraged (Fenton et al. 1977; Hecker and Brigham 1999) in response to lunar light intensity. It is unknown to what extent air temperature, wind speed, and moonlight visibility influence bats within the open space of estuarine wetlands and if these variables have the same effects as observed in other habitats. Therefore, I wanted to examine whether these climatic factors are correlated with general activity of *M. yumanensis* and *T. b. mexicana* in the Alviso wetlands.

Tidal Height

An estuary is an enclosed coastal water body with a free connection to the sea and a measurable saline quantity in its waters (Clark 1977). Sloughs in the South San Francisco Bay are subject to two high tides and two low tides daily, resulting in variable water height, flow, and salinity levels. Tidal flow provides important functions in estuaries by transporting nutrients and suspended organisms while flushing out wastes (Clark 1977). Tidal flow can also regulate patterns of locomotion activity in insect species (Craig 1970; Foster 1983; Foster et al. 1979). The emergence of an intertidal midge on the Japanese coast was synchronized with the tidal cycle (Saigusa and Akiyama 1995), and higher insect emergence rates were found in flooded agricultural fields (Moss et al. 2009). Because degree of flooding was correlated with insect emergence and *M. yumanensis* forages on emergent adult aquatic insects (Johnston 2002), this suggested a potential relationship between tidal height and bat foraging. I hypothesized that *Myotis yumanensis* and *Tadarida brasiliensis mexicana* feeding activity in open brackish water and brackish marsh habitats is correlated with tidal height. Wildlife species exhibit variable responses to the stress of tidal conditions. Marsh rice rats venture from the tidal marsh to uplands to seek refuge during high tide (Kruchek 2004). Sanderlings near

Bodega Bay, California, forage on outer beaches at high and medium tide but move to harbor sandflats at low tide. This corresponds to density of prey species, suggesting that sanderlings alternate between foraging habitats on a tidal basis to maximize prey consumption (Connors et al. 1981). Some aquatic insects retreat up plant stems to emergent parts during incoming tide (Davis and Gray 1966) while others can remain completely submerged (Brown 1948; Cameron 1976). Response by foraging bats to an increase or decrease in estuarine waters is poorly understood. Because *M. yumanensis* forages over tidal waters in the South San Francisco Bay (Johnston et al. 2003), I predicted that echolocation sequences with feeding buzzes would be correlated with periods of higher tidal height.

METHODS

Study Area

I chose Alviso, California (37°27′N, 121°57′W), as the general study locale because it is occupied by both *M. yumanensis* and *T. b. mexicana*, and it encompasses my four habitats of interest. I identified marsh habitats based on dominant percent vegetative cover, which I visually estimated using a square meter grid. I defined salt marsh as a patch of muted tidal marsh ≥15 m with pickleweed (*Salicornia virginica*) and/or alkali heath (*Frankenia salina*) representing ≥80% of the vegetative cover (Fig. 1). Muted marsh is wetland habitat that is managed for wildlife, and the amount of tidal inundation is regulated by the opening and closing of water control gates. I defined brackish marsh as a patch ≥15 m bordering a tidally influenced channel with California bulrush (*Scirpus* *californicus*) and/or alkali bulrush (*Scirpus robustus*) representing ≥80% of the vegetative cover (Fig. 2). Bulrush species dominate low marsh in brackish marsh habitat (Boursier et al. 2008; Goals Project 2000; Mitsch and Gosselink 1986). I identified open water habitats based on salinity level and physical structure. I defined open salt water as a permanent water body ≥15 m wide, ≥10 cm deep, and >15 parts per thousand (ppt) salinity (Fig. 3). I defined open brackish water as a permanent, linear water course with a free connection to the South San Francisco Bay (Fig. 4). The variable influence of freshwater flows and daily tides resulted in fluctuating salinity with levels ranging from 1.8−25.5 ppt. Open brackish water habitat included portions of Artesian Slough, Coyote Slough, and Coyote Creek. Coyote Creek is bordered by long, narrow strips of riparian forest as opposed to open, dense stands of bulrush.

FIG. 1.—Salt marsh habitat (New Chicago Marsh), Alviso, California. Dominant vegetation: pickleweed (*Salicornia virginica*); alkali heath (*Frankenia salina*). (Photo by Theresa M. Brickley.)

FIG. 2.—Brackish marsh habitat (between Artesian Slough and salt pond A16), Alviso, California. Dominant vegetation: California bulrush (*Scirpus californicus*). (Photo by Theresa M. Brickley.)

FIG. 3.—Open salt water habitat (salt pond A16), Alviso, California. (Photo by Theresa M. Brickley.)

FIG. 4.—Open brackish water habitat (Artesian Slough), Alviso, California.
(Photo by Theresa M. Brickley.)

My study was conducted in three contiguous areas in Alviso, California, each of which contained all four habitats (Fig. 5). The study areas included: 1) San José/Santa Clara Water Pollution Control Plant (WPCP); 2) Don Edwards San Francisco Bay National Wildlife Refuge, Environmental Education Center (EEC); and 3) Coyote Creek mitigation area (CC). Artesian Slough (AS) within the WPCP receives 386 million liters of treated wastewater daily from the adjacent wastewater treatment plant. Wastewater inputs contribute to the very high nutrient concentrations found in the South San Francisco Bay (Thébault et al. 2008). A16 and A18 are two of 25 salt ponds in Alviso, which is one of three pond complexes of the SBSPRP. Although bounded by levees, A16 and A18 are each fitted with one inlet and one outlet constructed as one-way tide culverts; the inlet allows brackish water from AS to enter the ponds at high tide while the outlet discharges pond water into AS at low tide (Thébault et al. 2008). A16

(98 hectares) and A18 (330 hectares) are expansive and shallow, with the latter having a mean depth of 0.5 m (Carpelan 1957) to 0.7 m (Thébault et al. 2008).

FIG. 5.—Placement of Anabat II® detectors to record *Myotis yumanensis* and *Tadarida brasiliensis mexicana* in four habitats of South San Francisco Bay wetlands; 10 August−9 October 2009, Alviso, California. WPCP = San José /Santa Clara Water Pollution Control Plant; EEC = Environmental Education Center, Don Edwards San Francisco Bay National Wildlife Refuge; CC = Coyote Creek mitigation area. (Map by Samatha Moturi, H.T. Harvey & Associates, by permission.)

Experimental Design

Measuring Habitat Use.—I used echolocation call sequences as an indicator of bat habitat use, and potentially, feeding frequency of individual free-flying *M. yumanensis* and *T. b. mexicana* in open salt water, salt marsh, open brackish water, and brackish marsh habitats. To detect echolocation calls, I used calibrated Anabat II® detectors and Zero-crossings Analysis Interface Modules (Z-CAIM) recorders (Titley Electronics, Ballina, New South Wales, Australia). I deployed detectors at 15 sampling points (stationary locations where acoustic equipment was physically positioned overnight) within each of the four habitats at three study areas (WPCP, EEC, and CC; Table 1).

TABLE 1.—Locations of acoustic sampling points of four habitats within WPCP, EEC, and CC[a] study areas from 10 August−9 October 2009, Alviso, California.

STUDY AREA	**HABITAT**			
	Open brackish water	**Brackish marsh**	**Open salt water**	**Salt marsh**
WPCP	Artesian Slough − Pond A18 outlet	E of Artesian Slough, <800 m upstream of Pond A18 outlet	Pond A18 − S/SW corner	E of Artesian Slough, SE of the Weir Bridge
	Artesian Slough − ~50 m upstream of the Weir Bridge			
	unnamed slough at S end of A18			
EEC	Artesian Slough − Pond A16 outlet	W of Artesian Slough, <450 m upstream of Pond A16 outlet	Pond A16 − SE corner	New Chicago Marsh
	Artesian Slough − floating dock at SE corner of A16	NE of the refuge gate	W of the pedestrian footbridge	W/SW of the parking lot
CC	Coyote Creek (tidal portion)	W of the Coyote Slough tide culvert (N side of the road)	Bird Island Pond − W side	Bird Island Pond − SE corner
	Coyote Slough − tide culvert	E of the Coyote Slough tide culvert (N side of the road)	Bird Island Pond − S side	W of NW corner of Bird Island Pond

[a] **WPCP** = San José /Santa Clara Water Pollution Control Plant; **EEC** = Environmental Education Center, Don Edwards San Francisco Bay National Wildlife Refuge; **CC** = Coyote Creek mitigation area.

Ideally, I would have sampled all four habitats on any given survey night, but as I had access to only two Anabat II® detectors, I sampled either saline or brackish habitat while making sure to sample both open and marsh each survey night (i.e., open salt water and salt marsh or open brackish water and brackish marsh). I randomized the study area and the locations of sampling points each survey night. I collected acoustic data over 30 survey nights (60 detector nights) from 10 August−09 October 2009 (WPCP: *n* = 9 survey nights; EEC: *n* = 12 survey nights; CC: *n* = 9 survey nights). I sampled saline habitats for 15 nights and brackish habitats for 15 nights. At each of the two randomly selected sampling points on a survey night, I housed the Anabat II® detector and Z-CAIM recorder in an ammo box and deployed it from sunset to sunrise with ≥90% of the projected area of the microphone covering one of the four habitats. I recorded throughout the night as opposed to three hours after sunset because levels of bat activity vary considerably within nights (Hayes 1997). I placed detectors within 3 m of the edge of open water or marsh at a 45° angle at ground level with no vegetation obstructing reception of bat echolocation calls (Seidman and Zabel 2001). However, at open brackish water sampling points, I had to secure detectors to a levee, bank, floating dock, or tide culvert elevated above the slough channel to protect them from tidal inundation. To ensure that all sampling points surveyed equal amounts of space (Menzel et al. 2005b), I set all detectors to a sensitivity of 5-6 and division ratio of 16. I tested acoustic equipment prior to deployment (Williams et al. 2006) and rotated equipment among sampling points to account for any variation among detectors (Seidman and Zabel 2001). I assumed that all sampling points had an equal chance of being used by *M. yumanensis* and *T. b. mexicana* and that all Anabat II® detectors had an equal ability of detecting bat echolocation calls. Furthermore, I recorded the relative abundance of specific species of insects while deploying detectors because food habits among bats are specific for a local area (Nagorsen and Brigham 1995).

I obtained approval for my study from the Institutional Animal Care and Use Committee of San José State University (Protocol #2009-B, Approval date 1 June 2009). I obtained access permits from the United States Fish and Wildlife Service, Don Edwards

San Francisco Bay National Wildlife Refuge (EEC study area) and City of San José, Environmental Services Department, San José/Santa Clara Water Pollution Control Plant (WPCP and CC study areas) to deploy Anabat II® detectors and Z-CAIM recorders within the four habitats over the 30 survey nights.

Analysis of Echolocation Calls.—I used Analook™ software to differentiate between recorded *M. yumanensis* and *T. b. mexicana* sequences. Each individual sequence represented one "bat pass" and was plotted on its own acoustic file representing frequency (kHz) x time display (Avila-Flores and Fenton 2005; Gillam and McCracken 2007; Parsons et al. 2000). Each acoustic file had a maximum recording time of one minute. I defined a bat pass as a series of ≥ 2 consecutive echolocation calls produced by a single bat as it flew within range of the microphone of a detector (Johnston 2002). Because detectors cannot discern the number of bats recorded, an individual bat may have been recorded more than once in or among habitats (Hayes et al. 2009; Seidman and Zabel 2001; Wund 2006). Thus, recordings served as a relative measure of activity rather than abundance (Seidman and Zabel 2001; Vaughan et al. 1997; Walsh et al. 2002). The number of recorded passes per sampling point per habitat over the 30 survey nights served as an estimate of bat activity within open salt water, salt marsh, open brackish water, and brackish marsh (Walsh et al. 2002). I qualitatively identified recorded echolocation calls to species or genus by matching them to known sequences from an acoustic library (Menzel et al. 2005a; Parsons 2002; Walsh et al. 2002). Acoustic parameters extracted from each sequence included bandwidth (the range of

frequencies in a call—Limpens 2002); pulse shape including frequency modulated (FM) and constant frequency (CF) components (Limpens and McCracken 2002; Rydell et al. 2002); minimum and maximum frequency (kHz—Aldridge and Rautenbach 1987; Broders et al. 2004; Gillam and McCracken 2007); call duration (ms; the duration of the extracted waveform—Parsons 2002); and repetition rate determined by the duration of pulses and inter-pulse intervals (Limpens 2002; Rydell et al. 2002). I was able to differentiate *M. yumanensis* and *T. b. mexicana* passes as the two species produce structurally different echolocation signals with different minimum frequencies.
M. yumanensis emits steep and shallow FM search calls with a minimum frequency of 45−50 kHz (O'Farrell et al. 1999; Fig. 6) while *T. b. mexicana* produces long CF signals with a minimum frequency of 20−25 kHz (Schwartz et al. 2007; Fig. 7). When I recorded an individual *M. yumanensis* and individual *T. b. mexicana* echolocation call at the same sampling point within one sample period (Fig. 8), I assigned one sequence to each of the two species.

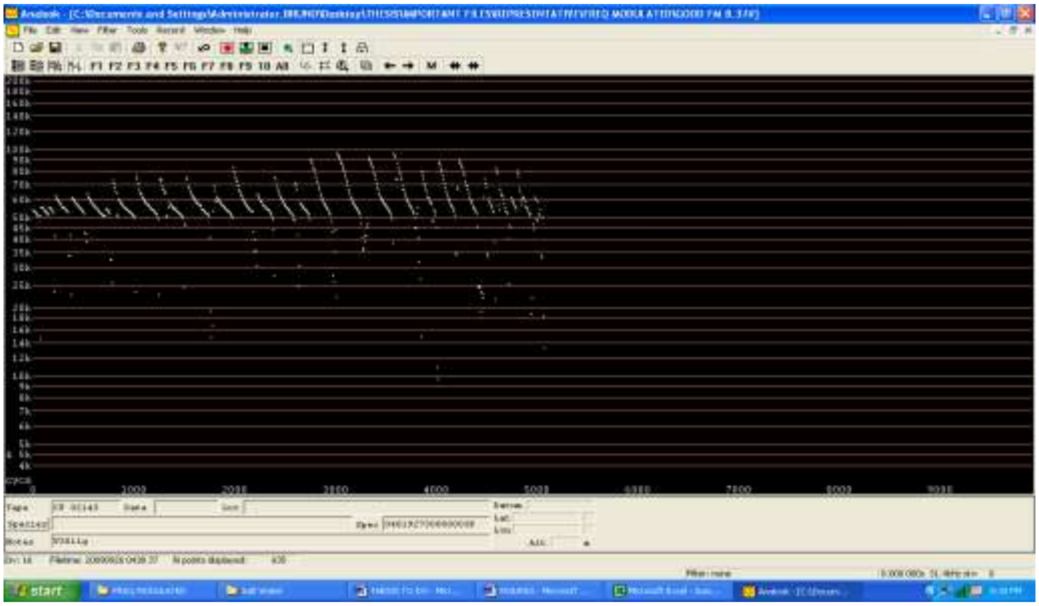

FIG. 6.—*Myotis yumanensis* frequency modulated (FM) search echolocation calls recorded on 26 September 2009, Alviso wetlands, California.

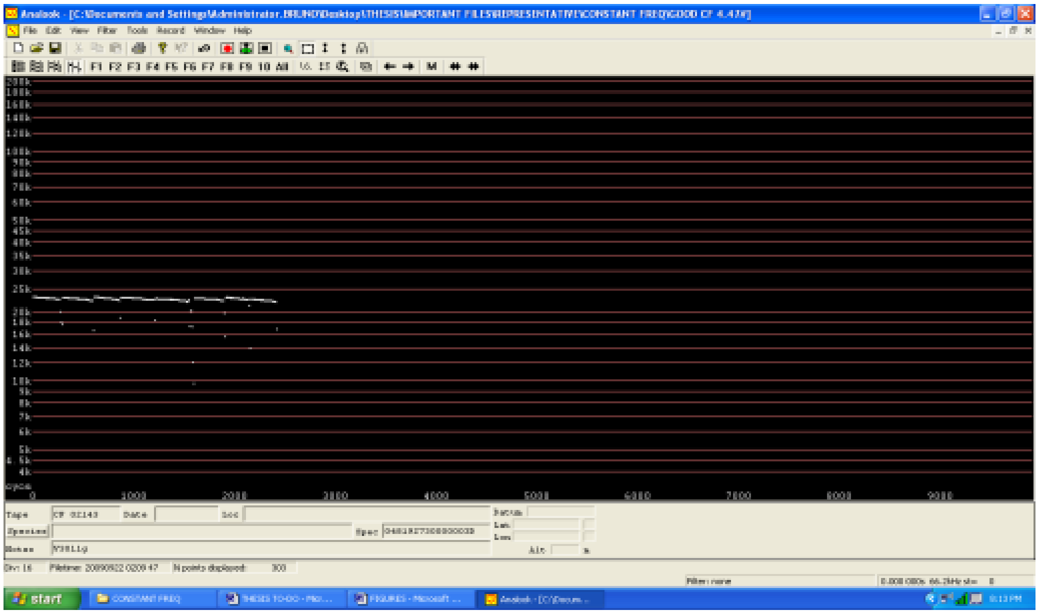

FIG. 7.—*Tadarida brasiliensis mexicana* constant frequency (CF) search echolocation calls recorded on 22 September 2009, Alviso wetlands, California.

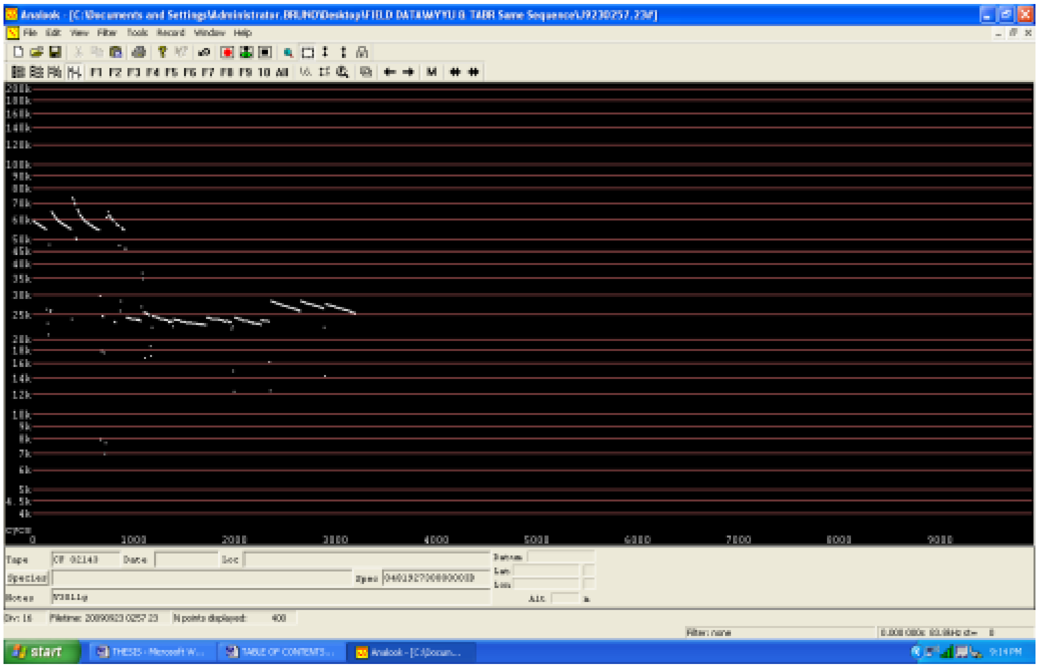

FIG. 8.—*Myotis yumanensis* and *Tadarida brasiliensis mexicana* echolocation calls recorded in the same acoustic file within one sample period; 23 September 2009, Alviso wetlands, California.

Although the acoustic signatures of *M. yumanensis* and a closely related species *Myotis californicus* are both 50 kHz (O'Farrell et al. 1999), I have confidence that the passes I attributed to *M. yumanensis* are in fact that species. Previous survey efforts in Alviso have never detected or captured *M. californicus* (D. S. Johnston, pers. comm.), and O'Farrell et al. (1999) has shown that calls from *M. californicus* approach and commonly exceed 100 kHz, are shorter in duration, and tend to be linear. Sequences that were atypical, too fragmentary, included extraneous noise (Broders et al. 2004), or contained only one search call were classified as "unidentified." Those with a minimum frequency of 35−40 kHz were classified as "*Myotis* spp." because closely related species of Myotis may not be acoustically identifiable due to similarities in calls (Johnston 2002).

Lastly, passes from non-target bat species such as western red bats (*Lasiurus blossevillii*) and hoary bats (*L. cinereus*) were identified but not subject to analyses.

Habitat Use

To determine if *M. yumanensis* and *T. b. mexicana* showed different habitat usage, I examined the relationship between the frequency of occurrence of each species and the different habitats. Frequency of occurrence was based on the number of sampling points per habitat (*n* = 15) in which $\geq$1 pass was recorded. For each species, I used a 2 x 2 Test of Independence using the Log-Likelihood Ratio Test (Sokal and Rohlf 1987) to determine whether there was a significant difference in presence of these species within the four habitats. The two variables were degree of salinity (saline/brackish) and degree of vegetation (open water/marsh).

I used a Randomized Complete Block Multivariate Analysis of Variance (RCB MANOVA; test statistic was Wilks' Lambda—Zar 2010) to determine if *M. yumanensis* and *T. b. mexicana* differed in use of open water and marsh within saline and brackish habitats. I analyzed data from saline and brackish habitat separately. The independent variable was degree of vegetation (open water/marsh) while the dependent variables were the mean number of passes for each species per survey night. To resolve whether sampling for saline and brackish habitat on different nights affected bat habitat use results, I used survey nights as the blocking variable (*n* = 30 blocks). Using a randomized-block design ensured that the acoustic data I collected reflected habitats sampled rather than nightly climatic variation. To examine effects of degree of vegetation on individual species, I used an RCB ANOVA (Zar 2010) for each species and each degree of salinity.

Air Temperature, Wind Speed, and Moonlight Visibility

I used a Canonical Correlation Analysis (Sokal and Rohlf 1987) to investigate whether there was a relationship between echolocation call frequencies of *M. yumanensis* and *T. b. mexicana* and environmental parameters. Measuring appropriate environmental parameters accounts for the variation in ambient conditions during sampling (Walsh et al. 2002). Thus, I recorded air temperature (°C) and wind speed (m/s) per hour between 2000−0600 h during each survey night (National Oceanic and Atmospheric Administration, National Weather Service 2009). Furthermore, sunset, sunrise, and moonlight visibility (%) per survey night were obtained for San Francisco Bay, Coyote Creek, Tributary #1 (the sampling station nearest my study areas) from Tide High and Low, Inc. (1999-2011). Moonlight visibility, or the percentage of the moon face illuminated (Ford et al. 2006; Rogers et al. 2006), indicated the amount of light available to bats during foraging. Because a high number of passes (>150) were recorded on three of the 30 survey nights, I used the log+1 transform of call frequencies of both species to reduce the effect of high outliers in the analysis. I computed the means of air temperature, wind speed, moonlight visibility, transformed call frequency of *M. yumanensis*, and transformed call frequency of *T. b. mexicana* for each of four 3-hour time intervals (0.0−2.9, 3.0−5.9, 6.0−8.9, and 9.0−11.9 h after sunset) over the 30 survey nights. The first suite of variables (species) included mean echolocation call frequencies of *M. yumanensis* and of *T. b. mexicana*; the analysis included sampling points with no recorded bat passes. The second suite of variables (environmental parameters) included mean values for air temperature, wind speed, and moonlight visibility. Variables with canonical loadings <0.3 were not considered significant in the interpretation. Finally, I separated the plotted time intervals into the respective degree of salinity (saline/brackish) and degree of vegetation (open water/marsh) to determine whether the correlations observed were a reflection of the particular habitat sampled.

I used Logistic Regression (Sokal and Rohlf 1987) analyses to determine whether or not the presence/absence of echolocation calls from *M. yumanensis* and from *T. b. mexicana* on any given survey night could be predicted from nightly environmental parameters. I computed the means of air temperature, wind speed, and moonlight visibility per survey night. For each of the two species, survey nights in which $\geq$1 pass was recorded were assigned a code of "1" meaning presence while nights with no passes were assigned a code of "0" meaning absence. Environmental parameters served as the independent or predictor variables while presence/absence served as the dependent variable. I ran separate analyses for each species of bat in which mean environmental parameters during presence versus absence were compared.

Tidal Height

To examine the effect of tidal height on *M. yumanensis* and *T. b. mexicana* foraging activity, I obtained tidal height (ft) at 15-min intervals during survey nights in which I sampled open brackish water and brackish marsh habitats (n = 15 survey nights).

Tidal height records were obtained with permission from the City of San José, San José/Santa Clara Water Pollution Control Plant, salt pond A18 database (E. G. Dunlavey, pers. comm.; accessed 1 August 2009). I identified feeding buzzes (Fig. 9) within echolocation sequences recorded from the two species at open brackish water and brackish marsh sampling points. Analyzing feeding buzzes separately allowed me to examine bat feeding behavior (Walsh et al. 2002). Feeding buzzes were distinctive and resembled known buzzes in the acoustic reference library. If multiple buzzes were recorded within the same acoustic file, I counted each buzz independently as opposed to attributing only one buzz to the sequence.

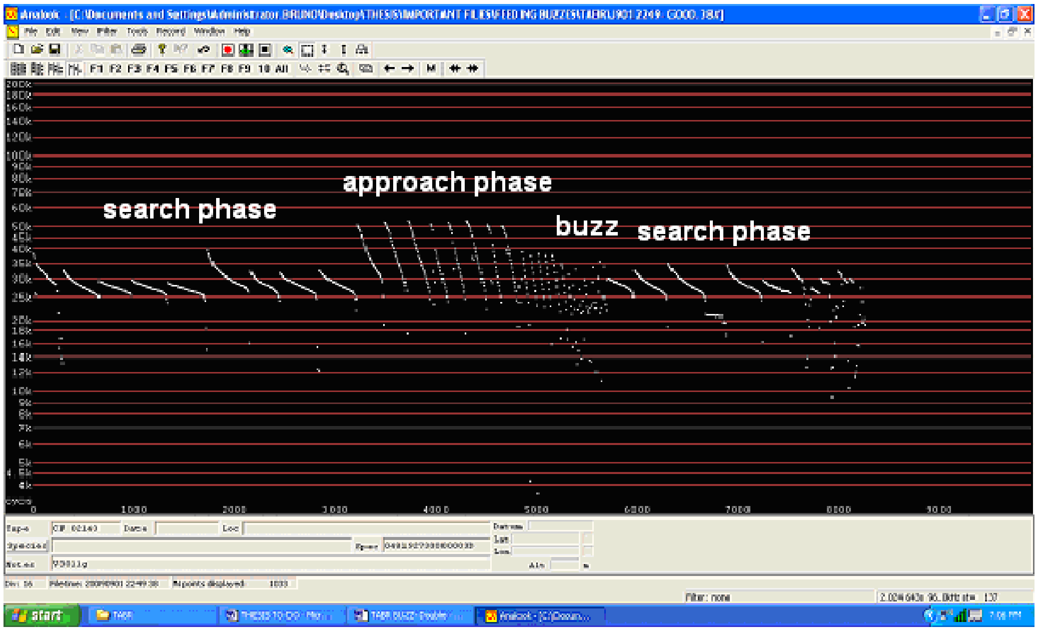

FIG. 9.—The changes in call structure through a complete foraging sequence of *Tadarida brasiliensis mexicana*, including a search phase, approach phase, feeding buzz, and another search phase; 1 September 2009, Alviso wetlands, California.

I used an Independent Samples *t*-test (Sokal and Rohlf 1987) to examine the difference between mean tidal height during *M. yumanensis* and *T. b. mexicana* passes with a feeding buzz and passes without a buzz. Because so few buzzes were recorded from *M. yumanensis* (*n* = 4), I combined both species in the analysis. Each *M. yumanensis* and *T. b. mexicana* pass recorded at open brackish water and brackish marsh sampling points was separated into whether a feeding buzz was present or absent and whether the tidal height was low (-1.0–1.99 ft), medium (2.0–5.99 ft), or high (6.0–9.0 ft) during the time the pass was emitted. Because the number of passes with a feeding buzz was small relative to the number of passes without a buzz, unequal sample size could create a bias in the *t*-test results. Therefore, I created 10 datasets, each of which contained the 20 feeding passes plus a random selection of 20 non-feeding passes and conducted the *t*-test for each dataset to determine if the results were consistent.

RESULTS

Habitat Use

Using Anabat II® detectors deployed at sampling points within open brackish water, brackish marsh, open salt water, and salt marsh habitats, I recorded 1,896 bat echolocation sequences (Table 2). The target species produced 1,828 sequences (96% of the total), 845 from *M. yumanensis* and 983 from *T. b. mexicana*. Table 3 shows the total number of *M. yumanensis* and *T. b. mexicana* passes within each of the four habitats over the 30 survey nights. Echolocation sequences from *M. yumanensis* and *T. b. mexicana* were recorded in open salt water on 13 out of 15 survey nights, making it the most frequently used habitat. However, open brackish water comprised the majority of sequences from the two species (1,053/1,828 passes). No bat passes were recorded on four of the 30 survey nights; three of these occurred at the end of sampling (7−9 October 2009) when it was foggy. Finally, 18 sequences included calls from both *M. yumanensis* and *T. b. mexicana* recorded within the same acoustic file. Sixteen of these occurred in open brackish water, one in brackish marsh, and one in open salt water habitat.

TABLE 2.—Classification of bat echolocation passes recorded from 10 August−9 October 2009, Alviso wetlands, California.

CLASSIFICATION	TOTAL # OF PASSES
Myotis yumanensis	845
Tadarida brasiliensis mexicana	983
Myotis spp.	13
Lasiurus blossevillii	11
Lasiurus cinereus	11
Unidentified	33

TABLE 3.—Total number of *Myotis yumanensis* and *Tadarida brasiliensis mexicana* echolocation passes recorded within each of four habitats; 10 August−9 October 2009, Alviso, California.

Habitat	Total passes	*M. yumanensis* passes	*T. b. mexicana* passes	Survey nights with passes
Open salt water	444	68	376	13/15
Salt marsh	0	0	0	0/15
Open brackish water	1,053	688	365	9/15
Brackish marsh	331	89	242	4/15

The Test of Independence indicated a relationship between the presence of *M. yumanensis* and *T. b. mexicana* and degree of vegetation (open water/marsh) for one of the two habitats. For both species, there was a significant difference in frequency of occurrence in open water versus marsh for saline but not for brackish habitats (*M. yumanensis*: $G = 5.935$, $P = 0.015$, *d.f.* = 1; *T. b. mexicana*: $G = 6.277$, $P = 0.012$, *d.f.* = 1; Fig. 10). The primary difference was that the two species produced ≥ 1 echolocation sequence in open salt water sampling points but no sequences in salt marsh.

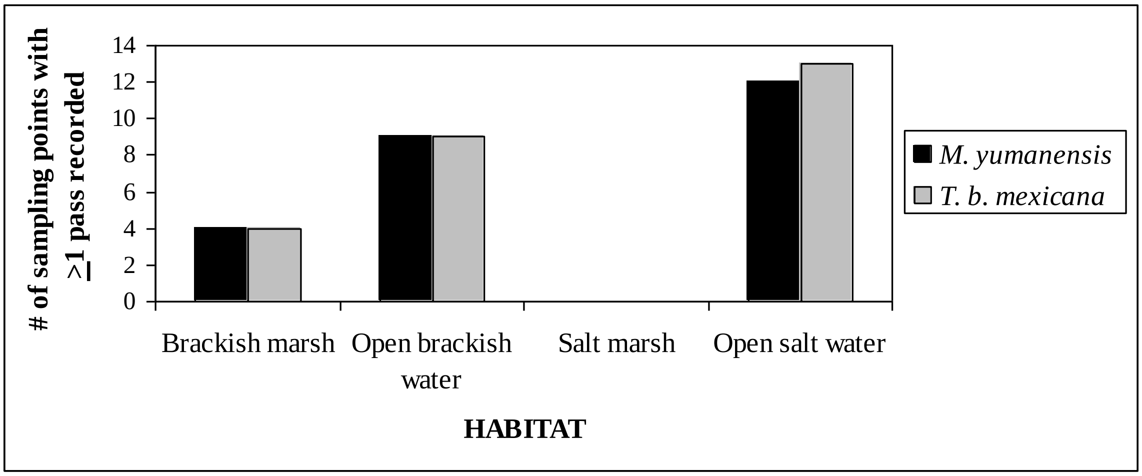

FIG. 10.—Results of 2 x 2 Test of Independence using the Log-Likelihood Ratio Test for testing differences in frequency of occurrence of *Myotis yumanensis* and of *Tadarida brasiliensis mexicana* within four habitats; 10 August–9 October 2009, Alviso, California. Frequency of occurrence was based on the number of sampling points per habitat ($n = 15$) in which ≥ 1 echolocation pass was recorded. The two variables were degree of salinity (saline/brackish) and degree of vegetation (open water/marsh).

The RCB MANOVA and RCB ANOVAs for saline habitats showed that both *M. yumanensis* and *T. b. mexicana* used open water and marsh differently (Table 4). The significant multivariate effect for degree of vegetation indicated that the two species used open water and marsh differently. The primary difference was that *T. b. mexicana* had a greater number of echolocation passes than *M. yumanensis* over open salt water (Fig. 11). The RCB ANOVAs demonstrated that both species used open salt water but did not use salt marsh. The blocking variable date was not significant in the analysis.

The RCB MANOVA and RCB ANOVAs for brackish habitats showed that there were no differences in echolocation passes between open water and marsh for either species (Table 5). The multivariate effect for degree of vegetation was not significant, indicating that the two species used open water and marsh relatively equally. The RCB ANOVAs also demonstrated that neither species differed in mean number of passes per survey night between open water and marsh habitats. The blocking variable date was not significant in the analysis.

TABLE 4.—Results of RCB ANOVAs and RCB MANOVA for testing differences in mean number of echolocation passes per survey night between degrees of vegetation (open water/marsh) in saline habitats; 10 August−9 October 2009, Alviso, California. The first analyses are RCB ANOVAs and the last is RCB MANOVA. The independent variable is degree of vegetation (open water/marsh), and the dependent variables are *Myotis yumanensis* and *Tadarida brasiliensis mexicana*. The blocking factor is date. Significant factors ($P < 0.05$) are in bold text.

		SOURCE	***d.f.***	***F* for Wilks' Lambda**	***P*-value**
RCB ANOVA	*M. yumanensis*	Degree of vegetation	1	51.858	**<0.001**
		Date (Block)	12	1	0.500
RCB ANOVA	*T. b. mexicana*	Degree of vegetation	1	10.505	**0.007**
		Date (Block)	12	1	0.500
RCB MANOVA	Multivariate	Degree of vegetation	2,11	23.770	**<0.001**
		Date (Block)	24,22	0.917	0.584

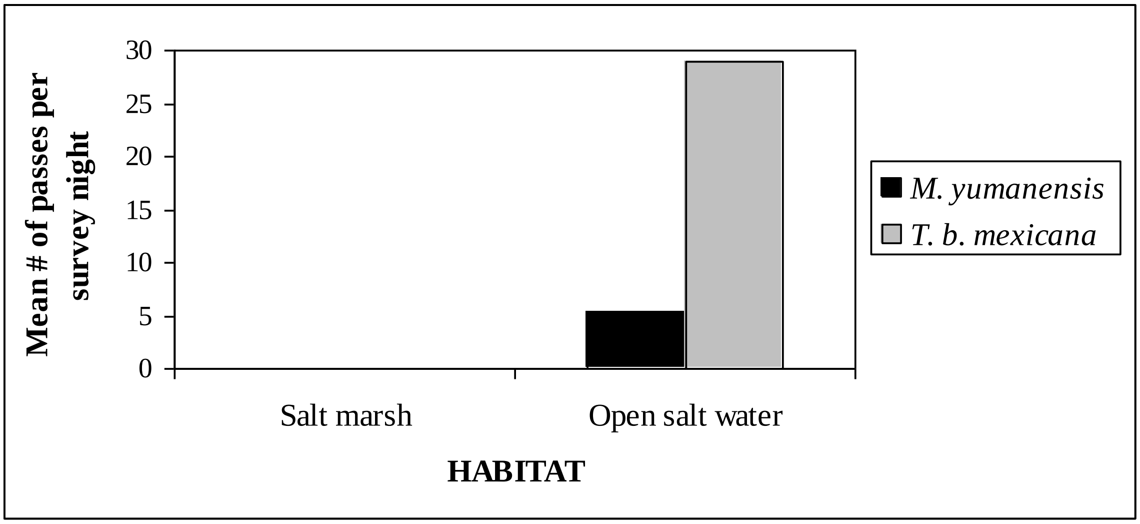

FIG. 11.—Results of the RCB MANOVA examining differences in mean number of *Myotis yumanensis* and *Tadarida brasiliensis mexicana* echolocation passes per survey night in open water versus marsh for saline habitats; 10 August–9 October 2009, Alviso, California.

TABLE 5.—Results of RCB ANOVAs and RCB MANOVA for testing differences in mean number of echolocation passes per survey night between degrees of vegetation (open water/marsh) in brackish habitats; 10 August–9 October 2009, Alviso, California. The first analyses are RCB ANOVAs and the last is RCB MANOVA. The independent variable is degree of vegetation (open water/marsh), and the dependent variables are *Myotis yumanensis* and *Tadarida brasiliensis mexicana*. The blocking factor is date.

		SOURCE	***d.f.***	***F* for Wilks' Lambda**	***P*-value**
RCB ANOVA	*M. yumanensis*	Degree of vegetation	1	3.698	0.079
		Date (Block)	12	0.790	0.655
RCB ANOVA	*T. b. mexicana*	Degree of vegetation	1	0.266	0.616
		Date (Block)	12	0.483	0.889
RCB MANOVA	Multivariate	Degree of vegetation	2,11	1.821	0.207
		Date (Block)	24,22	0.706	0.797

Air Temperature, Wind Speed, and Moonlight Visibility

The Canonical Correlation Analysis showed that air temperature and moonlight visibility were important environmental parameters for one of the two species of bats while wind speed was not important for either. Echolocation call frequency of *T. b. mexicana* increased ($R = 0.433$) significantly ($P = 0.003$) with increasing air temperature and, to a lesser extent, decreasing moonlight visibility (Fig. 12). There was no apparent difference between brackish and saline habitats or between open water and marsh habitats with respect to the canonical correlation. The small loading (0.296) for *M. yumanensis* indicated that there was no relationship between echolocation call frequency of that species and the three environmental parameters.

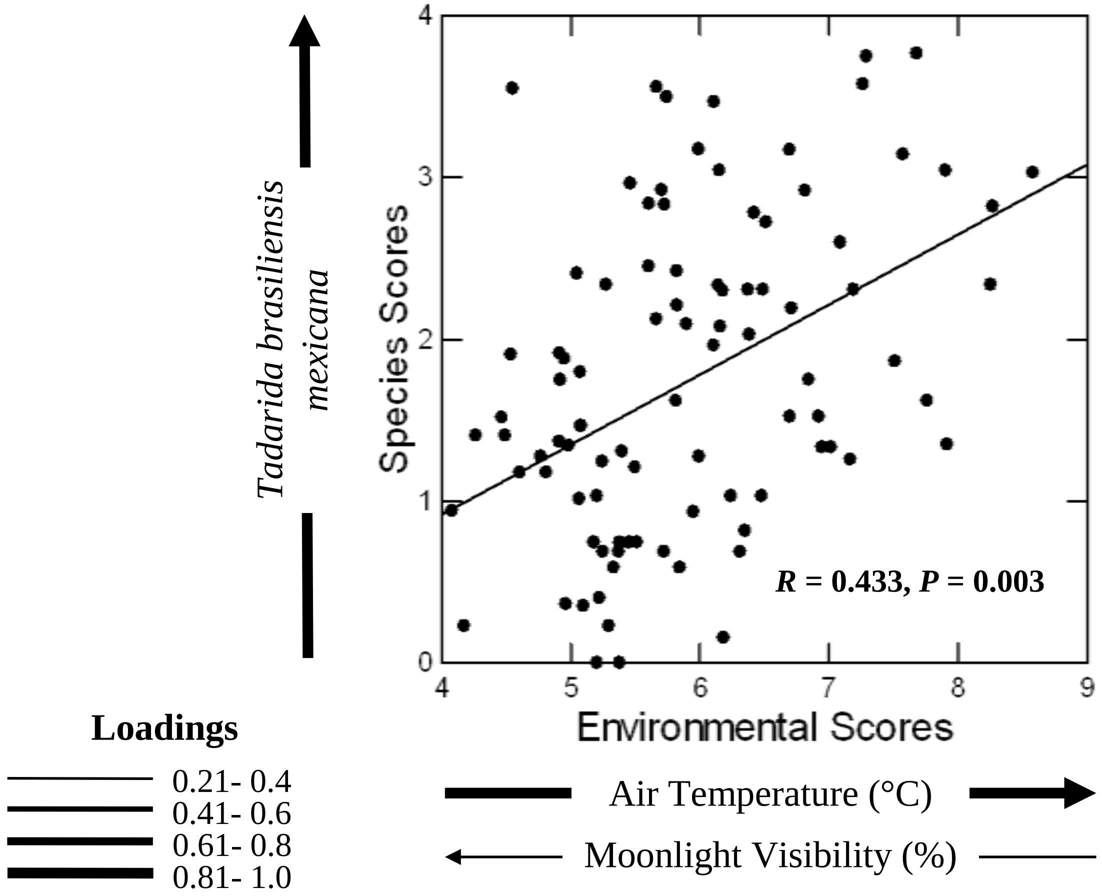

FIG. 12.—Canonical Correlation Analysis of the relationship between echolocation call frequency of *Tadarida brasiliensis mexicana* and environmental parameters (air temperature, wind speed, and moonlight visibility) from 10 August–9 October 2009, Alviso wetlands, California. All measurements were averaged within four 3-hour time intervals after sunset (up to 12 hours) over the 30 survey nights. Thickness of the arrows reflects canonical loadings. Variables with loadings <0.3 were not included in the plot.

The Logistic Regression analysis indicated that the presence/absence of echolocation calls from *M. yumanensis* and from *T. b. mexicana* could not be predicted from mean air temperature, wind speed, and moonlight visibility (Nagelkerke R^2 for *M. yumanensis* = 0.056, Overall Percentage of cases correctly predicted by the model =

85.3%; Nagelkerke R^2 for *T. b. mexicana* = 0.197, Overall Percentage of cases correctly predicted by the model = 89.5%).

Tidal Height

The Independent Samples *t*-test showed that mean tidal height did not differ between *M. yumanensis* and *T. b. mexicana* echolocation sequences with feeding buzzes and sequences without buzzes in brackish habitats ($P > 0.05$; Table 6). Twenty-eight feeding buzzes, 24 from *T. b. mexicana* and four from *M. yumanensis*, were recorded over the 30 survey nights. While all four feeding buzzes from *M. yumanensis* occurred in open brackish water, *T. b. mexicana* produced 10 buzzes in open brackish water, eight in brackish marsh, and six in open salt water habitat (Fig. 13).

TABLE 6.— Results of 10 Independent Samples *t*-tests for testing differences in mean tidal height during *Myotis yumanensis* and *Tadarida brasiliensis mexicana* echolocation passes in open brackish water and brackish marsh habitats; 10 August–9 October 2009, Alviso, California. The independent variable was feeding buzzes present (Yes or No). Because the number of feeding passes was small relative to the number of non-feeding passes, to account for unequal sample size, each test represented a random selection of 20 non-feeding passes.

RUN	***P*-VALUE**
1	0.609
2	0.064
3	0.676
4	0.858
5	0.430
6	0.211
7	0.236
8	0.837
9	0.862
10	0.941

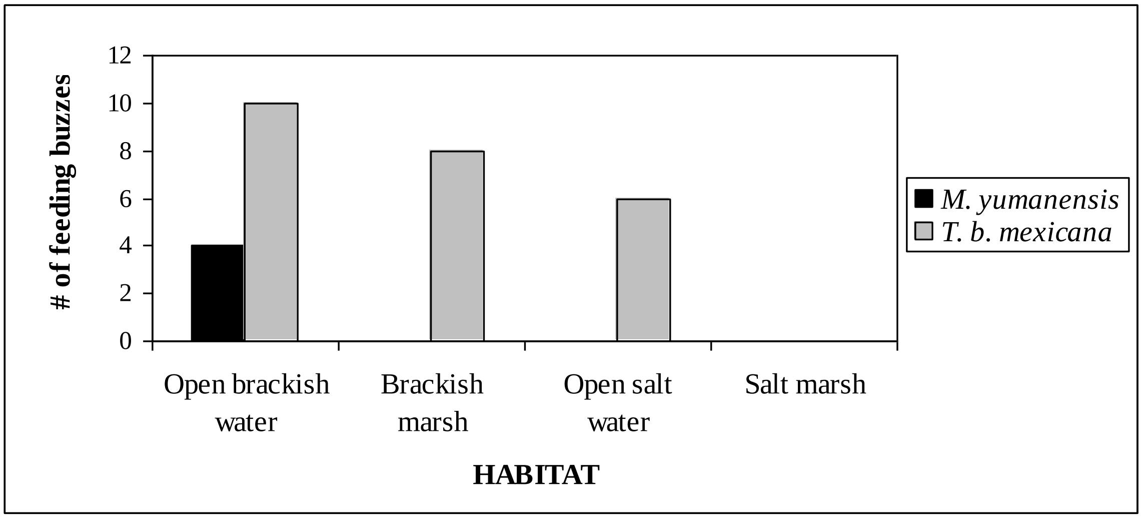

FIG. 13.—Number of *Myotis yumanensis* and *Tadarida brasiliensis mexicana* feeding buzzes recorded within each of four habitats; 10 August−9 October 2009, Alviso, California.

DISCUSSION

Habitat Use

Use of Saline Habitat.—Some bats selectively forage in certain habitats over others (Ball 2002; Gannon et al. 2003; Rogers et al. 2006; Williams et al. 2006). My results showed a preference of open salt water over salt marsh for both species, especially *T. b. mexicana*. Indeed, no echolocation sequences were recorded in salt marsh habitat. This observation may be attributed to the fact that salt marsh sampled in my study was muted and relatively dry. Discharge of tidal water into the marsh was minimal during the study period. Foraging bats exhibit high activity over rivers, lakes, ponds, streams, and other aquatic habitats (Walsh and Harris 1996). Water bodies contain high insect densities because many insects have aquatic larval stages (Voshell 2009; Walsh and Harris 1996). Seidman and Zabel (2001) found that stream channels with little water experienced greater bat activity than dry channels or upland sites. This suggests that sites containing water have greater insect presence and consequently greater bat presence than those that do not. Although my data did not include echolocation sequences over salt marsh, I previously recorded 88 sequences from *M. yumanensis* and 105 from *T. b. mexicana* during three preliminary surveys in Palo Alto, California. Additionally, Johnston et al. (2003) found that *M. yumanensis* in the South San Francisco Bay had eaten two dipteran species netted in salt marsh habitat. The target species use salt marsh to some extent, and research about the relative use of tidal salt marsh would be valuable in future estuarine studies.

This is the first study indicating that *Myotis yumanensis* and *Tadarida brasiliensis mexicana* forage over open salt water habitat. One explanation for this result is that foraging bats can easily access salt ponds due to their expansive size and openness. Schwartz et al. (2007) recorded *T. b. mexicana* flying back and forth 5−10 m above ponds and producing feeding buzzes as they took brief dives down to just above the surface. Similarly, Evelyn et al. (2004) found that radiotagged *M. yumanensis* on the San Francisco Bay Peninsula returned to forage over the same man-made reservoir each night. These studies indicate that both species forage over large bodies of water without clutter in search of insects.

Preference of open salt water habitat could also be attributed to high prey availability in Alviso salt ponds. The ponds provide a permanent nutrient-rich water source where insects can live year-round. Connectivity between salt ponds (Carpelan 1957) and discharge of tidal water from Artesian Slough (Thébault et al. 2008) are regulated by water control gates such that water constantly moves through the pond system. Thus, the ponds never desiccate and salinity levels remain relatively constant. Most importantly, fast phytoplankton growth and high accumulation of dissolved organics result in high primary productivity (Thébault et al. 2008). This supports large numbers of aquatic insects available to foraging bats. I found high concentrations of *Trichocorixa* spp. (water boatmen) and *Ephydra* spp. (brine fly) larvae and pupae at open salt water sampling points. Reticulated water boatmen (*T. reticulata*) prefer shallow saline water (Davis 1966; Jang and Tullis 1980) and are abundant in San Francisco Bay salt ponds (Carpelan 1957; Hodge 1996; Maffei 2000a). Guano analysis of *M. yumanensis* and *T. b. mexicana* in the Sacramento Valley showed that both species readily forage on water boatmen (Freeman Long et al. 1998). Furthermore, brine flies can swarm on the shores of South Bay salt ponds (Carpelan 1957; Maffei 2000b; Powell and Hogue 1979). Although brine flies are prevalent in the Alviso wetlands, there is no evidence that bats eat them. Dipterans found in *M. yumanensis* guano samples collected along the lower watershed of the Guadalupe River, Alviso, California (Johnston et al. 2003), were not brine flies (D. S. Johnston, pers. comm.). However, given that *M. yumanensis* feeds among swarms of aquatic insects (Brigham et al. 1992), it is possible that *M. yumanensis* and *T. b. mexicana* prey on brine flies.

Individual bats can exhibit high selectivity for particular groups of insects (Johnston and Fenton 2001), and prey abundance has been shown to be correlated with overall bat activity and foraging (Avila-Flores and Fenton 2005; Fukui et al. 2006). Access to a dependable food source is energetically profitable for small flying mammals such as bats (Vaughan 1980), and the abundance of water boatmen within Alviso salt ponds provides *M. yumanensis* and *T. b. mexicana* with a dependable food source. This gives these bats a motive to selectively and repeatedly use open salt water habitat.

Use of Brackish Habitat.—One explanation for relatively equal use of open brackish water and brackish marsh by *M. yumanensis* and by *T. b. mexicana* is that bats use tidal channels and the surrounding bulrush as commuting routes. Sixteen of the 18 sequences in which the two species were recorded during the same time sample occurred along open brackish water. It is likely that these bats were following the same flight path and using sloughs as "highways." Female pipistrelle (*Pipistrellus pipistrellus*) bats in Scotland traveled between foraging sites on a regular route in groups of two to six individuals (Racey and Swift 1985). Additionally, African insectivorous bats flew along regular courses in woodlands while producing search calls (Fenton et al. 1977). This suggests that different bats may routinely follow the same traveling routes while foraging. Linear landscape features such as hedgerows, treelines, streams, and rivers are used by bats for commuting and feeding (Walsh and Harris 1996). *M. yumanensis* along the San Francisco Bay Peninsula used streams as flight corridors between foraging and roost sites (Evelyn et al. 2004). Waterways create gaps that provide open flight zones, facilitating travel by bats (Evelyn et al. 2004; Seidman and Zabel 2001). In the Alviso estuary, *M. yumanensis* and *T. b. mexicana* may travel along open brackish water and brackish marsh because they are familiar, discrete habitats by which to navigate from roosts to feeding sites such as salt ponds. This promotes continuity of the landscape (Walsh and Harris 1996) and allows foraging bats to access different habitats.

In addition to commuting routes, open brackish water and brackish marsh also serve as foraging sites. Twenty-two of the 28 feeding buzzes recorded during this study occurred in brackish habitats. Estuaries are extremely productive in the diversity and amount of organic material (Clark 1977). They are inhabited by many types of aquatic insects including *T. reticulata* and *Ephydra* spp. (Maffei 2000a, 2000b; Powell and Hogue 1979). I found species of *Hesperocorixa* and *Trichocorixa* within Coyote Creek and flying water boatmen along the perimeter of brackish marsh. Furthermore, insect parts in *M. yumanensis* guano collected along the tidal portion of the Guadalupe River, Alviso, California, were identified as predominantly Hemiptera (*T. reticulata*—Johnston et al. 2003). This indicates that bats readily forage on water boatmen within brackish habitat. Considering that many bats prefer edge habitat (Walsh and Harris 1996), I suspect that slough/marsh interfaces may function as structural edges preferred by foraging bats. Brackish marsh is uniformly vegetated with tall, dense stands of bulrush. Vegetated habitats typically contain high insect densities (Vaughan et al. 1997) because many insects require shrubs for shelter (Menzel et al. 2005a). Bhattacharjee et al. (2009) found that insect presence was related to aboveground vegetation biomass. California bulrush and alkali bulrush along tidal sloughs in the Alviso wetlands probably provide insects with a safe place to oviposit and protection from wind, predators, and tidal inundation (Davis and Gray 1966). Reliance on open brackish water and brackish marsh as linear features in the landscape and the quality of both as foraging habitats contributed to the relatively equal bat use found in my study.

Air Temperature, Wind Speed, and Moonlight Visibility

Air Temperature.—I found a strong correlation between air temperature and echolocation call frequency of *T. b. mexicana* within four 3-hour time intervals after sunset over the 30 survey nights. However, the presence/absence of echolocation calls from *M. yumanensis* and from *T. b. mexicana* could not be predicted from mean temperature alone. These results indicate that although temperature does not explain why bats are or are not present in a particular area, *T. b. mexicana* exhibits increased activity during warmer nights. Several other studies (e.g., Anthony et al. 1981; Geluso 2007; Krutzsch 1955; Vaughan et al. 1997) also established a relationship between bat activity levels and ambient air temperature. Anthony et al. (1981) reported that the amount of time the little brown bat (*Myotis lucifugus*) spent roosting, and thus the amount of time spent foraging, was influenced by temperature. Night roosts were occupied for longer periods on cooler nights. Geluso (2007) found that the number of bats captured in nets over water and along flyways in New Mexico was positively, but not significantly, correlated with air temperature at dusk. Lastly, Krutzsch (1955) found that diurnal activity in a *T. b. mexicana* colony in southern California seemed to be influenced by temperature. Activity including squeaking, chattering, and scrambling around began in the morning on warm days while on cool or cloudy days, bats remained quiet and inactive until the temperature increased (Krutzsch 1955). Ambient temperature also affects insect distribution (Taylor 1963). Changes in the activity of prey subsequently influence activity levels of foraging bats (Fukui et al. 2006; Lang et al. 2006), and I predict the same holds true for the Alviso wetlands. Air temperature was an important covariate for general bat activity, but what remains unclear is whether it affects bats directly or indirectly through changes in insect activity (Erkert 1982).

Wind Speed.—I did not find a correlation between wind speed and echolocation call frequency of *M. yumanensis* or of *T. b. mexicana* within four 3-hour time intervals after sunset over the 30 survey nights. Also, the presence/absence of echolocation calls from the two species could not be predicted from mean wind speed alone. This concurs with Hecker and Brigham (1999) and Vaughan et al. (1997) who also found no relationship between wind speed and bat activity levels. Rogers et al. (2006) chose not to examine this parameter because it was negligible during the majority of data collection. The results in my study may partially be attributed to the fact that I could not measure wind speed per hour at each individual sampling point. Therefore, I could not account for small localized changes in wind speed due to levels of shelter (Vaughan et al. 1997). Another explanation is that the wind did not fluctuate enough or spike during the sampling period to produce a discernable difference. Mean wind speed from 2000−0600 h during all 30 survey nights was 1.66 m/s, and it never exceeded 4.9 m/s. Mean wind speed during three nights with a high number of recorded passes (>175) was 1.78 m/s versus a mean of 1.65 m/s during the other 27 nights. Moreover, the mean during four survey nights with no passes was 1.31 m/s. These data and my analyses show that wind speed was not an important environmental covariate for bat activity in the Alviso wetlands during my study. Because the wind remained low and relatively stable throughout the study, impact on bat flight was likely minimal resulting in no correlation detected. Relatively low wind speeds probably have little or no effect on bat activity until wind increases to the point that bats may avoid flight activity (Erkert 1982).

Observations of Pond A16 at 4.5 m/s wind speed showed a rippling effect over the water surface and minor wave action along the bank. This roughened water surface could affect *M. yumanensis* which forages low over flat waters (Barbour and Davis 1969; Williams et al. 2006). Rydell et al. (1999) found that Daubenton's bats (*Myotis daubentonii*) in southern Sweden selectively foraged over calm sections of a stream rather than an area with small ripples (<3 cm high), although insect abundance was higher over the ripples. The bats presumably avoided this area because the ripples produced echo clutter and ultrasonic noises in the form of transient pulses. Echoes from small-bodied insects are subtle and can be concealed by extraneous noise in the immediate environment (Rydell et al. 1999). Moderate to high wind speeds over large bodies of open water likely limit *M. yumanensis* echolocation by blocking their ability to detect small insects at the water surface. Thus, during periods of higher wind speeds when ripples are present, *M. yumanensis* likely doesn't glean insects at open salt water ponds and may switch to a different foraging habitat such as brackish marsh. However, interference with the echolocation calls of this species was probably negligible because wind speed was typically lower than 4.5 m/s during my sampling period and *M. yumanensis* demonstrated a preference of open salt water over salt marsh habitat.

Moonlight Visibility.—I found a negative correlation between moonlight visibility and echolocation call frequency of *T. b. mexicana* within four 3-hour time intervals after sunset over the 30 survey nights. However, the presence/absence of echolocation calls from *M. yumanensis* and from *T. b. mexicana* could not be predicted from mean moonlight visibility alone. These results suggest that although moonlight does not explain why bats are or are not present in a particular area, *T. b. mexicana* activity increased when moonlight levels decreased. Earlier studies have produced disparate results regarding the relationship between bat activity and moon phase. Lang et al. (2006) found that both katydids and Neotropical insectivorous bats were more active during the dark periods associated with a new moon compared to bright periods around a full moon. During full moon nights, bats emerged from their roost about 30 minutes earlier, spent more time in their roosts, and did not exhibit flight activity between 2300−0200 h (Lang et al. 2006). However, Anthony et al. (1981), Rogers et al. (2006), and Vaughan et al. (1997) found no direct correlation between bat activity and moonlight visibility. Other authors reported that moon phase may induce changes in the behavior of bats. Hecker and Brigham (1999) determined that insectivorous bats shifted their vertical height within the forest in response to changing lunar light. Furthermore, African insectivorous bats foraged above the canopy and along meadow/woodland edges on dark nights, but remained within the woodland on bright nights (Fenton et al. 1977). Moonlight may also affect bats indirectly through changes in behavior or availability of prey (Anthony et al. 1981; Hecker and Brigham 1999). Anthony et al. (1981) found that moon phase is related to nocturnal insect density, with the lowest densities occurring during bright nights in open areas used by foraging *M. lucifugus*. Bats are influenced by prey availability (Fukui et al. 2006) and may therefore become less active if insects are less active.

I did not find a correlation between moonlight visibility and *M. yumanensis* call frequency within four 3-hour time intervals after sunset over the 30 survey nights. Perhaps *M. yumanensis* forages in the shadows of tall bulrush along tidal sloughs on bright nights. *Myotis* spp. forage and commute close to vegetation (Limpens and Kapteyn 1991), and bats in southwest England were relatively more active in sheltered than exposed sections of sampled transects (Vaughan et al. 1997). Additionally, Reith (1982) found that *M. yumanensis* in central New Mexico flew in the shadows of riparian vegetation along a canal during nights with increased moonlight. The edges of vegetation are a more cluttered habitat (Schnitzler and Kalko 2001) because the vegetation physically interacts with flight and foraging abilities of bats (Ober and Hayes 2008b). *M. yumanensis* has echolocation (high frequency FM calls) and morphology (short, rounded wings) appropriate for maneuvering within cluttered conditions (Brigham et al. 1992) and detecting insects over a shorter distance. However, *T. b. mexicana* is restricted to foraging on aerial insects in relatively open habitats due to its low frequency CF calls and long, narrow wings (Aldridge and Rautenbach 1987). Foraging in the open exposes this species to risk of predation. Barn owls (*Tyto alba*) are present in the Alviso wetlands and hunt bats as prey. Twente (1954) observed barn owls in northwestern Oklahoma making repeated soaring attacks into the flying stream of Mexican free-tailed bats as the bats emerged at dusk from their cave. Predation risk can impact activity levels of nocturnal animals (Lang et al. 2006). Given that *T. b. mexicana* is adapted to foraging in the open, it makes sense that it may decrease its activity on bright nights so as not to be detected by barn owl predators. Predation pressure may have contributed to the fact that moonlight visibility was an important environmental covariate for this species of bat.

Tidal Height

My data suggest that mean tidal height is not correlated with feeding buzzes by *M. yumanensis* and *T. b. mexicana*. Although this environmental variable does not seem to influence bat foraging in the Alviso wetlands, samples were not evenly distributed throughout the tidal prism. If the acoustic sampling distance was increased to include points further upstream, closer to the connection with the South San Francisco Bay, I may have found a correlation. There were a limited number of sites in which I could deploy detectors in open brackish water due to challenges of vegetation obstruction and tidal inundation. It is possible that I missed feeding buzzes that occurred outside the sampling area of my detectors. Feeding buzzes are more difficult to detect than search phase calls due to their gradually decreasing pulse duration and increasing frequency (McCracken et al. 2008). Furthermore, because high-frequency sounds such as calls emitted by *M. yumanensis* have higher directionality and are quickly absorbed by the atmosphere, they have a more limited range than low-frequency sounds (Feldhamer et al. 2007; Griffin 1971). Surrounding vegetation also absorbs sound, especially at higher frequencies (Wund 2006). Dense patches of tall bulrush surround Artesian Slough and Coyote Slough while riparian forest borders Coyote Creek. During my study, I only detected four feeding buzzes from *M. yumanensis*, all of which were recorded in open brackish water habitat. Buzzes from this species could have been underestimated thereby making it more difficult to detect a relationship between bat foraging and tidal height.

The sheer size of the Alviso estuary could also have been a contributing factor for why I found no relationship between tidal height and bat foraging. Indeed, the San Francisco Bay estuary is the largest estuary along the Pacific Coast of North America (Stralberg et al. 2003). There is a wide network of tidal channels that connect to the South San Francisco Bay, and Artesian Slough also receives discharge from neighboring salt ponds and the wastewater treatment plant. According to Williams and Hamm (2002), insect species richness increases with estuary size. I presume that the expansiveness of the estuary probably supports great insect diversity for bats regardless of tidal height.

Although I did not find tidal height to be a significant variable, I suspect that high tide periods result in an increase in the amount of flat water habitat available to foraging bats. Previous studies have found a relationship between foraging space and wildlife activity. Carolina bays in South Carolina held more water one year following restoration, resulting in an increase in bat activity (Menzel et al. 2005a). Likewise, Seidman and Zabel (2001) found greater bat activity at medium and large streams compared to small streams and upland sites. As the amount of vegetation obstructing a stream decreased, bats that fed along the surface of the water exhibited greater activity due to easier access to foraging space (Ober and Hayes 2008b). Furthermore, wading birds in a New Jersey estuary were most abundant during medium and low tides when the mouths of tidal creeks, mudflats, and shallows were exposed (Maccarone and Brzorad 2005). These examples suggest that an increase in lacustrine waters during high tides results in a greater amount of surface area available for foraging. This creates better foraging opportunities for bats, especially species such as *M. yumanensis* that glean insects off the surface of open water. My study stresses the importance of tidal channels as both foraging and commuting habitat for bats. Thus, tidal height should be examined further in bat studies in estuarine systems.

CONCLUSIONS

Studies examining bat habitat use in an estuarine ecosystem are limited. This is the first study indicating that *Myotis yumanensis* and *Tadarida brasiliensis mexicana* forage over open salt water habitat. I found that both species prefer open salt water over salt marsh and equally use open brackish water and brackish marsh. Air temperature and moonlight visibility are important environmental covariates for *T. b. mexicana*, and there is no relationship between tidal height and foraging activity by *M. yumanensis* and *T. b. mexicana*. Prey availability and physical structure of habitats were likely key factors that influenced bat habitat selection. A significant long-term restoration project is currently underway within the South San Francisco Bay. In deciding retention of salt ponds versus conversion to tidal salt marsh, I advocate that restoration managers maintain some salt ponds in their present state. The expansive size of ponds provides bats an unobstructed flight zone while their productivity and shallow depth support high insect prey. Salt ponds also serve as important foraging habitat for waterfowl and shorebirds (Dias 2009; Takekawa and Marn 2000). Vegetation in wetlands contributes to prey availability and serves other important ecosystem functions. It converts, stores, and cycles nutrients, removes toxic materials from estuarine waters, reduces the sedimentation of channels, and protects shorelines from flooding and erosion (Clark 1977). Therefore, the presence of vegetation within and along the edges of water bodies is an important feature to preserve. This includes bulrush adjacent to open brackish water sloughs and pickleweed and alkali heath at open salt water sites. Water boatmen are important prey for foraging bats and birds due to their small body size and abundance. Managers should periodically monitor for the presence of these insects and maintain features used by them. Shallow ponds and pools with medium to high salinity and submerged pickleweed should be preserved to sustain population levels of corixid prey. Lastly, flight can be an energetically expensive activity for bats if roosts are distant from feeding areas (Johnston 2007; Walsh and Harris 1996). Roosting structures within estuaries including riparian trees, bridges, and buildings should remain undisturbed so bats will have easier access to preferred foraging habitats (Betts 1998; Ormsbee and McComb 1998). My study exemplifies the importance of saline wetlands to bat species. Bats are good indicators of the overall quality of habitats and ecosystems due to their longevity, mobility, and variety of feeding habits (Fenton 2003; Moreno and Halffter 2000). Thus, managers should consider bat distribution across the landscape when assessing the quality of restored habitats.

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