ABSTRACT

Winter Ecology of Migratory Brazilian Free-Tailed Bats (*Tadarida brasiliensis*)
in Bridges of the Southwestern U.S.

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Bats are diverse and ubiquitous mammals with a worldwide distribution. In the

U.S., especially the southwest, Brazilian free-tails (*Tadarida brasiliensis*: I. Geoffroy

Saint-Hilaire, 1824) are arguably the most abundant bat in the western hemisphere.

These insectivorous bats range from Nebraska to Latin America and from Oregon to

North Carolina. Populations migrate frequently (every year), great distances (>1,800

km), and seasonally (south for winter). In New Mexico and Texas, migrant Brazilian

free-tailed populations increase seasonally because of fecundity in local summer

populations as well as migration of individuals from more northern environments in

summer, to southern environments in winter. Surprisingly, apparently viable populations

persist in during mid-winter months suggesting winter residency of either localized

populations, northern migrants, or a combination of cryptic metapopulations. This

unexpected transient stop-over or residency in the geographic middle of the migration

pattern (southern New Mexico-central Texas) was puzzling and warrants scrutiny.

Although *T. brasiliensis* is abundant and commonly researched, the ecology of wintering

populations is poorly known. Research on bats has been traditionally confined to their

warm-season biology with sparse information available on winter activity. The broad

goals of this research on winter *T. brasiliensis* had four major conduits.

1. Describe basic population parameters of bridge populations such as species, abundances, and roost characteristics of bridge bats in New Mexico.

2. Determine the extent of bridge occupancy of *Tadarida brasiliensis* in terms of continuously occupied roosts, and year-round occupation in New Mexico and Texas.

3. Investigate winter variation in population composition, i.e. frequency and relative abundance of individuals, sex ratios, age classes, body mass, evidence of feeding, and distribution in Texas of *Tadarida brasiliensis*.

4. Investigate winter variation in diet composition, i.e. frequency and relative abundance of major food items in Texas *Tadarida brasiliensis*.

This research described bridge occupancy, diet and winter ecology of *T. brasiliensis* and reflected on the status of these wintering populations as either transients in the midst of extended migration, or marginal laggards tolerating less than optimal conditions in lieu of completing migration. Winter presence of metapopulations continuously roosting in bridges and actively feeding were previously unknown for this opportunistic bat.

Winter Ecology of Migratory Brazilian Free-Tailed Bats (*Tadarida brasiliensis*)
in Bridges of the Southwestern United States

by

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DEDICATION

       To Brianna and Avery, my true loves. And for my late father Oscar, my late uncle Wesley and my late grandmother Dorothy all who passed during this research . I believe they would appreciate this effort.

CHAPTER ONE

Winter Ecology of Migratory Brazilian Free-tailed Bats (*Tadarida brasiliensis*) in the
Southwestern United States

Introduction

Cosmopolitan in distribution, bats (Mammalia: Chiroptera) comprise nearly 25%

of the 5,416 extant species of mammals formally described (Wilson 1997; Wilson and

Reeder 2005). As an ordinal taxon of mammals, bats have versatile feeding strategies

and form diverse functional trophic groups. Their specialized niches, distinctly nocturnal

behavior, and responsive echolocation abilities account for radiation among bat families

with unique ecologies. Within the family Molossidae, or free-tailed bats, worldwide

distribution of nearly 90 species occurs primarily in pantropical areas throughout the

eastern and western hemispheres. Molossids are strictly aerial insectivores that garner

prey items on the wing and are known for extensive migrations and high flight speed

often from high altitudes (Barbour and Davis 1969; Hall 1981; Norberg and Rayner

1987; Davis and Schmidly 1994). Of the 14 genera of molossids, ten reside in the New

World. Seven species occur in North America from Canada to Mexico and the Atlantic

coastal states to California (Villa-R. and Cockrum 1962; Glass 1982; Jones et al. 1983;

Dalquest and Horner 1984), and are most prevalent in the southwestern United States.

Gaps in information concerning timing of migration, winter roosts and general

demographics of gender and spatial temporal scales are significant for species of

Molossidae.

Of the seven species occurring in North America, four have been vouchered in Texas (Davis 1960; Davis et al., 1962; Schmidly 1983; Davis and Schmidly 1994). *Tadarida brasiliensis* (Western Mastiff bat) *, Eumops perotis* (Brazilian free-tailed bat)*, Nyctinomops macrotis* (Big free-tailed bat)*, and *N. femorosacca* (Pocketed free-tailed bat) all temporarily reside and travel throughout Texas according to county record vouchers listed by Davis (1960) and Davis and Schmidly (1994). These four species migrate during summer into temperate areas such as Texas and more northern locales, and exploit prolific insect populations.

In North America the molossid, *Tadarida brasiliensis* (I. Geoffroy Saint-Hilaire, 1824), has been sighted or tracked by radar at 3,000 meters altitude (Davis et al., 1962; Williams et al., 1973), and banded individuals have been recovered after autumnal migrations of at least 1300 kilometers (Villa-R. and Cockrum 1962, Cockrum 1967, Glass 1982). Accounts from the latter half of the 20th century describe *T. brasiliensis* congregating into impressive summer colonies of 50 million individuals in Arizona (Mohr 1972; Hoffmeister 1986). However; current figures list Bracken Cave in Bexar County Texas as the largest colony known today with 20 million individuals (Hoffmeister 1986; Wilson 1997). Although impressive for their feats of mammalian aggregation and migration, our knowledge of flight and navigation by these mammals, timing of migration, winter roosts, general demographics of gender, and spatial temporal scales of life history is poor for molossids of North America in general and *T. brasiliensis* in particular.

Migration and Distribution

Tadarida brasiliensis (I. Geoffroy Saint-Hilaire, 1824), the Brazilian free-tailed bat, is a migratory species, attested to by diminishing populations and disappearance of the bats during the onset of winter in western North America (Allen 1922, Bailey 1928, Christensen 1947, Davis et al. 1962, Villa-R. and Cockrum 1962, Constantine 1967, Cockrum 1969, Glass 1982, Dalquest and Horner 1984). *Tadarida brasiliensis* is in reality a free-tailed bat of the Americas, North, Central, and South (Hoffmeister 1986), and a name far more fitting than 'Brazilian' based on the entirety of its distribution in the Western Hemisphere. This bat's North American range includes populations in caverns of central Mexico through the Yucatan peninsula. Populations east to North Carolina and west to California burgeon in summer. The northern expanse extends to southern Nebraska and southwestern Oregon approximating a 40° N latitude boundary (Hall 1981; Jones et al. 1983; Dalquest and Horner 1984). *T. brasiliensis* have been occasionally captured outside their understood range (Genoways et al. 2000). The ability to range far with robust flight result in sporadic, discrete representatives dispersed outside historic ranges described by Davis et al. (1962), Hall (1981) and Dalquest and Horner (1984). Summer mist-netting surveys reveal significant pioneering behavior by *T. brasiliensis* beyond "traditional" distribution boundaries (Figure 1).

Figure 1. Distributional map of *Tadarida brasiliensis* in North America (after Hall 1981).

In Texas, *T. brasiliensis* occur statewide and are historically documented from capacious caverns in karst regions typified by calcerous erosion of Cretaceous limestone in central and west Texas and buildings of east Texas (see Figure 2), Davis et al. (1962) recorded 20 million *T. brasiliensis* from Bracken Cave in 1956.. Summer colonies may number several million individuals in central and western states as well. For example, 10 to 20 million Brazilian free-tailed bats are historically reported for a cavern along the east side of Eagle Creek, south-southwest of Morenci, Greenlee County, Arizona (Hoffmeister 1986). Contemporary estimations, of these historically impressive cavern

populations, are significantly reduced (Betke et al. 2008). These smaller colonies are possibly a result of human decimation (e.g. pesticides, cavern destruction, guano mining pursuits), errors in direct visual observational techniques of earlier bat count numbers or a combination of factors.
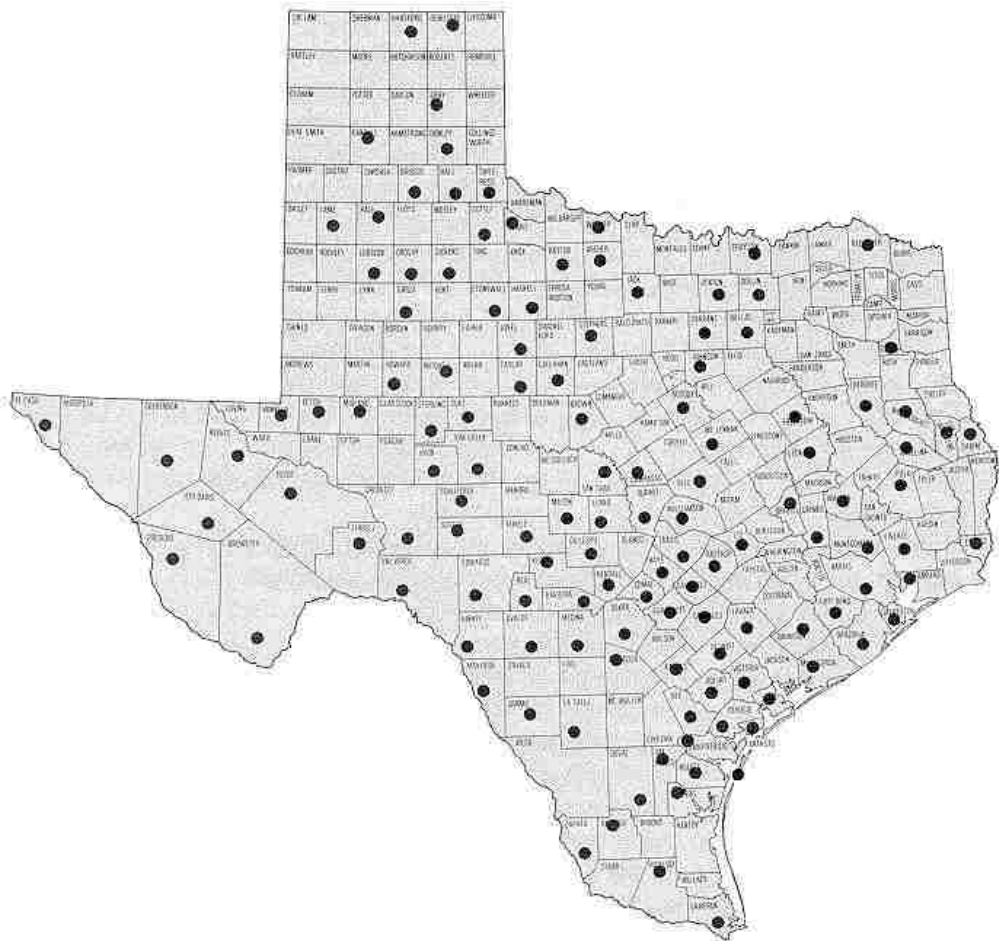
Figure 2: Distribution of Brazilian free-tailed bat in Texas based on known vouchered specimens as county records regardless of seasonality (Davis and Schmidly 1994).

Study Areas

To select appropriate study sites17 bridges associated with paved highways that crossed arroyos, small canyons, and the Rio Grande river were inspected in Doña Ana and Sierra Cos., New Mexico (Table 1). Texas bridges (*n*=47) in Bell, Bexar, Comal,

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Ellis, Evant, Hays, McLennan, Nueces, Travis, Williamson, and Zapata counties were inspected (as well as recommendations from TxDOT) for candidate roost sites. Bridges surveyed for bats were those constructed mainly from cement, metal, or both (I-beam bridges) and timber (New Mexico). Heights of bridges differed, but most spans examined for bats ranged from 1.2 m to greater than 15 m above the ground. Concrete-steel, steel, and timber bridges exist in Texas; however, I found no timber bridges, and none of the steel or concrete-steel composite bridges contained bats.

The likelihood of bridge occupancy by bats depended primarily on the presence of vertical expansion joints of variable depths on the underside of concrete spans regardless of traffic or proximity to nearby water sources. All concrete bridges with a vertical expansion joint feature sheltered at least one bat. Ease of transport, travel and time logistics to survey wintering *T. brasiliensis* were considerations in choosing and surveying concrete bridges as candidates for suitable, long term sampling sites. The best candidates contained a vertical expansion joint, since bat counts are easily facilitated and this bridge characteristic promotes its use as a viable roost. Nevertheless, only a limited number of surveyed bridges in these Texas counties (9%) had this structural expansion joint. Therefore, primary sampling were done on concrete bridges, with variable depth expansion joints, at five sites in Texas – three in central Texas and two in south Texas.

Site 1: McLennan Co., Waco, Hwy 484 bridge at Loop 340 intersection

Site 2: Bell Co., Belton, Hwy 386 bridge at Interstate 35 intersection

Site 3: Bell Co., four miles south of Highway 190 and Interstate 35, Lampasas River bridge on Interstate 35

Site 4: Kenedy Co., 3.5 miles south of Riviera on Hwy 77 southbound bridge span over Los Olmos Creek

Site 5: Kenedy Co., 3.6 miles south of Riviera on Hwy 77 northbound bridge
span at Los Olmos Creek

Vegetative Descriptions and Geography of Study Areas

Studies on New Mexico bat populations was conducted along the lower Rio
Grande valley in southern New Mexico from Truth or Consequences, Sierra County to
Radium Springs, Doña Ana County. We inspected 17 bridges associated with paved
highways that crossed arroyos, small canyons, and the Rio Grande (Table 1). Bridges
were constructed from timber or from a combination of concrete, metal, or both.
Vegetation varied from creosote bush (*Larrea tridentata*) and mesquite (*Prosopis
grandulosa*) on flat areas, Chihuahuan desert scrubland dominated by creosote bush on
rocky hills and slopes, and cottonwoods (*Populus deltoides*) and tamarisk species
(*Tamarix chinensis* and *T. ramosissima*) along edges of the Rio Grande and Caballo
Reservoir in the northern part of the study area. The southern half of the study area
contained agricultural fields in the low-lying flat areas bordered by screwbean mesquite
(*P. pubescens*), tamarisk along edges of the Rio Grande, and Chihuahuan desert
scrubland on rocky hills and slopes.

For studies on Texas populations of bats the area surrounding McLennan and Bell
Cos. -northern study area (sites 1, and 2); is mainly urban with anthropogenic modified
habitat, e.g. asphalt roads, service stations, channelized streamways, gravel dredged, and
agriculturally treated acerage. Site 3 also has agricultural modification and asphalt;
however, the area surrounding the northern study site is part of the central blackland
prairie and cross timbers and prairies vegetational regions (see map in Correll and
Johnston 1970) adjacent to the eastern boundary of the Edwards plateau as delineated by

relief of the Balcones Escarpment. This study site area is a mosaic of anthropogenic

modified habitats, e.g. asphalt roads, commercial business pursuits, channelized storm

sewers, agricultural modification as well as the Lampasas River. These bridges in Bell

County are located along Interstate-35. This Lampasas River riparian area is

characterized by these plants: southern shield fern (*Thelypteris ovata* var. *lindheimeri*),

inland sea-oats (*Chasmanthium latifolium*), saw greenbrier (*Smilax bona-nox*), hellfetter

(*S. tamnoides*), bird pepper (*Capsicum annuum* var. *glabriusculum*), American

beautyberry (*Callicarpa americana*), box elder (*Acer negundo),* black willow (S*alix

nigra*), cottonwood (*Populus deltoides*), Texas sugarberry (*Celtis laevigatus*), rough-leaf

dogwood (*Cornus drummondii*), green ash (*Fraxinus pennsylvanica*), possumhaw (*Ilex

decidua*), yaupon (*I. vomitoria*), Osage orange (*Maclura pomifera*), sycamore (*Plantanus

occidentalis*), wafer ash (*Ptelea trifoliata*), Carolina buckthorn (*Rhamnus caroliniana*),

American elm (*Ulmus americana*), chinaberry (*Melia azedarach*), glossy privet

(*Ligustrum lucidum*), Chinese privet (*L. sinense*), smooth sumac (*Rhus glabra*), Alabama

supple-jack (*Berchemia scandens*), poison ivy (*Toxicodendron radicans*), Virginia

creeper (*Parthenocissus quinquifolia*), tree-of-heaven (*Ailanthus altissima*), pecan (*Carya

illinoinensis*), black walnut (*Juglans nigra*), and eastern red cedar (*Juniperus virginiana*).

Dominant vegetation away from riparian influence, occurred on Cretaceous limestone

substrates and included sideoats grama (*Bouteloua curtipendula*), hairy woollygrass

(*Erioneuron pilosum*), whitetop (*Tridens albescens*), little bluestem (*Schizachyrium

scoparium*), prairie spiderwort (*Tradescantia humilis*), agarito (*Berberis trifoliata*), coral

berry (*Symphoricarpos orbiculatus*), jara dulce (*Baccharis neglecta*), mesquite (*Prosopis

grandulosa*), Texas persimmon (*Diospyros texana*), Texas redbud (*Cercis canadensis

var. *texensis*), prairie flame-leaf sumac (*Rhus lanceolata*), cedar elm (*Ulmus crassifolia*), prickly-pear (*Opuntia engelmanii*), ashe juniper (*Juniperus ashei*), mesquite (*Prosopis grandulosa*), lime pricklyash (*Zanthoxylum clava-herculis)*, Mexican buckeye (*Ungnadia speciosus*), Mexican plum (*Prunus mexicana*), woollybucket bumelia (*Sideroxylon lanuginosum*) and plateau live oak (*Quercus fusiformis*).

The Kenedy County site (site 4 and 5) is transected, under bridge spans, by Los Olmos Creek, a brackish water stream, varying in widths influenced by tide. The area surrounding the southern study sites (Kenedy County) is part of the Tamaulipan brushland biotic province of Texas (biotic province map in Gould 1962; 1969) and transected beneath bridge spans by Los Olmos Creek, a brackish water stream. This stream varies in widths by tidal influence and supports coastal saltgrass (*Distichus spicata*), sea oxeye daisy (*Borrichia frutescens*), saladillo (*Varilla texana*), Texas bluebells (*Eustoma russellianum* [*E. grandiflorum*]) and vidrillos (*Batis maritimas*) at the littoral interface. Also in the surrounding area are Spanish dagger (*Yucca treculeana*), Rhodes grass (*Chloris gayana*), Sarita rosette-grass (*Dichanthelium nodatum*), giant panic grass (*Panicum antidotale*), Bailey's ball moss (*Tillandsia baileyi*), velvetleaf (*Abutilon theophrasti*), bee-brush (*Aloysia gratissima*), Texas lantana (*Lantana urticoides*), Texas verbena (*Verbena halei*), Texas rabbit-tobacco (*Pseudognaphalium austrotexanum*), fetid marigold (*Dyssodia papposa*), Caribbean purple everlasting (*Gamochaeta antillana*), smallflower groundcherry (*Physalis cinerascens* var.*spathulifolia*), beaked mock vervain (*Glandularia quadrangulata*), prairie vervain (*Glandularia bipinnatifida* var. *bipinnatifida*) American snoutbean (*Rhynchosia americana*), Texas pricklypoppy (*Argemone aurantiaca*), Texas ragwort (*Senecio*

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ampullaceus), barbas de chivato (*Clematis drummondii*), anaqua (*Ehretia anacua*), brasil (*Condalia hookeri*), desert hackberry (*Celtis pallida*), jara dulce (*Baccharis neglecta*), desert yaupon (*Schaefferia cuneifolia*), lotebush (*Ziziphus obtusifolia*), blackbrush acacia-chaparro prieto (*Acacia rigidula*), huisache (*A. farnesiana*), retama (*Parkinsonia aculeata*), prickly-pear (*O. engelmanii*), cenizo (*Leucophyllum frutescens*), amargosa (*Castela erecta*), mesquite (*Prosopis grandulosa*), colima (*Zanthoxylum fagara*), and coastal live oak (*Quercus virginiana*) occur in the surrounding study site area. The study sites were separated north to south by at least 563 km.

Bridges as PrimaryRroosts

Bridges are accessible and viable alternatives to natural caves for various life-history stages and ecologies of bats in North America (Stager 1943, Davis and Cockrum 1969, Hirshfeld et al. 1977, Fraze and Wilkins 1990, Lewis 1994, Lance and Garrett 1997, Arnett and Hayes 2000, Lance et al. 2001, Johnson et al. 2002, Trousdale and Beckett 2002, 2004, Feldhamer et al. 2003, Sgro and Wilkins 2003, Keeley and Keeley 2004, Ferrara and Leberg 2005). Bats in temperate regions often use these structures for various functions and behaviors, depending on the time of year (Kunz 1982; Perlmeter 1996). In the primary literature, information regarding the choice and use of various winter roosts is limited, and the extent, distribution, and pattern of use of various roost structures by nonhibernating bats in winter is not documented.

Bridge roosts are vital sites for essential life-history functions such as rest, grooming, hibernation, copulation (Mink, *per. obs*. 2007), bearing and raising young, consumption and digestion of food. Given their diverse functionality, roosting sites differ

greatly among bat species (Kunz 1982). Even populations of a single species may use a variety of roosts depending on sex, season, and time of day (Hill and Smith 1984). Seasonal distribution of bats utilizing roost structures, e.g. bridges, has largely been analyzed as exclusively day occupation versus strictly occupancy at night (Feldhammer et al. 2003), or as maternity or male and nonreproductive female roosts (Adam and Hayes 2000; Kunz 1982) during warm months. Winter surveys have not been done. Humphrey (1975) proposed that availability of roosting sites might be a limiting resource for bats, and when suitable roosts are denied, bats may disappear from areas or their abundance, distribution, and demographics may change (Constantine 1967, Findley 1987, Lewis 1995, Fenton 1997). I propose that bridges should be investigated as significant supplements to roost site availability and as alternative habitat space for a variety of bat species.

Paths of Research Effort

My research followed four approaches to understanding the wintering ecology of bats. These approaches cover population characteristics of bridge bats in New Mexico and Texas, diet, response to climatic conditions, and insight into the migratory origin or residency of the central and south Texas wintering Brazilian freetails.

Population Ecology of Wintering Tadarida brasiliensis

Literature has well-established *T. brasiliensis* migrating south from summer populations in Texas, and other states leaving before December and January based on research spanning the last century (Allen 1922, Bailey 1928, Christensen 1947, Davis et al. 1962, Villa-R. and Cockrum 1962, Findley and Jones 1964, Constantine 1967,

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Cockrum 1969, Griffin 1970, Hall 1981, Glass 1982, Dalquest and Horner 1984, Hoffmeister 1986). However, there are individual *T. brasiliensis* that remain in northern areas, perhaps employing a strategy that avoids the risks associated with migration. These individuals possibly remain at northern regions in winter until fat stores are minimal or depleted and therefore, migrate south only when forced to. It is unclear as to the extent that individuals might hibernate in bridges, buildings, caves, caverns, sinkholes or in other northern areas where they overwinter (Barbour and Davis, 1969).

My research verified and documented that bridges are important, i.e. continually occupied, wintering roost sites for bats, especially *T. brasiliensis*, in New Mexico and Texas. With seven species known to roost in bridges in Arizona and Texas (Davis and Cockrum 1963, Fraze and Wilkins 1990), bridges clearly are important roosting sites for bats in Texas. In December 2005 my discovery of *Tadarida brasiliensis* roosting in some Bell county bridges (sites 2 and 3) throughout winter indicated that not all individuals migrate from or fully through Texas during cold months, and that bridges are significant winter roosts (Mink *pers.obs*,. See tables 1-9). It is probable that bridges have historically benefited bats in other parts of the state augmenting natural sites by providing additional roost sites either temporally or spatially.

Paucity of winter data could be attributed to a lack of natural history knowledge. Surveys of wintering bats are long overdue and should be conducted in Texas and other southwestern states. Resulting data would likely reveal bats as active biotic components of our winter ecosystems. In this study I examined activity and natural history of *T. brasiliensis* using bridges as study sites from December through February. Hereafter, I define winter as December through February. This period corresponds to the duration of

hibernation for bats observed in southern Bell County, Texas; e.g. cave myotis, *Myotis velifer* and eastern pipestrelle, *Pipestrellus subflavus* (Mink *per. obs.* Field Notes 2006-2008).

Predictions. I predicted that roosts would be consistently occupied suggesting winter residency. I further predicted that bridge roost use in winter is predicated by expansion joint occurrence in bridge construction, and contains both sexes and various age classes in winter despite roost use as bachelor or maternity colonies during summer months.

Across study sites I expected time of capture to influence body mass and that mean body mass would increase by February across gender or age class. In either sense, I hypothesized captured bats would increase in mass during nightly foraging bouts, regardless of gender or age, and bats captured in February, i.e. end of winter, would display the highest mean body mass during winter sampling. I predicted that the body mass of *T. brasiliensis* in the southern site would not only be maintained overwinter but increase because foraging activity would positively correlate with higher mean winter ambient temperatures (USDA 2012) and subsequent increased insect activity and thus higher insect availability. In other words during the winter months *T. brasiliensis* in the southern locale (with warmer temperatures favoring food availability) would be significantly heavier than those bats in the northern sites. I expect January captures to express the lowest overall mass across sexes and sampling sites for volant individuals, and that January would have the lowest capture rates of bats regardless of study site.

Winter Diet of Tadarida brasiliensis (I. Geoffroy Saint-Hilaire, 1824):

Diet of Brazilian free-tailed bats has been studied and varies greatly across nights, different localities, temporal spans (e.g. diel (Whitaker et al 1996)), and warm seasons (Whitaker and Rodriquez-Duran 1999, McWilliams 2005). The winter diet of *Tadarida brasiliensis* populations has not been studied. In the United States, only two studies have documented bats feeding in winter. Whitaker et al. (1997) confirmed that *Lasiurus borealis* (Eastern red bat) feeds in winter in North Carolina and Virginia, and Geluso (in press) found that four species (*Pipistrellus hesperus*, *Lasionycteris noctivagans*, *Myotis californicus*, and *Tadarida brasiliensis*) commonly feed December-February in New Mexico. In summer nocturnal foraging bouts, *T. brasiliensis* consumes a variety of insects (e.g., McWilliams 2005). Moreover, McWilliams (2005) found great variation in orders of Insecta eaten by *T. brasiliensis* from spring through summer to fall at Carlsbad Caverns, Eddy County, New Mexico. Typical food items include moths, beetles, flies, wasps, true bugs and flying ants. Examination of this species diet during winter months in south-temperate and subtropical regions would reflect on the economic value of *Tadarida brasiliensis* consuming important agricultural pests. (e.g. Cleveland et al., 2006).

Predictions. I predicted that *T. brasiliensis* actively feeds in winter and that diet composition of these winter bats*,* measured by frequencies, volumes and relative importances would differ from December to February. I further predict a more varied forage base with higher diversity at southern study site versus northern study site. I

predict that diets between genders and among age classes would not be significantly different, within or between sites. *T. brasiliensis* is an opportunist and in winter they likely encounter markedly different quality and quantity of prey during spring, summer and autumn. These shifts would be reflected in diet analysis.

CHAPTER TWO

Use of Bridges by Brazilians Free-Tailed and Other Bats in the Lower Rio Grande
Valley, New Mexico

Abstract

Bats roost in bridges for various life-history functions, but little is known about
use of bridges in the southwestern United States. During a 2-year study, we documented
eight species of bats using bridges in the lower Rio Grande valley of New Mexico as day
roosts. Of 17 bridges surveyed, 88% contained day-roosting bats and at least 8 bridges
contained maternity colonies. Individuals roosted in many sites in bridges, but about
99.9% roosted in narrow cracks and crevices. A total of 36,629 day-roosting bats were
counted, with 99.8% observed in timber bridges and 0.02% observed in I-beam bridges
constructed of concrete, metal, or both. The Yuma myotis (*Myotis yumanensis*), Arizona
myotis (*M. occultus*), and Brazilian free-tailed bat (*Tadarida brasiliensis*) formed
maternity colonies in bridges. The California myotis (*M. californicus*), fringed myotis
(*M. thysanodes*), silver-haired bat (*Lasionycteris noctivagans*), big brown bat (*Eptesicus
fuscus*), and pallid bat (*Antrozous pallidus*) only roosted infrequently in bridges. Use of
bridges by day-roosting bats differed seasonally, with most individuals occupying bridges
April-October. From November to March, relatively few individuals of *T. brasiliensis*
occupied bridges. Other bats discovered in colder months included 2 individuals of *M.
yumanensis* in January and 12 individuals of *M. yumanensis* and a single *L. noctivagans*

in March. We observed evidence of night roosting in every bridge. Our study

demonstrates that bridges represent important roosting sites for bats in New Mexico,

especially in summer. Bridges throughout the southwestern United States likely serve

similar life-history functions for bats, and should be managed as a resource, especially

those occupied by maternity colonies or large numbers of individuals.

Resumen

Murciélago el gallinero en los puentes para las diversas funciones de la vida-

historia, pero poco se sabe sobre el uso de puentes en los Estados Unidos al sudoeste.

Durante un estudio de dos años, documentamos ocho especies de murciélagos usando los

puentes en el valle más bajo de Rio Grande de New México como gallineros del día. De

17 puentes examinados, el 88% contenido los murciélagos día-roosting y por lo menos 8

puentes contuvieron a las colonias de maternidad. Los individuos roosted en muchos

sitios en puentes, pero cerca de 99,9% roosted en grietas y grietas estrechas. Un total de

36.629 murciélagos día-roosting fueron contados, con 99,8% observados en puentes de la

madera y 0,02% observado en los puentes del Yo-haz construidos del hormigón, del

metal, o de ambos. El myotis de Yuma (*Myotis yumanensis*), el myotis de Arizona (*M.*

occultus), y el murciélago brasilensis (*Tadarida brasiliensis*) formaron a las colonias de

maternidad en puentes. El myotis de California (*M. californicus*), el myotis franjado (*M.*

thysanodes), el murciélago cano (*Lasionycteris noctivagans*), el murciélago marrón

grande (*Eptesicus fuscus*), y el murciélago pálido (*Antrozous pallidus*) roosted solamente

infrecuentemente en puentes. El uso de puentes por los murciélagos día-roosting

diferenció estacional, con la mayoría de los individuos ocupando los puentes abril-

octubre. De noviembre a marzo, relativamente pocos individuos del *T. brasiliensis*

ocuparon los puentes. Otros murciélagos descubiertos en meses más fríos incluyeron 2

individuos de *M. yumanensis* en enero y a 12 individuos del *M. yumanensis* y *L.*

noctivagans de los solos en marzo. Observamos pruebas de la noche el roosting en cada

puente. Nuestro estudio demuestra que los puentes representan los sitios roosting

importantes para los murciélagos en New México, especialmente en verano. Los puentes

en la vida-historia similar del servicio probable al sudoeste de Estados Unidos funcionan

para los murciélagos, y se deben manejar como un recurso, especialmente ésos ocupados

por las colonias de maternidad o un gran número de individuos.

Introduction

Humans have created declines, or jeopardized populations of bats throughout the

United States and world (Hill and Smith 1984, O'Shea and Bogan 2003), but certain

human influences benefit bats and augment their conservation. These bat populations

have been aided by establishment of permanent water sources (e.g., stock tanks) in arid

regions (Geluso 1978, Tuttle et al. 2006), by implementing educational programs that

emphasize the values of bats and encourages their protection (Fenton 1997), and by

constructing structures used for shelter (e.g., buildings, bridges, culverts, tunnels, and

mines; Kunz 1982, Fenton 1997). Many human-made structures function as roosting

sites for many species (e.g., Barbour and Davis 1969, Davis and Cockrum 1963, Sandel

et al. 2001), even though most were not intended to originally house them. Throughout

the United States, bridges commonly are inhabited by many species of bats, as these

structures serve as various types of roosts, including daytime shelters (Stager 1943, Davis

and Cockrum 1963, Fraze and Wilkins 1990, Lance and Garrett 1997, Arnett and Hayes

2000, Lance et al. 2001, Trousdale and Beckett 2002, 2004, Feldhamer et al. 2003,

Keeley and Keeley 2004, Ferrara and Leberg 2005), night roosts (Hirshfeld et al. 1977,

Lewis 1994, Adam and Hayes 2000, Johnson et al. 2002), maternity roosts (Davis and

Cockrum 1963, Trousdale and Beckett 2002, 2004), bachelor colonies (Davis and

Cockrum 1963), and transient roosts (Davis and Cockrum 1963, Fraze and Wilkins 1990)

and seasonally (Kunz 1982, Geluso and Mink 2009).

Despite the important functions that bridges provide for many species,

documentation and conservation of bridges as vital roosting sites is minimal priority in

many states. Protection of roosts is important because they provide places for important

life-history functions such as copulation, bearing and raising of young, consumption and

digestion of food, rest, grooming, and hibernation. Given their diverse functionality,

roosting sites differ greatly among bats (Kunz 1982), and even a single species may use

different roosts depending on sex, season, and time of day (Hill and Smith 1984).

Humphrey (1975) proposed that availability of roosting sites might be a limiting resource

for bats, and when roosts are absent or removed, bats may disappear from areas or alter

their abundance, distribution, and demographics (Constantine 1967, Findley 1987, Lewis

1995, Fenton 1997).

In the southwestern United States, bats are known to roost in bridges (Keeley and

Tuttle 1999), but few specific details are known on how and when they use bridges

throughout the year. In New Mexico, almost no information exists on whether the 29

species that inhabit the state use bridges as roosts. Thus far, only the Brazilian free-tailed

bat (*Tadarida brasiliensis*) and eastern pipistrelle, or tri-colored bat, (*Pipistrellus*

[*Perimyotis*] *subflavus*) have published accounts of roosting in bridges. Constantine

(1967) reported that *T. brasiliensis* roosts throughout the year in bridges of southern New Mexico, and Geluso et al. (2005) reported the first record of an eastern pipistrelle (*Perimyotis subflavus*) in the state from under a bridge. Other species are known to roost in bridges in Arizona and Texas (Davis and Cockrum 1963, Fraze and Wilkins 1990, Keeley and Tuttle 1999), and we predicted that bridges also serve as important roosting sites for bats in New Mexico. For this project, we examined use of bridges by bats in the lower Rio Grande valley of New Mexico. We investigated which species roost in bridges, the functions bridges serve for them, seasonal variation in bridge use, where individuals roost in bridges, and what characteristics of bridges are associated with day roosting.

Methods

Study Site Description

We conducted this study along the lower Rio Grande valley in southern New Mexico from Truth or Consequences, Sierra County to Radium Springs, Doña Ana County. We inspected 17 bridges associated with paved highways that crossed arroyos, small canyons, and the Rio Grande (Table 1). Bridges were constructed from timber or from a combination of concrete, metal, or both. Vegetation varied from creosote bush (*Larrea tridentata*) and mesquite (*Prosopis grandulosa*) on flat areas, Chihuahuan desert scrubland dominated by creosote bush on rocky hills and slopes, and cottonwoods (*Populus deltoides*) and tamarisk species (*Tamarix chinensis* and *T. ramosissima*) along edges of the Rio Grande and Caballo Reservoir in the northern part of the study area. The southern half of the study area contained agricultural fields in the low-lying flat areas

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bordered by screwbean mesquite (*P. pubescens*), tamarisk along edges of the Rio Grande, and Chihuahuan desert scrubland on rocky hills and slopes.

Bridge Bat Census

Bridges were examined one day each month April 2004-March 2006. During daylight hours, we systematically searched in cracks, crevices, and other small spaces under and on sides of bridges. Under each bridge, we also inspected all surfaces not associated with narrow spaces, and hereafter, we refer to these surfaces as open areas. For each bat or group of individuals, we recorded the location of the roost and whether individuals were in narrow spaces or open areas. At each roost, we counted the numbers of each species, including non-volant young when present. At many sites, bats roosted in deep cracks and were stacked atop one another at least 2-4 individuals. Numbers reported herein represent only those bats in the lowest layer. Our counting method underestimated the total number roosting in bridges 1) when individuals were stacked, 2) when bridges crossed the Rio Grande containing fast unsafe currents for us to observe bats ($n = 4$, Table 1), and 3) when bridges were too high for observation (Percha Creek, Table 1). During colder months, flow of the Rio Grande was reduced allowing access to additional spans; bats counted in those spans are not reported hereafter, except where explicitly stated in Results and Discussion.

A more accurate count of individuals at roosts was not obtained because we attempted to minimize disturbance. At the beginning of our study, we captured a number of individuals; however, when removing them, nearby bats always crawled lengthwise down cracks and some individuals flew from roosts, especially groups of *M. yumanensis*. Throughout the project, we occasionally captured individuals to verify species or to

determine sex, age, body mass, and reproductive condition. For almost all individuals, we identified them to species visually by illuminating narrow spaces with hand-held lights. Most spans were relatively low to the ground (1.1 to 4.1 m), allowing observation at close distances. If identification of bats was in question, we reported them as unknown species.

We also examined each bridge for evidence of night roosting by searching for fecal pellets on the ground in areas not associated with narrow spaces occupied by bats during the day. On I-beam bridges, we also searched for fecal pellets on sides of walls and on small ledges associated with lower edges of beams.

Bridge Architecture

Bridges examined consisted of those constructed from mainly timber ($n = 12$) and those constructed from mainly concrete, metal, or both (I-beam bridges, $n = 5$). Architecture of timber bridges generally had more spans, but spans were shorter and thus supported by relatively more trusses; I-beam bridges generally had fewer trusses but longer spans. Heights of bridges differed, but most spans examined for bats ranged from 1.2 m to 4.5 m above the ground. I-beam bridges generally lacked narrow spaces, and some had a few. In contrast, all timber bridges had narrow spaces, and some had many.

Results

Species and Numbers of Bats using Bridges

We observed 8 species of bats roosting in bridges during the day (Table 2). In summer, the Yuma myotis (*Myotis yumanensis*), Arizona myotis (*M. occultus*), and

Brazilian free-tailed bat formed maternity roosts in at least 8 bridges; adult males of these species also were present during warmer months. The California myotis (*Myotis californicus*), fringed myotis (*M. thysanodes*), silver-haired bat (*Lasionycteris noctivagans*), big brown bat (*Eptesicus fuscus*), and pallid bat (*Antrozous pallidus*) roosted infrequently in bridges, and we did not observe maternity colonies of these species or evidence of reproductively active females.

A total of 36,629 day-roosting bats were counted in bridges April 2004-March 2006 (Table 2). *Tadarida brasiliensis* was the most abundant species observed followed by *M. yumanensis* and *M. occultus*, and these species were observed at most bridges (Table 2). The pallid bat was the only other species with multiple sightings, and all 5 individuals handled were adult males. Only single individuals of the 4 remaining species were observed; including an adult female *M. californicus* on 3 April 2004, an adult male *E. fuscus* on 15 June 2004, a male *M. thysanodes* on 26 September 2004, and a male *L. noctivagans* on 13 March 2005.

We observed evidence of night roosting by bats at all timber and I-beam bridges. The largest deposits of guano from night-roosting individuals were discovered under timber bridges. Some accumulations of guano from night roosting were greater than from accumulations under the larger groups of day-roosting individuals.

Monthly Fluctuations of Bats in Bridges

Use of bridges by day-roosting bats differed monthly, and most occupied bridges April-October (Table 3). In 2004, totals of all individuals peaked in July, and in 2005, individuals peaked in June. *Myotis yumanensis* and *M. occultus* were most numerous in June and July, and *T. brasiliensis* was most numerous in August and September (Table

3). Compared to warmer months, relatively few individuals of *T. brasiliensis* (20 to 520 bats) roosted in bridges November-March. Other species observed in colder months included 2 individuals of *M. yumanensis* in January and 12 individuals of *M. yumanensis* and a single *L. noctivagans* in March (Table 3; 1 of the *M. yumanensis* observed in January was in an additional span of bridge only accessible during low flows in winter, and this individual is not recorded in Tables 2 or 3). We observed none of the species using bridges as hibernacula, and we observed the fewest number of individuals in January or February. In spring, the majority of bats appeared in April and May, and in autumn, most vacated roosts in September and October (Table 3). *Myotis yumanensis* was absent from bridges November, December, and February, and *M. occultus* was absent October-March. We observed *A. pallidus* roosting in bridges 3 April-26 September.

Roosting Sites in Bridges

We observed 99.8% of bats in timber bridges and 0.02% (61 individuals) in I-beam bridges. The most bats counted in a single bridge was 1313 (King Canyon), although other larger bridges with spans over the Rio Grande likely contained many more bats. Day-roosting bats were observed in 100% of timber bridges, but some bridges were used more frequently than others. Only 3 of 5 (60%) I-beam bridges were used by day-roosting bats in this study. Day-roosting bats roosted significantly more often in timber bridges than in I-beam bridges ($U = 59$, $d.f. = 5,12$, $p = 0.001$, Mann-Whitney test). The lowest height of a span used by *T. brasiliensis* was 1.4 m, the lowest for *M. yumanensis* was 1.1 m, and the lowest for *M. occultus* was 1.1 m.

Bats roosted in numerous sites on bridges, about 99.9% of individuals ($n =$ 36,611) roosted in narrow cracks and crevices, and only 18 individuals were observed in open areas during daylight hours. Narrow spaces in bridges consisted of two main types. In timber bridges, 95.0% of bats roosted in spaces formed by parallel-running pairs of large adjacent beams, hereafter referred to as double beams (Table 1). Along lengths of most spans, these pairs of beams have separated and created a narrow, deep, and dark space that measured about 38 cm deep with widths ranging from 1 to 25 mm. The largest number of bats counted in a single span in a double beam was 453, which included mainly *M. yumanensis*, a few *M. occultus*, and a few *T. brasiliensis*. This count of individuals only represented those in the lowest layer of bats and numbers likely were at least double. We observed all species in spaces between double beams except *L. noctivagans* and *E. fuscus*.

In narrow crevices between double beams, we commonly observed multiple species in a crevice along a single span. Generally, the majority of individuals of each species were observed in species-specific groups, with groups commonly adjacent to one another and sometimes touching. In large species-specific groups, we usually observed a few individuals of other species interspersed within. On a number of occasions, however, crevices were packed with 2 species in a relatively random manner with many individuals of different species side by side.

The other narrow space frequently used in timber bridges was located above the supports at ends of each span. Atop bridge supports, ends of large timber beams that cross spans terminated. Here, opposing timber beams from each side of the span laid next to one another for only the width of the support (about 29 cm), and some contained

no space between timber beams but others had spaces of various widths. We observed 5% of bats in timber bridges in these spaces. Although bats commonly roosted in these small spaces, the largest number of individuals in a single space was about 35-50 individuals. We observed 6 species roosting in these narrow spaces—*T. brasiliensis*, *M. yumanensis*, *M. occultus*, *A. pallidus*, *E. fuscus*, and *L. noctivagans*. The most frequently observed bats in these spaces were solitary male *M. occultus*. In these narrow spaces, groups of individuals usually consisted of a single species.

In the timber bridge spanning King Canyon, we measured widths of all narrow spaces above the supports of each span because all were accessible and frequently occupied by bats. Spaces ranged from 1 to >150 mm in width. In June, July, and August 2005, bats roosted in these spaces on 67 occasions in this bridge. Mean width of spaces occupied by bats was 16.8 mm and occupied spaced ranged from 8 to 35 mm. In this range of widths (8-35 mm), we documented a total of 87 spaces in the bridge, and in contrast, we observed no bats in the 11 spaces <8 mm and 76 spaces >35 mm in width.

Another narrow space used by bats formed when large beams that crossed spans separated from the lignified wood materials above these timber beams. To our knowledge, only a few of these spaces existed, and we discovered them only when chattering bats alerted us to their presence. We only captured bats from 1 of these sites, and it contained *M. yumanensis*.

We observed open areas under timber bridges to be used infrequently by bats, with a total of 17 individuals observed roosting on sides of beams including 16 individuals of *M. yumanensis* and a single *M. occultus*. All individuals were discovered near abutments of bridges where it was darkest. These observations were reported May-

October, and at least 11 individuals were adults. Male and female *M. yumanensis* were observed, and the single *M. occultus* was male.

Relatively few bats (*n* = 61) were observed day-roosting on I-beam bridges. Many of these individuals (13 *T. brasiliensis* and 15 *A. pallidus*) were discovered in narrow spaces associated with joints between spans or at the ends of bridges. Several individuals were discovered in small spaces associated with anomalies of the bridge. On six occasions, for example, a single *M. yumanensis* roosted between a concrete wall and small piece of wood; the space was only a few cm deep. Other observations included 25 individual bats (species unknown) behind a metal plate that had separated from concrete associated with railing on the bridge, a solitary male *M. yumanensis* roosting in a partially broken nest of a cliff swallow (*Petrochelidon pyrrhonota*) on 29 June 2005, and a volant young male *M. yumanensis* roosting in the open on the side of a concrete I-beam on 30 July 2005.

Discussion

Species in Bridges and Functions of Bridges for Bats

Seven of 8 species observed in this study represented species previously not documented roosting in bridges in New Mexico (*M. yumanensis*, *M. occultus*, *M. californicus*, *M. thysanodes*, *L. noctivagans*, *E. fuscus*, and *A. pallidus*). Most species, however, have been documented in bridges elsewhere in the United States (Keeley and Tuttle 1999). In Arizona, *M. yumanensis*, *E. fuscus*, *T. brasiliensis*, and *A. pallidus* are known to use bridges as maternity roosts (Davis and Cockrum 1963), and in Texas, *T. brasiliensis* also has been reported in bridges (Fraze and Wilkins 1990, Keeley and

Keeley 2004). In southern New Mexico, the present study demonstrated that older timber bridges serve as important sites for maternity colonies of *M. yumanensis*, *M. occultus*, and *T. brasiliensis* (Table 4), transient roosts for *M. californicus*, *M. thysanodes*, *L. noctivagans*, *E. fuscus*, and bachelor roosts for *A. pallidus*.

Frequency, abundance, and use of bridges by *M. occultus* was unexpected because this species previously was not reported in bridges in Texas, New Mexico, and Arizona (Davis and Cockrum 1963, Findley et al. 1975, Hoffmeister 1986, Schmidly 1991). In New Mexico and Texas, records of *M. occultus* are scarce along the Rio Grande. Findley et al. (1975) reported only 4 localities of *M. occultus* along the Rio Grande, and most records of this species in New Mexico are from mountainous areas. Allen (1922) reported the only *M. occultus* from the lower Rio Grande valley in New Mexico, and in Texas, only a single record of *M. occultus* is known in the state (Schmidly 1991) at a locality near Fort Hancock. The only other account of this species in a bridge is from southern California (Stager 1943).

Occupation of 100% of timber bridges and 60% of I-beam by day-roosting bats is noteworthy because several other studies in the United States report relatively low occupancy of bats in bridges. For example, Trousdale and Beckett (2002) observed day-roosting bats under 8% (8 of 99) of bridges in southern Mississippi, and Feldhamer et al. (2003) reported day-roosting bats in 6.5% (15 of 232) of bridges in southern Illinois. We suspect the proximity of bridges to permanent sources of water in this arid region and lack of naturally occurring candidate roosts near water may account for the high frequency of occupancy for bridges in southern New Mexico.

Bridges in our study also served as night roosts. Functions of night roosts generally differ from those of day roosts, serving as sites for consumption of prey, digestion, energy conservation, rest, shelter, and social function (Kunz 1982). Several timber bridges appeared to be large night roosts based on large quantity of guano under open areas of bridges. We were unable to determine presence of night roosts of bats under portions of bridges over water.

Monthly Fluctuations of Bats in Bridges

In temperate regions of North America, bats are most active in warmer months, and during colder months, bats migrate, hibernate, or both (Kunz 1982, Jones et al. 1983). In southern parts of the United States, several studies demonstrate that some bats remain active in winter (Cross 1965, O'Farrell et al. 1967, Ruffner et al. 1979, Padgett and Rose 1991, Geluso 2007, 2008). In the present study, most bats used bridges in warmer months (April to October, Table 2), and total numbers peaked in June and July when non-volant young also were included in counts. Increases of use in April and May correspond to bats arriving from distant wintering grounds or from nearby winter hibernacula, and decreases in autumn represent individuals vacating roosts to migrate or hibernate. The peak of *T. brasiliensis* in August and September suggests that individuals from other nearby roosts or from more northerly colonies use bridges as transient stopover sites during migration.

Observations of *T. brasiliensis* roosting in bridges throughout winter (Table 3) demonstrates that not all individuals migrate from or through New Mexico during the cold months. From October to February, we accessed 12 additional spans under the timber bridge at Radium Springs. During this time, we observed more *T. brasiliensis* in

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these additional spans than in the 7 spans over dry land. In October 2004, we observed

1102 *T. brasiliensis* in spans usually over water compared to 203 individuals in spans

over dry land, in November (531 versus 142), December (69 versus 38), January 2005

(382 versus 1), February (444 versus 5), November (1072 versus 51), December (1071

versus 78), January 2006 (unknown number versus 40), and February (1174 versus 52).

Although most individuals left roosts during the cold months, it is uncertain whether

remaining individuals represent a small percentage of individuals from local summer

populations or those from more northerly populations, such as in southern Colorado

(Svoboda and Choate 1987, Freeman and Wunder 1988). In New Mexico, small groups

of *T. brasiliensis* previously have been reported from Carlsbad Cavern and bridges in

Eddy County during winter (Christensen 1947, Constantine 1967, Geluso and Geluso

2004), but Geluso (2008) observed more individuals than expected throughout the entire

winter at the cavern. Winter use of bridges is interesting because bats are not buffered

from low ambient temperatures as they would be roosting in caves. We predict that use

of bridges during cold months in southern New Mexico is positively correlated with

night-time temperatures and with insect abundance. That is, winters with an extended

number of nights with temperatures below freezing should have fewer individuals

compared to winters with overall warmer night-time temperatures. Although *T.*

brasiliensis is not known to hibernate, individuals readily enter torpor (Barbour and

Davis 1969) and thus feed in winter in southern New Mexico (Geluso 2007, 2008) under

benign climatic conditions. Further studies on the natural history of wintering Brazilian

free-tailed bats are warranted in the southern United States.

Several individuals of *M. yumanensis* in bridges were observed during cold

months (2 in January and 12 in March, Table 3). These records represent some of the

only winter records of this species throughout its entire range (Hoffmeister 1986). In

Arizona, Hoffmeister (1986) reported that of 37 localities where individuals were

captured in summer, there is only 1 locality where they are known in winter. Hoffmeister

(1986) suggested that the Yuma myotis generally migrates out of the state in autumn and

returns to Arizona in spring, but also suspected that this species is present in lower,

warmer parts of the Colorado River and northern Mexico in winter. We suspect that *M.

yumanensis* does not migrate long distances from summer roosts in the Southwest. The

occurrence of a few individuals at known summer roosts in winter suggests that this

species hibernates nearby, or arouses periodically from hibernation and subsequently

occupies bridges during these times.

Roosting Sites Used by Bats

Davis and Cockrum (1963) stated that most bridges can serve as night roosts for

bats, but only those with specific construction e.g., bridges with narrow spaces or those

containing large cave-like chambers at terminal foundations appear to provide the

necessary conditions to serve as day roosts. This study (Geluso and Mink 2009), as well

as others, demonstrate that many species of bats occupy narrow spaces for day roosts

(Fraze and Wilkins 1990, Arnett and Hayes 2000, Feldhamer et al. 2003), but some

species, such as Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), may select to

roost in more exposed areas under bridges (Lance et al. 2001, Ferrara and Leberg 2005).

In Arizona, Davis and Cockrum (1963) also stated that type of construction and not

construction material appears to be the critical factor in determining use by day-roosting

bats. Recent studies across the United States further demonstrate that bats roost in bridges constructed of different materials, but timber bridges containing fresh creosote hamper roosting activity by bats (Constantine 1967, Adam and Hayes 2000, Lance et al. 2001). In our study, timber bridges coated with creosote were occupied by bats, but in these bridges, creosote was not fresh and it is not known how long bats have occupied these bridges.

Newer styles of bridges may not provide adequate spaces for day-roosting bats (Davis and Cockrum 1963, Lance et al. 2001, Johnson et al. 2002, this study). For example, Davis and Cockrum (1963) commented that recent trends towards use of metal longitudinal undersupports results in most newer bridges being unsuitable as day roosts. Our study demonstrated that day-roosting bats occurred more frequently in older timber bridges (99.8%) compared to some of the more recent I-beam bridges (0.02%). We suspect the paucity of individuals day-roosting in I-beam bridges reflects lack of narrow spaces in these structures and not the construction materials or date constructed. Although construction of new bridges may lack roosting sites for bats, Arnett and Hayes (2000) demonstrated that installing boxes containing narrow crevices under bridges promoted day and night roosting by bats in western Oregon.

Bats in the lower Rio Grande valley of New Mexico appear to select narrow spaces in bridges that are relatively dark and provide protection from predators. In contrast, narrow spaces in timber bridges did not provide bats protection from rain. On a number of occasions, we observed bats soaked with water, even in areas containing maternity colonies, because road surfaces above bridges were permeable to water. Other

studies have suggested that temperatures under bridges are warmer than surrounding potential roost sites, thus promoting use by bats (Adam and Hayes 2000).

Management Issues Associated with Bats in Bridges

This study demonstrated that bridges represent important roosting sites for a number of species in New Mexico. Because roosts provide sites for important life-history functions, bridges used by bats could be managed as a resource to promote the conservation of bats, especially those occupied by maternity colonies or large numbers of individuals. During our study, one timber bridge was demolished and replaced with a new I-beam bridge that lacked narrow spaces. The conversion of older timber bridges to metal or concrete I-beam bridges will reduce availability of roosting sites for bats in New Mexico. Whether this may limit distributions of bats, reduce their numbers, or alter demographics such as number of reproducing females, has yet to be determined or studied.

One alternative to demolishing antiquated timber bridges currently occupied by bats is to preserve them in place and to construct new I-beam bridges adjacent to them, such as Radium Springs. The older timber bridge at the latter site is a registered historic structure, serves as a pedestrian foot bridge, and to date, we never observed a bat roosting on the adjacent I-beam bridge while thousands of bats have been observed in the narrow crevices of the timber bridge. It seems advantageous that some bridges never be removed to promote the conservation of bats. Until retrofitting bridges with "bat houses" is demonstrated to provide bats with appropriate roosting sites for large numbers of individuals, demolishing timber bridges could negatively affect many bats and the

ecosystem processes influenced by bats, such as the consumption of many night-flying insects (Cleveland et al. 2006).

Timing of bridge demolition is important to consider because of the seasonality of life-history aspects of bats. During this study, the bridge containing the 2nd highest monthly count of bats (by our counting methods and limitations, see Materials and Methods), including robust maternity colonies of *M. yumanensis* and *T. brasiliensis*, was demolished and razed in June 2005 upon completion of the new, adjacent I-beam bridge. Unrecognized or ignored by demolition crews and the New Mexico Department of Transportation, removal of the bridge coincided during the period when young bats cannot fly. The demolition likely killed 1,000s of bats, and unfortunately Brazilian free-tailed bats do not retrieve fallen young (K. N. Geluso, personal observation at Carlsbad Cavern) as well as possibly Yuma myotis. With planning and an understanding of bat biology, it is possible to prevent the destruction of bats when removing bridges, especially those used as maternity sites. As demonstrated by monthly fluctuations in numbers of individuals using bridges in this study (Table 3), demolition of bridges should be done when most bats are absent or when all individuals can fly, such as before birth in June or after young become volant by August.

After talking with both the New Mexico Department of Game and Fish and the New Mexico Department of Transportation after the demolition of the bridge, we learned that the most limiting constraint on communication between the 2 agencies to prevent further destruction of bridges with large concentrations of bats was the overall lack of knowledge about use of bats in bridges in the state. We hope that data presented in this study will aid bats throughout the southwestern United States as well as other regions

because bats are important natural components of many ecosystems throughout the world. Coexistence with bats depends on our understanding of their needs throughout the year in both natural and human-made environments.

Table 1. Bridges examined for bats along the Rio Grande valley in southern New Mexico. For bridges constructed of wood, double beams represent 2 adjacent parallel beams with areas containing deep narrow crevices between them commonly occupied by bats (see text). Numbers in parentheses represent numbers of double beams in each span.

Location	New Mexico Highway	Latitude and longitude	Construction type	Over water	Number of spans	Double beams
Sierra County						
1. Elephant Butte State Park	51	33°08.701'N, 107°12.556'W	Wood	Yes	10[1]	No
2. Truth or Consequences	51	33°08.957'N, 107°13.286'W	Wood	Yes	12	Yes (1)
3. Palomas Creek	187	33°03.659'N, 107°17.934'W	I-beam	No	5	--
4. King Canyon	187	33°02.323'N, 107°18.169'W	Wood	No	8	Yes (2)
5. Seco Creek	187	32°59.101'N, 107°18.254'W	Wood	No	8	Yes (2)
6. Animas Creek	187	32°58.017'N, 107°18.660'W	I-beam	No	4	--
7. Eagle Point, Caballo Lake	187	32°56.631'N, 107°18.770'W	Wood	No	7	Yes (2)
8. Oasis	187	32°55.794'N, 107°18.975'W	Wood	No	3	Yes (2)
9. South of Oasis	187	32°55.345'N, 107°19.071'W	Wood	No	4	Yes (2)
10. Percha Creek	187	32°53.968'N, 107°18.707'W	Wood	No	9[2]	No

Table 1 continued. Bridges examined for bats along the Rio Grande valley in southern New Mexico. For bridges constructed of wood, double beams represent 2 adjacent parallel beams with areas containing deep narrow crevices between them commonly occupied by bats (see text). Numbers in parentheses represent numbers of double beams in each span.

Location	New Mexico Highway	Latitude and longitude	Construction type	Over water	Number of spans	Double beams
Sierra County						
11. North of Arrey	187	32°51.096N, 107°19.180W	Wood	No	8	Yes (2)
12. South of Arrey	187	32°50.034N, 107°19.239W	Wood	No	7	Yes (2)
13. North of Derry, Old[3]	187	32°48.559N, 107°18.284W	Wood	Yes	21[4]	Yes (1)
14. North of Derry, New[5]	187	32°48.564N, 107°18.284W	I-beam	Yes	5	--
Doña Ana County						
15. Northeast of Placitas	187	32°40.895N, 107°11.370W	I-beam	Yes	6	--
16. Radium Springs-Wood	185	32°29.234N, 106°55.543W	Wood	Yes	19[6]	Yes (2)
17. Radium Springs-I-beam	185	32°29.234N, 106°55.539W	I-beam	Yes	5[7]	--

[1]Due to high flows of the Rio Grande, we only examined 4 spans of bridge.
[2]Due to height of bridge, we only examined the 2 outermost spans of bridge.
[3]Bridge was dismantled and removed June 2005, thus we discontinued searching for bats in May 2005.
[4]Due to high flows of the Rio Grande, we only examined 14 spans of bridge.
[5]Bridge was built in Spring 2005 and completed in June 2005. We began searching for bats in June 2005.
[6]Due to high flows of the Rio Grande, we only examined 7 spans of bridge in summer months. In winter, I examined all spans.
[7]Due to high flows of the Rio Grande, we only examined 2 spans of bridge.

Table 2. Species of bats occupying bridges along the Rio Grande valley in southern New Mexico, April 2004-March 2006. Number of individuals represent total numbers of individuals counted at all bridges. Number of bridges indicates number of bridges with detection of that species from a total of 17 bridges. Number of maternity roosts indicate number of different bridges with non-volant young observed at least once during study.

Scientific name	Common name	Number of individuals	Number of bridges	Number of maternity roosts
Tadarida brasiliensis	Brazilian free-tailed bat	18,261	12	6
Myotis yumanensis	Yuma myotis	13,997	14	7
Myotis occultus	Arizona myotis	4,081	9	2
Antrozous pallidus	Pallid bat	84	3	0
Eptesicus fuscus	Big brown bat	1	1	0
Myotis californicus	California myotis	1	1	0
Myotis thysanodes	Fringed myotis	1	1	0
Lasionycteris noctivagans	Silver-haired bat	1	1	0
Unknown individuals		202	4	

Table 3. Monthly totals of bats observed roosting in bridges along the lower Rio Grande valley of New Mexico, April 2004-March 2006. These numbers only reflect bats counted in spans accessible every month, and numbers do not include bats observed in spans when additional spans were accessible because of low flows in the Rio Grande.

Date	All species	*T. brasiliensis*	*M. yumanensis*	*M. occultus*
3 April 2004	317	234	80	0
31 May 2004	3748	1773	1660	312
15 June 2004	3762	1504	1568	537
16 July 2004	4378	1636	1799	931
24 August 2004	3692	2488	863	304
26 September 2004	1631	1251	333	18
28 October 2004	792	772	19	0
20 November 2004	210	210	0	0
25 December 2004	38	38	0	0
26 January 2005	37	36	1	0
18 February 2005	20	20	0	0
13 March 2005	26	21	4	0
28 April 2005	1032	271	713	39
17 May 2005	2117	704	1134	275
29 June 2005	3901	646	2506	748
30 July 2005	3366	1102	1646	615
20 August 2005	2366	1041	1043	265
15/16 September 2005	2634	2041	540	37
10 October 2005	1164	1083	80	0

Table 3 cont. Monthly totals of bats observed roosting in bridges along the lower Rio Grande valley of New Mexico, April 2004-March 2006. These numbers only reflect bats counted in spans accessible every month, and numbers do not include bats observed in spans when additional spans were accessible because of low flows in the Rio Grande.

Date	All species	*T. brasiliensis*	*M. yumanensis*	*M. occultus*
30 November 2005	248	248	0	0
6 December 2005	226	226	0	0
4 January 2006	115	115	0[1]	0
9 February 2006	281	281	0	0
18 March 2006	528	520	8	0

[1]A single *M. yumanensis* was observed in an additional span where we could only observe bats during reduced flows of the Rio Grande.

Table 4. Bridges with maternity colonies of bats in the lower Rio Grande valley of southern New Mexico. Bridges not listed did not contain maternity colonies during the study.

	Tadarida brasiliensis	*Myotis yumanensis*	*Myotis occultus*
Sierra County			
Truth or Consequences	No	Yes	No
King Canyon	Yes	Yes	Yes
Seco Creek	Yes	Yes	Yes
Animas Creek	Yes	Yes	No
North of Arrey	No	Yes	No
South of Arrey	Yes	No	No
North of Derry, Old[1]	Yes	Yes	No
Doña Ana County			
Radium Springs-wood	Yes	Yes	No

[1]Bridge was demolished in June 2005.

CHAPTER THREE

Bridge Occupancy as an Overwintering Strategy for Brazilian Free-Tailed Bats:
Demographics of Winter Residents in Texas

Abstract

Migration maximizes fitness and seasonal energy benefits in mobile organisms by enabling a species to occupy multiple environments across widely varying landscapes. Flexible timing and behavior of migratory organisms can optimize fitness and seasonal energy benefits associated with migration. Engineered structures such as bridges along historic migration routes are potential alternative winter habitat for bats. This study of winter *Tadarida brasiliensis* populations occupying bridges in Texas offers insight into variation in migratory patterns, and describes demographics of previously undescribed winter populations found midway along an expected U.S. to Mexico migration route. Bridge populations of day-roosting bats were censused at two sites in central and south Texas, 563 km apart, through six winters (2005-2011). Mean counts during winter months were consistently several thousand (Bell County $\bar{x} = 3,132$; Kenedy County $\bar{x} = 2,699$). Mist-net sampling of *Tadarida brasiliensis* through three winters from 2007-2009 yielded consistent captures (*n*=975) at bridge sites. Body mass, gender, feeding status and age were recorded for bats captured. Contrary to previous reports for migratory *Tadarida brasiliensis*, both sexes, all age classes, and active feeding were observed at all bridge sites throughout winter. Body mass for each population (*n*=975) declined initially (December to January), but increased from January to February. Body mass varied across sites, months, sex and age class (*p*<0.0001). Variations among sites

across years (F=25.99; $p<0.0001$), and winter months across sexes (F=6.96; $p=0.001$) were also significant. Adult males were significantly heavier than juvenile males (F=15.43; $p<0.0001$); however, females were not. Sex ratio (M:F) shifted but females were present during all winter months regardless of age class or site. No fewer than 58% of bats sampled were juveniles, and various feeding activity rates were detected throughout winter. Our results suggest that bridge habitats are advantageous beyond serving as roost alternatives in response to habitat loss. Winter occupancy of bridges likely serves as a viable alternative to historic migratrion strategies by demoting certain hazards associated with migration, competition or food resources. Flexible migration patterns, heterothermic capacities, and consistent exploitation of bridge roosts during winter months, may promote commensalism of *Tadarida brasiliensis* with humans.

1. Roosting behaviors by *Tadarida brasiliensis* in natural caverns and bridges, and continuous occupation during winter have important implications for migrating populations of these insectivorous bats and for winter ecosystems.

2. We describe winter-month fluctuations in *Tadarida brasiliensis* populations at four bridges and two locations separated geographically north-south by 563 km.

3. We evaluated demography, sex ratio, age class, feeding activity and mass over winter months and found dynamic shifts in these categories.

4. Juveniles comprised 58% of sampled bats, however, all four age classes and both sexes were captured in all winter sampling sessions. Feeding activity was high and consistently detected in captured bats throughout winter.

5. Representation of all age categories throughout winter suggests adaptation or acclimatization to bridge roosts as a viable winter strategy for *Tadarida brasiliensis* bats.

6. Bridge occupation is advantageous as an alternate winter strategy to migration. This winter roost behavior is likely a result of behavioral plasticity or a predisposition to a commensal relationship with humans rather than unrelenting habitat loss.

Key words: Brazilian free-tailed bat, *bridge roost, commensalism, sex ratio,* Tadarida brasiliensis*, winter ecology, winter residency, winter mass, winter population structure*.

Resumen.

La migración maximiza aptitud y ventajas estacionales de la energía en organismos móviles permitiendo a una especie ocupar ambientes múltiples a través de paisajes extensamente diversos. La sincronización y el comportamiento flexibles de organismos migratorios pueden optimizar la aptitud y las ventajas estacionales de la energía asociadas a la migración. Las estructuras dirigidas tales como puentes a lo largo de las rutas de migración históricas son hábitat alternativo potencial del invierno para los murciélagos. Este estudio de las poblaciones del *brasiliensis* del Tadarida del invierno que ocupan los puentes en Tejas ofrece la penetración en la variación en modelos migratorios, y describe el demographics de las poblaciones sines descripción previa del invierno encontró mitad del camino centra a lo largo de un Estados Unidos previstos a la ruta de migración de México. Las poblaciones del puente de murciélagos día-roosting censused en dos sitios en Tejas central y del sur, 563 kilómetros aparte, con seis inviernos (2005-2011). Las cuentas del medio durante meses de invierno eran constantemente

varios miles (x̄ del condado de Bell = 3.132; x̄ del condado de Kenedy = 2.699). El

muestreo de la Niebla-red del *brasiliensis* del Tadarida tres inviernos rindió a través a

partir de 2007-2009 las capturas constantes ($n = 975$) en los sitios de puente. La masa del

cuerpo, el género, la situación de alimentación y la edad fueron registrados para los

murciélagos capturados. El contrario a los informes anteriores para el *brasiliensis*

migratorio del Tadarida, ambos sexos, todos los grupos de edad, y la alimentación activa

fueron observados en todos los sitios de puente en invierno. La masa del cuerpo para

cada población ($n = 975$) disminuyó inicialmente (diciembre a enero), pero aumentó de

enero a febrero. Masa del cuerpo variada a través de sitios, de meses, de sexo y del grupo

de edad ($P< 0.0001$). Sitios a través de los años (F = 25.99; $P < 0.0001$), y meses de

invierno a través de los sexos (F = 6.96; $P = 0.001$) eran también significativos. Los

varones adultos eran perceptiblemente más pesados que los varones juveniles (F = 15.43;

$P < 0.0001$); sin embargo, las hembras no eran. Proporción por sexo (M: F) desplazado

solamente las hembras estaba presente durante todos los meses de invierno sin importar

grupo de edad o sitio. No más poco los que 58% de murciélagos muestreados eran

jóvenes, y las diversas tarifas de actividad de alimentación fueron detectadas en invierno.

Nuestros resultados sugieren que los hábitats del puente sean ventajosos más allá de la

porción como alternativas del gallinero en respuesta a pérdida del hábitat. La ocupación

del invierno de puentes sirve probablemente como alternativa viable a las estrategias

históricas del migratrion degradando ciertos peligros asociados a los recursos de la

migración, de la competencia o del fodd. Los modelos flexibles de la migración, las

capacidades heterothermic, y la explotación constante de los gallineros del puente durante

meses de invierno, pueden promover el commensalism del *brasiliensis* del Tadarida con los seres humanos.

Introduction

Temperate bats employ migratory movement (Miller 1897), hibernation (Johnson 1931), or a hybrid of strategies and destinations to accommodate seasonal insect supplies (Christensen 1947) and environmental constraints of winter. Similar to migrating birds, insectivorous temperate bats respond to climatic stress and migrate toward benign environments during winter as an energetically efficient strategy. Bats select winter destinations based on temperatures and available winter resources but may also be related to individual species traits associated with broader adaptability or temperature tolerances. Rapid arousal from torpor (Bailey 1933, Ransome 1971, Avery 1985) is also a documented behavioral response of some bat species. Hybrid strategies such as hibernation after migrating to benign environments to accumulate fat reserves may also be used by bats (Jones et al. 1983) and likely correlate with species vagility and flight performance. Migration strategies also may be sex specific in bats, see Fleming and Eby (2003) for treatment of known bat migration behaviors. Unfortunately, factors driving variation in migration, including male-specific migration (Villa 1956, Glass 1959; 1982), partial migration (Geluso 2007) and migratory adaptability (Villa 1956, Geluso 2008, Geluso and Mink 2009) in bats are largely unknown.

Bridges are viable, accessible alternatives to natural caves for various life-history stages and ecologies of bats in North America (Stager 1943, Davis and Cockrum 1963, Hirshfeld et al. 1977, Fraze and Wilkins 1990, Lewis 1994, Lance and Garrett 1997, Adam and Hayes 2000, Arnett and Hayes 2000, Lance et al. 2001, Johnson et al. 2002,

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Trousdale and Beckett 2002, 2004, Feldhamer et al. 2003, Keeley and Keeley 2004,

Ferrara and Leberg 2005, Geluso and Mink 2009). Bats periodically use bridges for

various functions and different behaviors, depending on the species (Geluso and Mink

2009) and time of year (Kunz 1982; Perlmeter 1996, Geluso and Mink 2009). Research

regarding factors determining the choice and use of various winter roosts such as bridges

is limited (Geluso 2008; Geluso and Mink 2009), particularly in regards to permanence of

occupancy or relative length of stay. However, Geluso and Mink (2009) reported

persistent *Tadarida brasiliensis*(Brazilian free-tailed bat) occupancy in various New

Mexico bridges during winter months. Despite the convenience of bridges for research

and their known occupation by bats, details of bat population structure and distribution in

bridge colonies (Keeley and Keeley 2004), especially during winter months, are poorly

understood for non-hibernating Brazilian free-tailed bats.

   Tadarida brasiliensis (Brazilian free-tailed bat) is a ubiquitous, semi-tropical bat

of the Americas. It is seasonally conspicuous, extensively distributed and locally

abundant throughout its range in North America (Cockrum 1969, Hall 1981, Hoffmeister

1986). These mammals are prominent faunal components of the southwestern United

States and may congregate in such seasonal profusion that they become the most

abundant mammal species in the Edward's Plateau region of Texas (Cagle 1950). Their

proclivity for limestone caverns, immense maternity colonies (Mohr 1948, Eads et al

1957, Villa and Cockrum 1962, Constantine 1967), and frequent roosting in engineered

habitats such as buildings (Krutzsch 1955, Spenrath and LaVal 1974) and bridges

(Geluso and Mink 2009) is well documented for warm and cool months. Populations of

T. brasiliensis are highly vagrant and annually migrate substantial (<1840 km) distances

(Villa 1956, Glass 1958, 1959; Villa and Cockrum 1962, Glass 1982). Winter disappearance of colonies of *T. brasiliensis* from their summer habitats coincides with shorter days and colder temperatures (Villa 1956, Glass 1982). However, despite their mass migrations during winter, many individual bats sporadically reside or linger within various states, including Texas (Villa and Cockrum 1962, Spenrath and LaVal 1974, Keeley and Keeley 2004). Winter dispersal patterns of *Tadarida brasiliensis* funnel south to Mexico from locations northern (Kansas, Oklahoma), western (Nevada, Utah, Colorado) and southwestern (Arizona, New Mexico, Texas) United States (Glass 1958, 1959; Findley and Jones 1964; Griffin 1970; Glass 1982; Dalquest and Horner 1984). *Tadarida brasiliensis* have been recovered in northern states of Mexico (Coahuila, Nuevo Leon, Sonora, Sinaloa, and Tamaulipas) and as far south as Jalisco in west-central Mexico during winter months (Villa 1956; Glass 1958, 1959; Villa and Cockrum 1962; Cockrum 1969; Glass 1982). Although *T. brasiliensis* commonly migrates from the central and southwestern United States into Mexico during fall, observed roost sites southward, along putative migratory routes shift considerably. For example, bats banded at Carlsbad Caverns in New Mexico are expected to migrate south along the Sierra Oriental Mountain range to Sinaloa or Sonora, in a western putative route (Villa 1956, Short et al. 1960, Villa and Cockrum 1962, Cockrum 1969, Glass 1982), but recoveries occur in more eastern locations (Eads et al 1957, Short et al. 1960, Glass 1958, 1959; Short et al. 1960). Bailey (1905, 1928), Christensen (1947) and Barbour and Davis (1969) suggested that some populations may migrate intermediate distances and overwinter in areas north of their expected southern destination; throughout the Mexican Plateau (Glass 1958, 1959; Cockrum 1969, Glass 1982).

Infidelities to established migration patterns for some *T. brasiliensis* suggest a phenology of migrational strategies, or movement based on individual bat proclivities. Genomes of *T. brasiliensis* show no significant fidelity to a geographic region or to a predictable migration behavior (Svodboda et al 1985, McCracken et al. 1994, McCracken and Gassel 1997, Russell et al 2005). Based on these data from banding at different points of origins and recoveries from multiple cavern destinations, many cavern populations are homogenized by free exchange of bats (Eads et al 1957, Short et al. 1960, Glass 1958, 1959; Short et al. 1960, Villa and Cockrum 1962, Constantine 1967, Cockrum 1969, Glass 1982). This blending coupled with anecdotal speculations, sporadic seasonal captures throughout its range and genetic studies data indicates that gene flow among North American *T. brasiliensis* prevents clear distinction of origins, flyways and destinations of this bat species. The dispersal capacity of *T. brasiliensis* likely magnifies gene flow and therefore has prevented these studies from detecting genetic lineage and phylogeographical patterns of this bat. Thus these bats essentially comprise a single North American gene pool, regardless of migration proclivity, or geographic behavioral variation. Therefore, characterizing or elucidating separate geographic races based on *T. brasiliensis* behavior, are likely overemphasized, or inaccurately assessed (Davis et al. 1962, Barbour and Davis 1969, Cockrum 1969, Hall 1981, Schmidley 1983).

Observations of *Tadarida brasiliensis* occupying habitats during winter in Texas include buildings (Spenrath and LaVal 1974), bridges (Keeley and Keeley 2004), and caverns (Krutzch and Sulkin 1958) but have not been consistent or subsequently substantiated (Keeley and Keeley 2004). One report documents *T. brasiliensis* in Texas

during winter from a cavern in central Texas (Krutzch and Sulkin 1958); however, others failed to find subsequent populations at this location (Spenrath and LaVal 1974). These discrepancies in cavern occupancy and roosting behavior are consistent with the irregular band returns of previous researchers during other seasons (Villa 1956; Glass 1958, 1959; Villa and Cockrum 1962; Constantine 1967; Cockrum 1969; Glass 1982). Davis et al. (1962) speculated that *T. brasiliensis* would only overwinter in thermally favorable buildings, implying temperature as a limiting factor. Spenrath and LaVal (1974) described winter activity only when temperatures at dusk were 10º C or more. However; Ruffner et al. (1979) captured nine *T. brasiliensis* during nights below 10º C during January and February in Utah. Captive migrating *T. brasiliensis* from Texas, demonstrated a pattern of lowered body temperature and metabolic rates when maintained at 5º C, suggesting migrating populations are thermally labile by withstanding lowered temperatures based upon laboratory trials (Orr 1958; Herreid 1963). Geluso (2007) mist-net captured *T. brasiliensis* at temperatures of 1º C, suggesting that these low temperatures do not limit volant activity of *Tadarida brasiliensis*.

Despite scant published data on late fall and winter activity of migratory populations of *T. brasiliensis* from the Southwest (Hoffmeister 1986, Geluso 2007; Geluso 2008; Geluso and Mink 2009), Geluso and Mink (2009) described the significance of bridges as year-round roosts in New Mexico, and noted limited, but persistent, populations during winter.

Despite the potential for populations of Brazilian free-tailed bats (*Tadarida brasiliensis*) to overwinter along migratory routes, validation of continuous roost occupancy in different habitats, and information on winter age demography and body mass comparisons is currently unavailable for this highly abundant and vagile species.

The purpose of this study was to interpret winter demography data of *T. brasiliensis* in central and south Texas. I also describe winter occupancy, absolute abundances, and seasonal fluctuations in four bridge roosting bat populations that are separated spatially (north-central Texas versus southern Texas) and differ in landscape context (urban influence versus ruderal influence). I expected date of capture to associate with body mass and predicted that mean body mass will increase in February across gender and age class. Male bats were expected to have higher mean body mass through winter and juvenile bats are expected to have the lowest mean body mass regardless of sex. I hypothesized that sex ratios would be male-biased based on greater mean body mass versus comparable female mean mass during other seasons (Eads et al. 1957 and Davis et al. 1962). Lastly, I expected bat activity, insect availability and temperature constraints to be revealed by body masses of winter captured *T. brasiliensis*.

Methods and Materials

Study Site Locations

This study was conducted at three sites in two counties of central and southern Texas (Figure 3). Forty-seven Texas bridges were surveyed in fall and winter of 2005 in Bell, Bexar, Comal, Ellis, Evant, Hays, McLennan, Nueces, Travis, Williamson, and Zapata counties, and recommendations were sought from the Texas Department of Transportation for roost sites as candidates for study. Two bridges were in north-central Texas and two bridges in south Texas. Transport, travel time and data collection logistics to sample wintering *T. brasiliensis* influenced choice of bridges suitable for long-term investigation. The northern site included two central Texas bridges in Bell County; 1)

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Hwy 317 bridge at Interstate 35 intersection (31° 02′N, 97° 28′W; elev. 581 ft) and, 6.4 km south of Highway 190 at 2) Lampasas River bridge on Interstate 35 (31° 00′N, 97° 29.31'W; elev. 503 ft.).

Study Site Descriptions

   The area surrounding the northern study site is part of the central blackland prairie and cross timbers and prairies vegetational regions (see map in Correll and Johnston 1970) adjacent to the eastern boundary of the Edwards plateau as delineated by relief of the Balcones Escarpment. This study site area is a mosaic of anthropogenic modified habitats, e.g. asphalt roads, commercial business pursuits, channelized storm sewers, agricultural modification as well as the Lampasas River. These bridges in Bell County are located along Interstate-35. This Lampasas River riparian area is characterized by these plants: southern shield fern (*Thelypteris ovata* var. *lindheimeri*), inland sea-oats (*Chasmanthium latifolium*), saw greenbrier (*Smilax bona-nox*), hellfetter (*S. tamnoides*), bird pepper (*Capsicum annuum* var. *glabriusculum*), American beautyberry (*Callicarpa americana*), box elder (*Acer negundo),* black willow (S*alix nigra*), cottonwood (*Populus deltoides*), Texas sugarberry (*Celtis laevigatus*), rough-leaf dogwood (*Cornus drummondii*), green ash (*Fraxinus pennsylvanica*), possumhaw (*Ilex decidua*), yaupon (*I. vomitoria*), Osage orange (*Maclura pomifera*), sycamore (*Plantanus occidentalis*), wafer ash (*Ptelea trifoliata*), Carolina buckthorn (*Rhamnus caroliniana*), American elm (*Ulmus americana*), chinaberry (*Melia azedarach*), glossy privet (*Ligustrum lucidum*), Chinese privet (*L. sinense*), smooth sumac (*Rhus glabra*), Alabama supple-jack (*Berchemia scandens*), poison ivy (*Toxicodendron radicans*), Virginia creeper (*Parthenocissus quinquifolia*), tree-of-heaven (*Ailanthus altissima*), pecan (*Carya illinoinensis*), black

walnut (*Juglans nigra*), and eastern red cedar (*Juniperus virginiana*). Dominant

vegetation away from riparian influence, occurred on Cretaceous limestone substrates

and included sideoats grama (*Bouteloua curtipendula*), hairy woollygrass (*Erioneuron

pilosum*), whitetop (*Tridens albescens*), little bluestem (*Schizachyrium scoparium*),

prairie spiderwort (*Tradescantia humilis*), agarito (*Berberis trifoliata*), coral berry

(*Symphoricarpos orbiculatus*), jara dulce (*Baccharis neglecta*), mesquite (*Prosopis

grandulosa*), Texas persimmon (*Diospyros texana*), Texas redbud (*Cercis canadensis*

var. *texensis*), prairie flame-leaf sumac (*Rhus lanceolata*), cedar elm (*Ulmus crassifolia*),

prickly-pear (*Opuntia engelmanii*), ashe juniper (*Juniperus ashei*), mesquite (*Prosopis

grandulosa*), lime pricklyash (*Zanthoxylum clava-herculis)*, Mexican buckeye (*Ungnadia

speciosus*), Mexican plum (*Prunus mexicana*), woollybucket bumelia (*Sideroxylon

lanuginosum*) and plateau live oak (*Quercus fusiformis*).

The southern site included two bridges in Kenedy County 5.6 km south of

Riviera, Texas on Hwy 77 at Los Olmos Creek (northbound 27° 16´N, 97° 48´W and

southbound spans; 27° 15´N, 97° 48´W; elev. 3-5 ft.). The area surrounding the southern

study site (Kenedy County) is part of the Tamaulipan brushland biotic province of Texas

(biotic province map in Gould 1962; 1969) and transected beneath bridge spans by Los

Olmos Creek, a brackish water stream. This stream varies in widths by tidal influence

and supports coastal saltgrass (*Distichus spicata*), sea oxeye daisy (*Borrichia frutescens*),

saladillo (*Varilla texana*), Texas bluebells (*Eustoma russellianum* [*E. grandiflorum*]) and

vidrillos (*Batis maritimas*) at the littoral interface. Also in the surrounding area are

Spanish dagger (*Yucca treculeana*), Rhodes grass (*Chloris gayana*), Sarita rosette-grass

(*Dichanthelium nodatum*), giant panic grass (*Panicum antidotale*), Bailey's ball moss

(*Tillandsia baileyi*), velvetleaf (*Abutilon theophrasti*), bee-brush (*Aloysia gratissima*),
Texas lantana (*Lantana urticoides*), Texas verbena (*Verbena halei*), Texas rabbit-tobacco
(*Pseudognaphalium austrotexanum*), fetid marigold (*Dyssodia papposa*), Caribbean
purple everlasting (*Gamochaeta antillana*), smallflower groundcherry (*Physalis
cinerascens* var.*spathulifolia*), beaked mock vervain (*Glandularia quadrangulata*),
prairie vervain (*Glandularia bipinnatifida* var. *bipinnatifida*) American snoutbean
(*Rhynchosia americana*), Texas pricklypoppy (*Argemone aurantiaca*), Texas ragwort
(*Senecio ampullaceus*), barbas de chivato (*Clematis drummondii*), anaqua (*Ehretia
anacua*), brasil (*Condalia hookeri*), desert hackberry (*Celtis pallida*), jara dulce
(*Baccharis neglecta*), desert yaupon (*Schaefferia cuneifolia*), lotebush (*Ziziphus
obtusifolia*), blackbrush acacia-chaparro prieto (*Acacia rigidula*), huisache (*A.
farnesiana*), retama (*Parkinsonia aculeata*), prickly-pear (*O. engelmanii*), cenizo
(*Leucophyllum frutescens*), amargosa (*Castela erecta*), mesquite (*Prosopis grandulosa*),
colima (*Zanthoxylum fagara*), and coastal live oak (*Quercus virginiana*) occur in the
surrounding study site area. The study sites were separated north to south by at least 563
km.

Bridge Census

　　　To document year-round occupation, bat census counts began in January 2006
and were collected through all months from December 2007 to March 2011. These
census counts were made simultaneously with winter mist-net sampling and separately
during spring, summer, and fall months (March-November). Occasionally, multiple
counts were made at the same site during particular months and mean census data were
recorded instead of absolute counts during these instances. Roosting bats were visually

distinguished to species and counted by illuminating the expansion joints and counting faces, or noses visible in the lowest layer. This method likely underestimated the total number of *Tadarida brasiliensis* roosting in bridges when individuals were stacked, or when bridges across waterways had current flow too swift (rain events) or deep (tidal influence) to allow adequate observation.

Demography Data

Fieldwork and census counts were conducted 2006-2011 during 127 sampling trips. Bats were netted as early as 14 December and as late as 28 February (29 netting episodes). Bats were netted during winter months only (December, January and February) hereafter referred to as winter. Mist nets (50 denier/ 2ply; 38 mm mesh; 2.6x12-18; Avinet, Inc., Dryden, New York, U.S.A.) were deployed before civil twilight. Nets were deployed at several locations adjacent to bridge roosts but not directly over waterways. Captured bats were temporarily held in 16-oz waxed paper cups, with opaque plastic lids, for meristics and guano collection and released within seven hours of capture. Most bats were marked by felt pen on the dorsal surface of patagium including areas of pelage to document repeat capture status during a mist-netting session. We sampled bats from sunset until flight activity and audible bat vocalizations decreased noticeably, which typically lasted from sunset to 22:00 ($\bar{x}$ = 3.29 hr).

Recorded data for all individuals included time of capture, presence of insect parts in the buccal cavity, mass (Pesola® 30-g or 60-g spring-scale, Kapuskasing, Ontario, Canada), forearm length, sex, and placement in one of four age classes. Assessment of age classes was based on a modified criteria generated by Davis et al (1962) on tooth wear: class I - all canine teeth noticeably pointed with glassine, unblemished tooth

staining; class II - one canine obviously blunted and slight dullness observed on molar cusps; class III - at least two canine blunted, tooth blemishing noticeable and consistent cusp wear on all molars observed; class IV - three or all canines blunted, tooth blemish obvious, significant cusp wear on all molars, including the absence of teeth and observable gomphotic gingiva. Perry and Herreid (1969) tested the validity of age categories using known-age bats and placed most *T. brasiliensis* bats (87.5%) in the correct age class based on tooth wear criteria of Davis et al (1962), most errors occurred in classification of aged bats, not juveniles. Errors in assessment related to actual tooth wear versus fracturing, may have produced slight overlap between adjacent age categories, but misplacement of individuals from adult (class II, III or IV) to juvenile (class I) is doubtful based on scaled graduation of tooth-wear by one observer in our study. After isolating a captured bat in a waxed cup for approximately one hour I counted the number of fecal pellets in individual cups, noted presence of insect fragments in buccal cavity as well as abdominal distention, and time of release. Fecal pellet uniformity in color and size indicate recent feeding based on Whitaker and Rissler (1993). I used a modification of Geluso's (2007) method of feeding activity confirmation, and determined feeding by production of three or more fecal pellets within an hour of capture. In other words all captured bats were considered actively feeding by rapid gut transit time and the lack of non-uniformity in fecal pellet shape. I released all bats at the site of capture except for 48 individuals retained as voucher specimens. The paucity of vouchered winter captures of any bat species in Texas dictated I retain specimens for winter records, county records, and to preserve tissues for other investigations.

Bridge-roosting populations of *T. brasiliensis* occurred in central and south Texas throughout the winter months; all study sites were occupied on every census trip (*n*=198) from December 2005 to March 2011. A total of 392,651 day-roosting bats were counted December 2005 to March 2011 (198 observations) between the four bridges (Figures 4 and 5). The highest census counts, regardless of month, occurred in Bell Co. (14,426 bats) on 29 August 2008 and in Kenedy Co. (6,470 bats) on 25 Oct 2010.

Winter monthly mean counts were consistently several thousand (Bell County $\bar{x}$ = 3,132; Kenedy County $\bar{x}$ = 2,699) and ranged from 400-6,233 (Bell Co.) and 589-4,536 (Kenedy Co.). The fewest bats encountered varied based on location and time of winter; Bell County bridges were least occupied in January ($\bar{x}$ =2,175; min. 400, max. 5,321), in contrast Kenedy County had the fewest bats in December ($\bar{x}$ =2,380) although a low value of 589 bats was counted in January 2011, and the greatest number encountered was in February 2009 (6,233 bats).

Bridge populations occupied day-roost heights as low as 0.70 m in Bell Co. and 0.37 m in Kenedy Co. The mean minimum day-roosting height occupied by at least one bat recorded for all months, bridge spans, and sites was $\bar{x}$ = 1.86 m (*n*=396 observations of roost heights). In all cases, higher, unoccupied sites were available.

In addition to census counts, mist-net captures of actively-feeding *T. brasiliensis* confirmed habitual roost occupancy and viability of bridges as winter roosts in Texas (Table 5; Figures 6 and 7). Both sexes were captured across all months, years and sites, except south Texas sampling in February 2009 (Table 6). Bats were captured during every mist-net capture session 2007-2009 (*n*=28 sessions), and yielded 975 *T.*

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brasiliensis. Additional bat species were occasionally encountered in association with bridge roosting; 591 cave myotis (*Myotis velifer*) and two tri-colored bat (*Perimyotis subflavus*) were identified in captures and/or counts. All *M. velifer* were associated with the Lampasas River bridge in Bell Co.: sixty-six *M. velifer* were documented using this bridge as a day roost during winter months, and individuals were encountered as single captures or in day-roosting aggregations of up to 77 individuals (10 March 2008) during counts outside of winter. These individuals represent the first documentation of bridge occupation by *M. velifer* in Texas. One *P. subflavus* in Bell Co. (28 February 2009) and one *P. subflavus* in Kenedy Co. (24 January 2009) were captured. The individual vouchered from Kenedy Co. represents a new county record for *P. subflavus* in Texas, and both individuals are the first documentation of bridge use by this species in Texas.

Age structure of winter populations, as assessed by tooth wear, was juvenile dominated, in other words Age Class I (Bell County captures 51-78% juveniles; Kenedy County captures 57-100% juveniles); however, all age classes were present (Age Class II, III, and IV) across all months and years with the exception of Kenedy County in February 2009 (Figures 4 and 5). Low captures (*n*=5), and all Age Class I male individuals for Kenedy County in February 2009 result in a lack of sex ratio, age class or overall statistical robustness for that date. Regardless of categorical placement of age class or assessment of age (see alternate categories in Davis 1962); there is clear indication that a diverse age group was present during all capture events, and locations. No winter population by gender, month, or location contained only juvenile or young-of-year (YOY) bats as laggard waifs.

Sex ratios (M:F) were male skewed and variable for all sites (Bell Co. 1.8-10.3:

Kenedy Co. 1.9-9.8), however, December and February mist-net captures yielded higher

female captures, regardless of sites (Figure 8). A total of 975 bats sampled revealed the

greatest number of females encountered occurred in Bell Co., February 2007 (1.8 sex

ratio), and Kenedy Co. February 2008, (1.4 sex ratio). All January captures were male

dominated and displayed the highest M:F sex ratio values Kenedy Co. 9.8 (January 2007)

and Bell Co.10.3 (2009) across sites and years (Table 6 & Figure 8) Although highly

variable across months, each site demonstrated similar temporal patterns and overall

winter sex ratio was not significantly different across sites ($\chi^2 = 0.3312$, df = 1, $P =$

0.565).

Based on fecal pellet data, feeding activity in Bell County *T. brasiliensis* captures

(*n*=540 bats) were lowest in December and increased through winter (December 59.7%;

January 64.7%; February 85.4%). Kenedy County fecal samples (*n* = 401 bats) revealed

the following individual feeding activity based on percent of captures during winter

(December 82.9%; January 75.0%; February 86.3%). However, the amount of dietary

items during feeding bouts was significantly higher in Bell County adult bats throughout

winter and all Bell County bats in February compared to categories in Kenedy County

(Figure 9).

Mean body mass of captured bats varied by sex and winter month. For statistical

analyses (*R* for Mac® version 2.11.1) we combined age class II, III, and IV as adult and

age class I as juvenile for comparisons of mass between age class and sexes. Mean body

mass, of male bats was significantly greater than that of females (Tables 7 and 8), and

mean body mass for all bats was significantly lower in January than December or

February (n = 924 bats). Significant mean body mass differences were found between sex and month (F=6.96, P = 0.001), adult male versus juvenile male (F=15.43, P = 0.0001), and across months, years and sites (F=18.62, P < 0.0001). The lowest monthly mean mass for Bell Co. bats of both sexes occurred in January 2007 [♂♂ x̄ = 11.60 g (9.5-13.5 g); x̄ = 11.00 g (9.5-14.5 g)]. Similarly Kenedy Co. masses for both sexes were lowest in January 2007 [♂♂ x̄ = 10.94 g (9.0-12.5 g); x̄ = 10.13 g (10.0-12.5 g)]. The highest mean mass for both counties occurred in December: Bell Co., December 2008 [♂♂ x̄ = 13.66 g (11.5-17.0 g)], December 2009 [x̄ = 14.09 g (12.0-15.5 g)]; Kenedy Co., December 2008 [♂♂ x̄ = 12.66 g (11.0-15.5 g); x̄ = 13.25 g (11.0-14.5 g)]. These December masses represent the greatest overall mean for both sites during winter (n = 178 bats) and the only observation that female mass was greater than male mass across all captures during winter. Contrary to our predictions, mean masses for captured bats in north-central Texas (Bell County) were significantly higher (Table 7; Figure 10 & Figure 11) versus Kenedy County, across months for two of three winter seasons (Table 7).

Discussion

The continuous and persistent occupation of bridges in Texas during our study suggests winter activity and residency for *T. brasiliensis* is not as novel or uncommon as previously thought. Texas bridges are consistently occupied throughout the year. I hypothesize that the resident Texas populations of *T. brasiliensis* of December—February are an ambit composed of these fluxes:

1) Habitual, resident bridge bats that consist of full-time/ non-migratory individuals. All study sites contained a minimum of 400 day-roosting bats for each sampling trip (*n=127*).

2) Northern arrivals maintaining an "inconsistent fidelity" to that bridge roost. All study sites showed variation in age class, especially periodic increases in juvenile bats.

3) Migratory bats that supplement bridge populations by stop-over but likely continue southward based on weather conditions. Pulse of bridge occupancy and population numbers, as well as sex ratios varied between months.

Winter Occupancy

Our observations of Texas winter populations of *T. brasiliensis* support the existence of flexible migration strategies that include discrete, adaptive populations exploiting engineered habitats. Seasonal and spatial variation in availability of environmental resources stimulates volancy or migratory behavior, especially in highly mobile organisms. Indeed, well-documented variation among migratory behaviors of Neotropical bird guilds suggests a range of successful strategies and demands for habitat breadth associated with diminishing resources (Rabenold 1992; Rolando 1998). Considering that the physiological demands of migration in bats, are similar to those of insectivorous birds, bat volant activity probably involves similar flexibilities in behavior. It follows that neither migratory nor sedentary behaviors are necessarily genetically hard-wired (Ehmlen 1967a, 1967b; Alerstam et al 2003). Flexible volant behaviors are likely adaptive and efficient, and thereby may offer a selective advantage in exploiting novel habitats. Flexible migratory behaviors can rapidly emerge or senesce within a few

generations (Berthold 1999). Varied migratory behaviors within an extensive population

of *T. brasiliensis* may result in meta-populations spanning a variety of adaptive peaks.

Variation in adaption to constantly changing climatic conditions and habitat availability

may be responsible for lack of evidence from previous studies to document winter

occupancy of Texas *Tadarida brasiliensis*. These bats most likely accommodate

dynamic periods of body mass and gain during winter months based upon low ambient

temperatures and fluctuating insect availability.

Age

The majority of our winter captures were juvenile (Age Class I) YOY bats at both

study sites. The northern site bridges are maternity roosts in summer so I expected

juveniles in winter captures as laggards who failed to migrate or are casually late

migrants from more northern latitudes. In contrast, our capture of juveniles at the

southern, non-maternity roost site confirms irregular, or irruptive, transient movement

from the north or west (See Lack 1954, Newton 1970, and Bock and Lepthien 1976 for

description and discussion of irruptive movements). Similarly, banding studies have

revealed a southern and eastern movement of *T. brasiliensis* into south Texas from

northern and western cavern locales (Eads et al 1957, Short et al. 1960, Villa and

Cockrum 1962, Constantine 1967, Cockrum 1969, Glass 1982). Our mist-net captures at

both study sites, across all sampling months revealed a full range of age classes

occupying bridges during winter. A portion of juvenile bats are likely successful winter

residents with no pressure to continue migration southward. However, captures

dominated by juveniles coincided with low incidence of feeding evidence.

Sex

Fewer females were captured than males, but females were captured at every sampling session except for a late February 2009 mist-netting in south Texas. Curiously, captures of females were not significantly less at the northern site (Table 7) where daily mean minimum winter temperatures were 8.3 °C colder than Kenedy County (USDA 1990). Apparently these colder temperatures do not constrain female volancy more than that of males in *T. brasiliensis*. Pearson et al (1952) found that the percentage of females decreased in areas of increased winter severity, but I found no association of climatic constraints on sex ratio based on location (Table 6; Figure 8). I expected females to be less active and more vulnerable to lower temperatures based on previous studies (Pearson et al 1952; Avery 1985); however, females were consistently volant. Frequency of captures and the consistent female component of sex ratios signify that the most vulnerable sex remains successful throughout the winter in Texas.

Feeding Activity and Body Mass

I expected winter severity and feeding success to impact body mass and fecal pellet counts. In the United States, only five species of bats are documented to feed in winter (Ross 1967, Whitaker et al 1997, Geluso 2007). Geluso (2007, 2008) confirmed *T. brasiliensis* feeding in winter during January and February, but not December. Data collected in our study documents feeding in all winter months in Texas, although monthly feeding patterns revealed the greatest feeding activity per individual bat occurring in south Texas (Kenedy County). However; in terms of the amount of food items consumed per individual bat, in bats that displayed evidence of feeding, the Bell Co. *T. brasiliensis* consumed significantly more than the Kenedy *T. brasiliensis* in foraging bouts during

February 2007-2009 (Figure 9). Additionally, significant differences were detected in feeding activity across age classes in Bell County but not so in Kenedy County (Figure 9).

Avery (1985) showed that the hibernating bat, *Perimyotis* [*Pipestrellus*] *subflavus*, would arouse and feed in any month, and this activity correlated with temperature. Thus, for non-hibernating *T. brasiliensis* I expected to body mass and feeding activity to reflect the ecological consequences of winter residency and distinguish critical winter time periods. Feeding activity occurred throughout winter months across all study sites based on fecal pellet count, visual inspection of abdominal distention, and observations of insect parts in mouths of captured individuals. Feeding activity was highest for all study sites in February and site-specific variation occurred between months. Although body mass of bats in Bell County was greatest in December regardless of sex and age class the lowest detected feeding activity occurred during this month. The capture of non-feeding individuals may reflect recent transients rather than insect availability or environmental situations.

Body masses in December and February were highest across all sexes, age classes and sites (Table 7; Figures 10 & 11). In January the masses were significantly lower suggesting loss of fat reserves and that January is the critical month of winter for Texas *T. brasiliensis*. Interesting trends in body mass data demonstrate its association with winter month; mean body mass of bats decreased in both Bell County (-10.1%) and Kenedy County (-9.6%) for both sexes and all age classes from December to January. Overall mean masses subsequently increased across sexes and age classes from January to February (Bell Co. +3.6%; Kenedy Co. +3.7%). These data contrast with those of

Geluso (2008) who found bats losing up to 15% of their body mass from November to March, without periods of increase, in New Mexico *T. brasilinesis* from Carlsbad Caverns. Our data suggest that January is the constraining winter month in Texas, regardless of location, and pre-winter months (fall) are not as critical for procurement of insect food for *T. brasiliensis*. December conditions of high mean body mass coupled with lower bat feeding activity may characterize casual feeding resident bats, irruptive migrants, or quality food. Alternatively, the increase in mean body mass from January to February may reflect mortality losses of physiologically stressed individuals in captures, leaving more robust winter survivors to comprise the majority of the population (Table 7; Figures 10 & 11). These data may also suggest movement further southward by some bridge bats for better food resources. Body mass of bridge populations decreases initially but recovers by the end of February. This pattern may suggest that bridge populations cope with winter conditions more successfully than cave populations. Based on mean body mass our study demonstrates January as a critical month of winter and not the entire winter period as in published data from winter cavern populations (Geluso 2008).

Winter Bridge Benefits

Bridge populations of *Tadarida brasiliensis* in Texas during winter months are evidence for an interesting shift in behavior from the traditionally accepted life history strategy for this species. These engineered landscapes offer select individual *T. brasiliensis* alternative, energetically sound opportunities to linger and supplement their energy budget, or fully overwinter in mid migration while other individuals migrate southward (Table 5; Figures 4 & 5). Temperature during winter does not appear to limit survival nor growth as indicated by the higher mean body mass in the more northern

population (Figures 10 & 11). Food availability is likely a more significant winter

selection pressure encountered by these populations based on feeding activity data.

Migration can be costly and dangerous behavior (Mink 2003), thus if individuals can

survive at more northern areas, without a committed migration, a bridge strategy may be

adaptively advantageous.

The advent of industrialization, especially enrichment of biota associated with

agriculture, combined with urban sprawl may provide advantageous environments for

insect activity and persistence and thereby ample food resources for bats. As a generalist

insectivore, (see McWilliams 2005) *T. brasiliensis* may have a unique blend of traits to

exploit the engineered habitat of bridges, nutritionally benefit from agriculturally

enhanced insect base (Cleveland et al 2006) and to survive Texas winters. The

characteristics of bridge roosts may benefit the energetics of *T. brasiliensis* and promote

their occupation beyond being a default alternative to declining cave roosts and habitat

eradication by human activity. These microenvironments may have a significant impact

on migratory success or overwintering survival, e.g. transient refuges, winter habitat or

both. Bridges likely increase survivability of winter bats by reducing competition for

roost sites and removing hazards encountered with steadfast migration.

Implications of Bridges

Bridges may have adaptive significance by affecting bat migration and likely

contribute to an expanding commensalism between bats and human activities. In

geographic areas lacking significant caves, e.g. north-central and south Texas, bats can

exploit bridge roost habitat to have access to previously unavailable food resources.

Bridges are exploited most during the summer and house a diverse number of

southwestern U.S. bat species including various maternity roosts (see Geluso and Mink 2009 for bat species). These bridge maternity roosts in Texas promote higher postnatal growth compared to postnatal growth in cave roosts for *T. brasiliensis* (Allen et al 2010). This growth emphasizes that bridges provide adaptive value for *T. brasiliensis* and that behavior and plasticity in *T. brasiliensis* is more dependent on local ecological conditions than on biogeographic patterns.

The ability of *T. brasiliensis* to occupy a variety of habitats, exploit a range of roost choices, and survive and possibly thrive in differing thermal climes and in engineered as well as natural structures suggests a broad range of tolerance across its distribution. The geography of winter migration has been aptly described in the literature. However, geographic location of a summer population may not dictate an individual bat's winter exodus or residency. The winter residency of discreet populations is dynamic and flexible. Geographic behavioral differences in *T. brasiliensis* may not be characterized by a single behavioral outcome in discreet populations but consists of multiple behavioral strategies within populations across North America. Our data indicates that bridges are geographically available and facilitate irregular, or irruptive, movements. Bridge availability and subsequent residency by bridge populations may promote these dynamic behaviors, e.g. irruptive movements, in *Tadarida brasiliensis*.

Given the increased construction of interstates, toll roads and new structures under NAFTA, the purposeful installment of bridges with vertical expansion joints would probably augment *T. brasilinesis* populations, and their benefits to the agricultural community, throughout Texas and other southwestern states. Although behavioral traits are labile and thus difficult to critically evaluate, the advent of bridge structures appears

to be adaptive for *T. brasiliensis*. However, the adaptive nature of this flexible behavior within the geographic range of a species remains poorly understood, and drivers of commensalism with human activity are not defined. The relative increase or decrease in the number of northern immigrant bats roosting in Texas bridges, the residency of bridge populations and the comprehensive phenology of winter aggregations are vaguely understood. In any event, populations of *T. brasiliensis* associated with bridges are important components of winter fauna throughout central and south Texas and warrant efforts to further understand winter bat ecology throughout the southwestern United States.

Table 5. Number of *Tadarida brasiliensis* captures, county location and number of mist-netting nights, Bell and Kenedy Cos., Texas 2007-2009 (*n* = 975).

	Winter 2007		Winter 2008			Winter 2009			Total
	Jan	Feb	Dec	Jan	Feb	Dec	Jan	Feb	
Mist-netting nights	3	4	4	4	4	3	3	3	28
Bell Co captures	78	113	70	64	98	64	34	65	586
Kenedy Co. Captures	43	103	48	49	89	28	24	5	389
TOTALS	121	216	118	113	187	92	58	69	975

Table 6. *Tadarida brasiliensis* captures by sex for winter months of Bell and Kenedy Cos., Texas, 2007-2009 ($n = 925$).

		Bell County		Kenedy County	
		♂♂	♀♀	♂♂	♀♀
Winter 2007	January	56	22	39	4
	February	72	41	84	19
Winter 2008	December	53	17	38	10
	January	56	8	32	17
	February	74	24	52	37
Winter 2009	December	53	11	22	6
	January	31	3	21	3
	February	57	8	5	0
All winter totals		452	134	293	96
Pooled winter sex ratio (♂♂:♀♀)		3.37: 1		3.05: 1	

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Table 7. Body masses (g), means and ranges for Texas *Tadarida brasiliensis* during winter months, Bell and Kenedy Cos., Texas, 2007-2009 and Kenedy Cos., 2007-2009 (n = 924).

		Bell Co.			Kenedy Co.		
		♂♂	♀♀	Overall Mean	♂♂	♀♀	Overall Mean
Winter 2007	January	11.610g (9.5-13.5g)	11.000g (9.5-14.5g)	11.522g (n=69)	10.949g (9.0-12.5g)	10.125g (10.0-12.5g)	10.872g (n=43)
	February	11.656g (9.5-14.0g)	11.607g (9.5-13.5g)	11.638g (n=76)	12.399g (9.5-15.5)	12.000g (9.5-14.0)	12.325g (n=103)
Winter 2008	December	13.660g (11.5-17.0g)	13.382g (10.5-16.0g)	13.593g (n=70)	12.662g (11.0-15.5g)	13.250g (11.0-14.5g)	12.796g (n=44)
	January	12.830g (10.5-15.5g)	11.625g (10.0-13.0g)	12.680g (n=64)	11.922g (11.0-13.5g)	11.897g (11.0-12.5g)	11.913g (n=49)

Table 7 continued. Body masses (g), means and ranges for Texas *Tadarida brasiliensis* during winter months, Bell and Kenedy Cos., Texas, 2007-2009 (*n* = 924).

	Bell Co.			Kenedy Co.		
	♂♂	♀♀	Overall Mean	♂♂	♀♀	Overall Mean
Winter 2008 February	13.189g (10.0-16.5g)	12.146g (9.0-16.0g)	12.934g (*n*=98)	11.481g (10.0-13.5g)	11.757g (9.5-12.5g)	11.596g (*n*=89)
December	13.255g (10.5-14.5g)	14.091g (12.0-15.5g)	13.398g (*n*=64)	12.568g (11.5-15.0g)	13.167g (12.5-14.0g)	12.696g (*n*=28)
Winter 2009 January	12.403g (9.5-14.0g)	11.833g (9.5-14.0g)	12.353g (*n*=34)	11.905g (10.0-13.0g)	12.167g (12.0-12.5g)	11.938g (*n*=24)
February	13.254g (11.0-15.0g)	12.125g (11.0--13.0g)	13.115g (*n*=65)	11.100g (10.0-11.8g)	--	11.375g (*n*=4 ♂♂)

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Table 8. Winter demography factors and their interactions with bridge population data for *Tadarida brasiliensis* in Bell and Kenedy Cos., Texas, (2007-2009)

ANOVA (Denom.)	DF: 899		
	numDF	F-value	*P*-value
(Intercept)	1	127501.37	<0.0001
County	1	88.65	<0.0001
Year	1	138.74	<0.0001
Month	2	51.78	<0.0001
Sex	1	18.06	<0.0001
Ageclass	1	34.82	<0.0001
County:Year	1	25.99	<0.0001
County:Month	2	0.24	0.7872
Year:Month	2	14.42	<0.0001
County:Sex	1	0.08	0.7744
Year:Sex	1	1.4	0.2377
Month:Sex	2	6.96	0.001
County:Ageclass	1	2.06	0.1516
Year:Ageclass	1	1.42	0.2336
Month:Ageclass	2	2.78	0.0628
Sex:Ageclass	1	15.43	0.0001
County:Year:Month	2	18.62	<0.0001
County:Year:Sex	1	0.03	0.8611
County:Month:Sex	2	2.11	0.1223

Table 8. continued. Winter demography factors and their interactions with bridge population data for *Tadarida brasiliensis* in Bell and Kenedy Cos., Texas, (2007-2009).

ANOVA (Denom.)	DF: 899		
	numDF	F-value	*P*-value
County:Year:Ageclass	1	1.77	0.1843
County:Month:Ageclass	2	1.44	0.2381
Year:Month:Ageclass	2	0.82	0.4419
County:Sex:Ageclass	1	0.39	0.5305
Year:Sex:Ageclass	1	1.63	0.2018
Month:Sex:Ageclass	2	0.15	0.8607
County:Year:Month:Sex	2	1.39	0.2488
County:Year:Month:Ageclass	2	0.15	0.8587
County:Year:Sex:Ageclass	1	0.16	0.6874
County:Month:Sex:Ageclass	2	3.5	0.0305
Year:Month:Sex:Ageclass	2	0.01	0.995
County:Year:Month:Sex:Ageclass	2	2.65	0.0712

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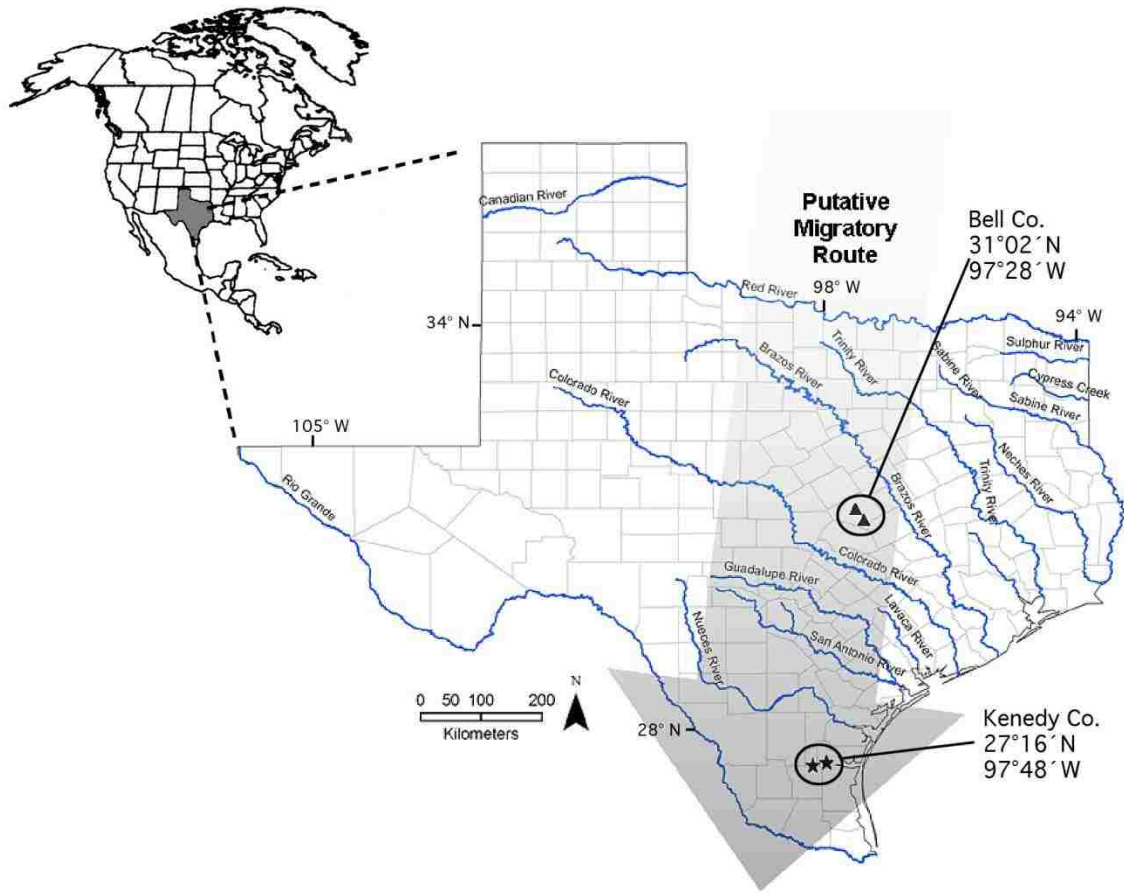
Figure 3. Locations of mist-netting sites in central and south Texas during winter 2006-2009. Closed triangles represent sites of northern captures, stars represent southern captures in respect to putative route adapted from Cockrum's (1969) and Hall's (1981) respective maps of North American *Tadarida brasiliensis* distribution and migration pathways.
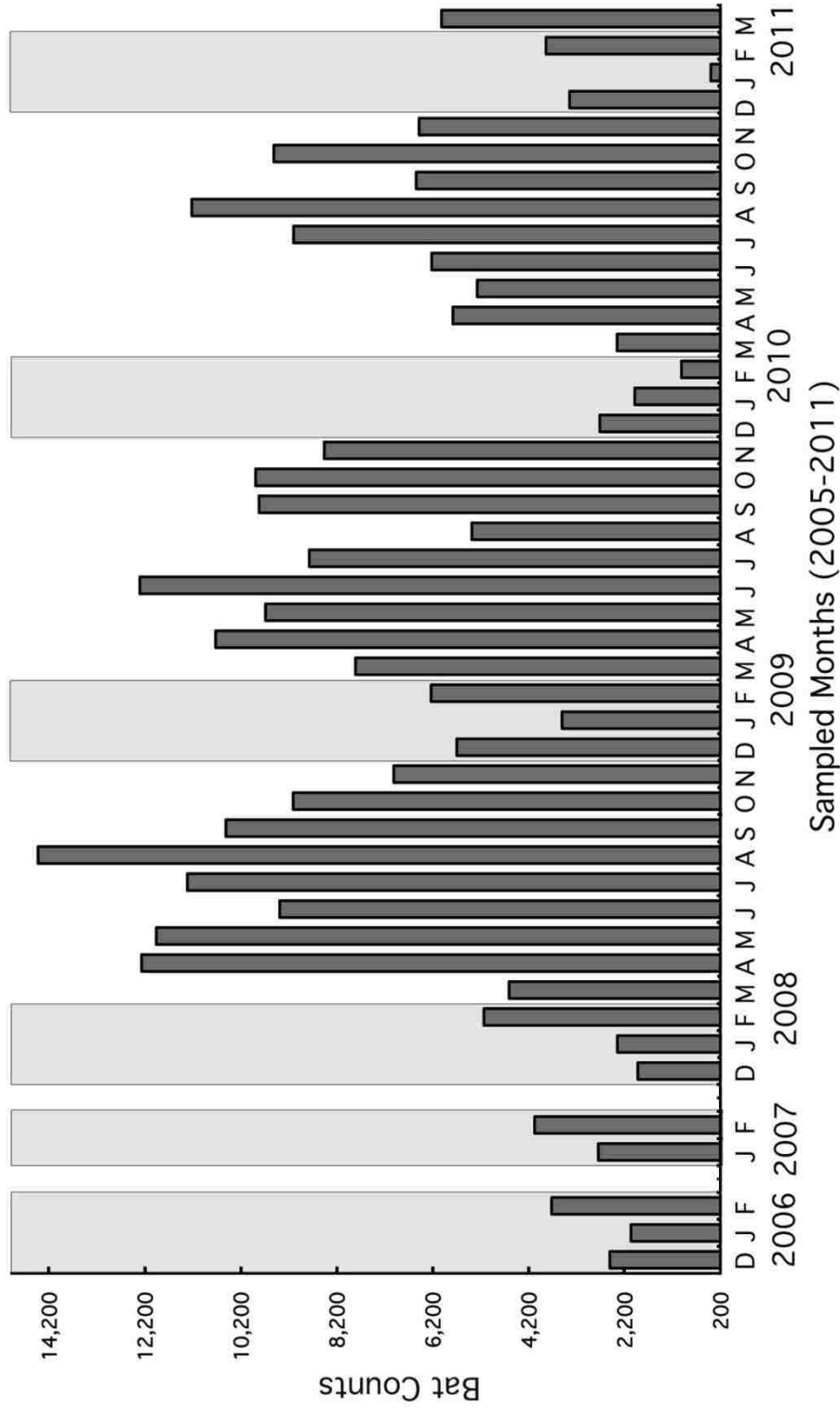
Figure 4. Monthly census of *Tadarida* brasiliensis occupying bridges in Bell County, Texas (2005-2011). Shaded areas represent data from December, January and February.
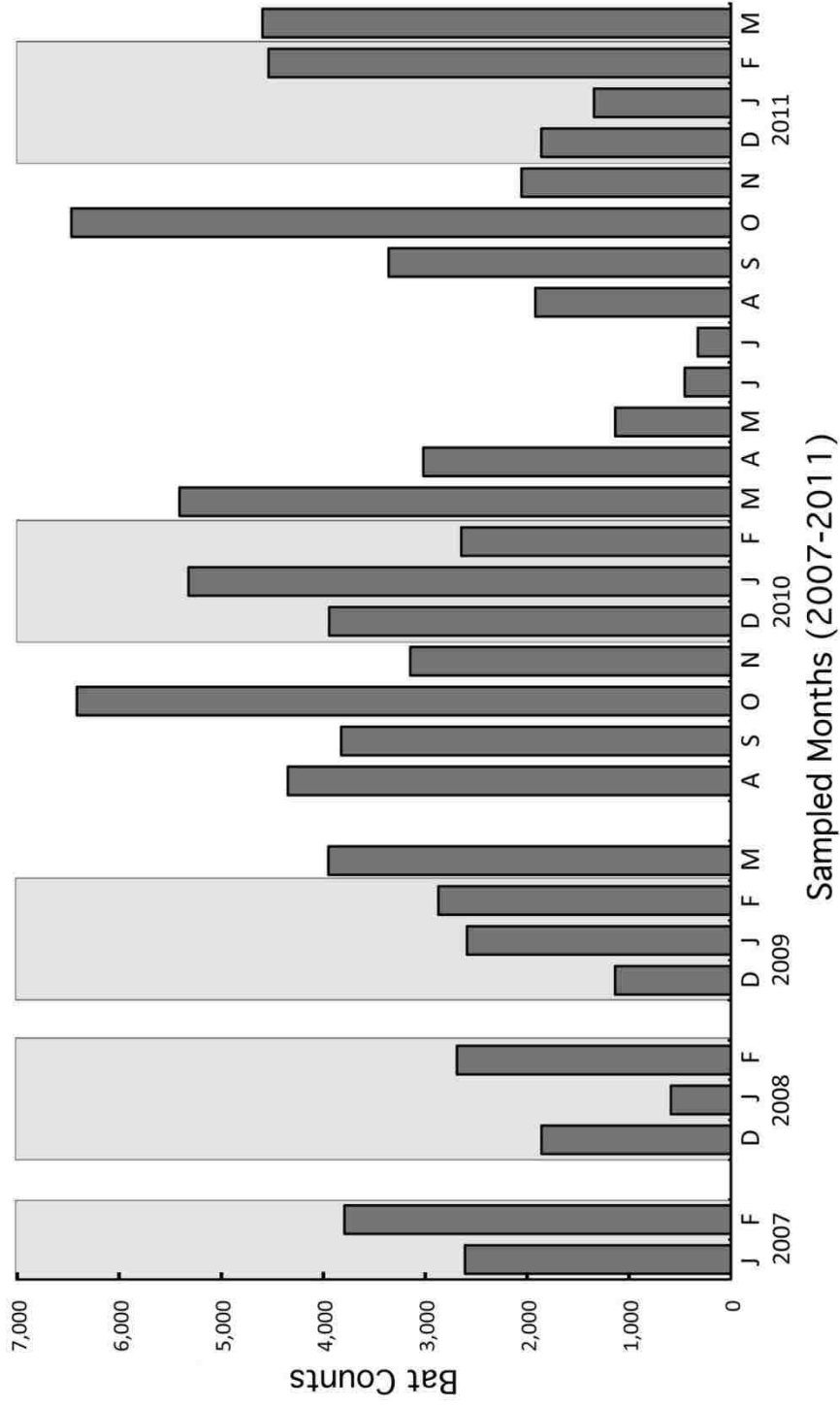
Figure 5. Monthly census of *Tadarida* brasiliensis occupying bridges in Kenedy County, Texas (2007-2011). Shaded areas represent data from December, January and February
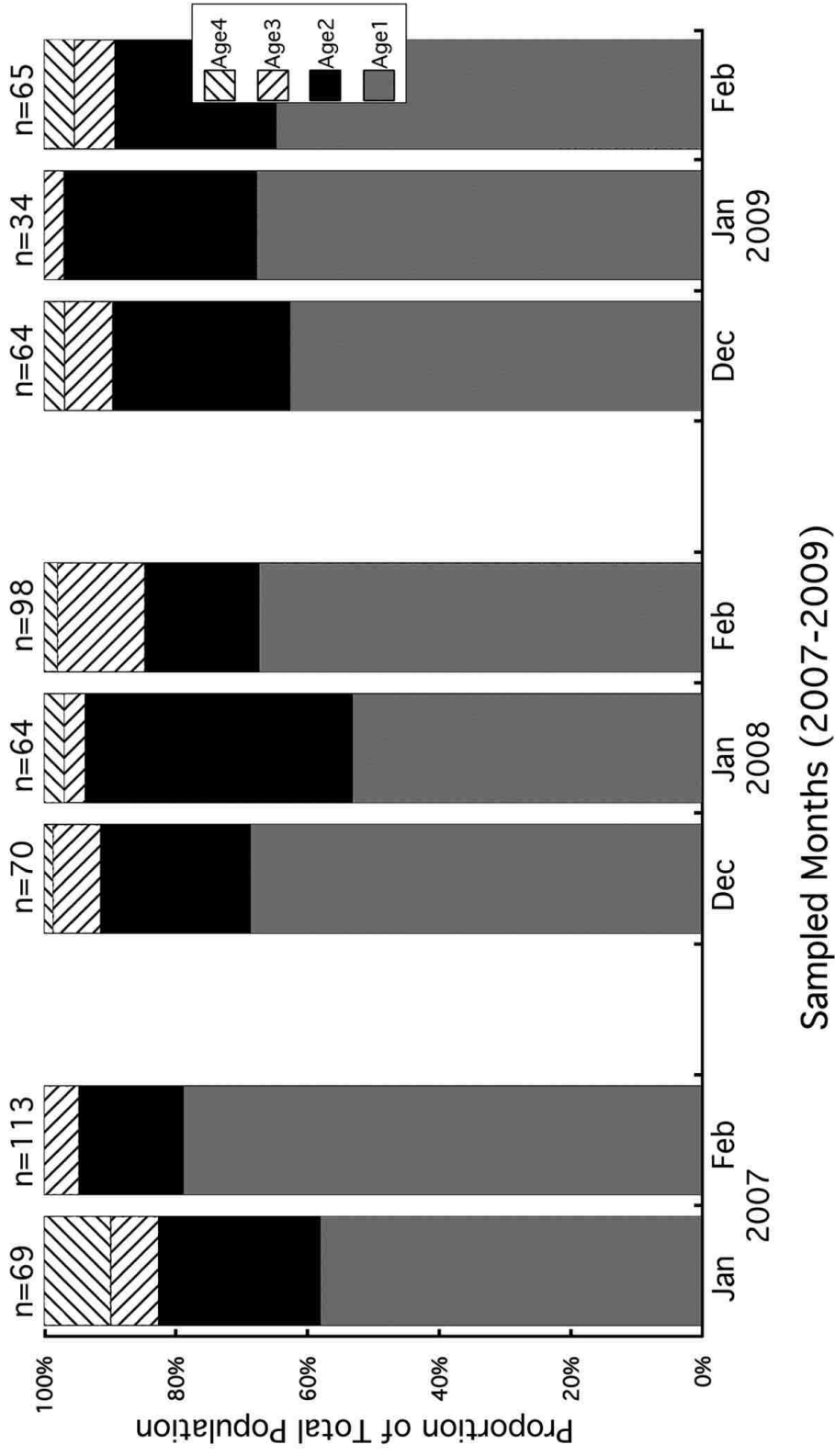
Figure 6. Age structures of *Tadarida brasiliensis* captured during winter months 2007-2009 in Bell County, Texas (*n* = 586).
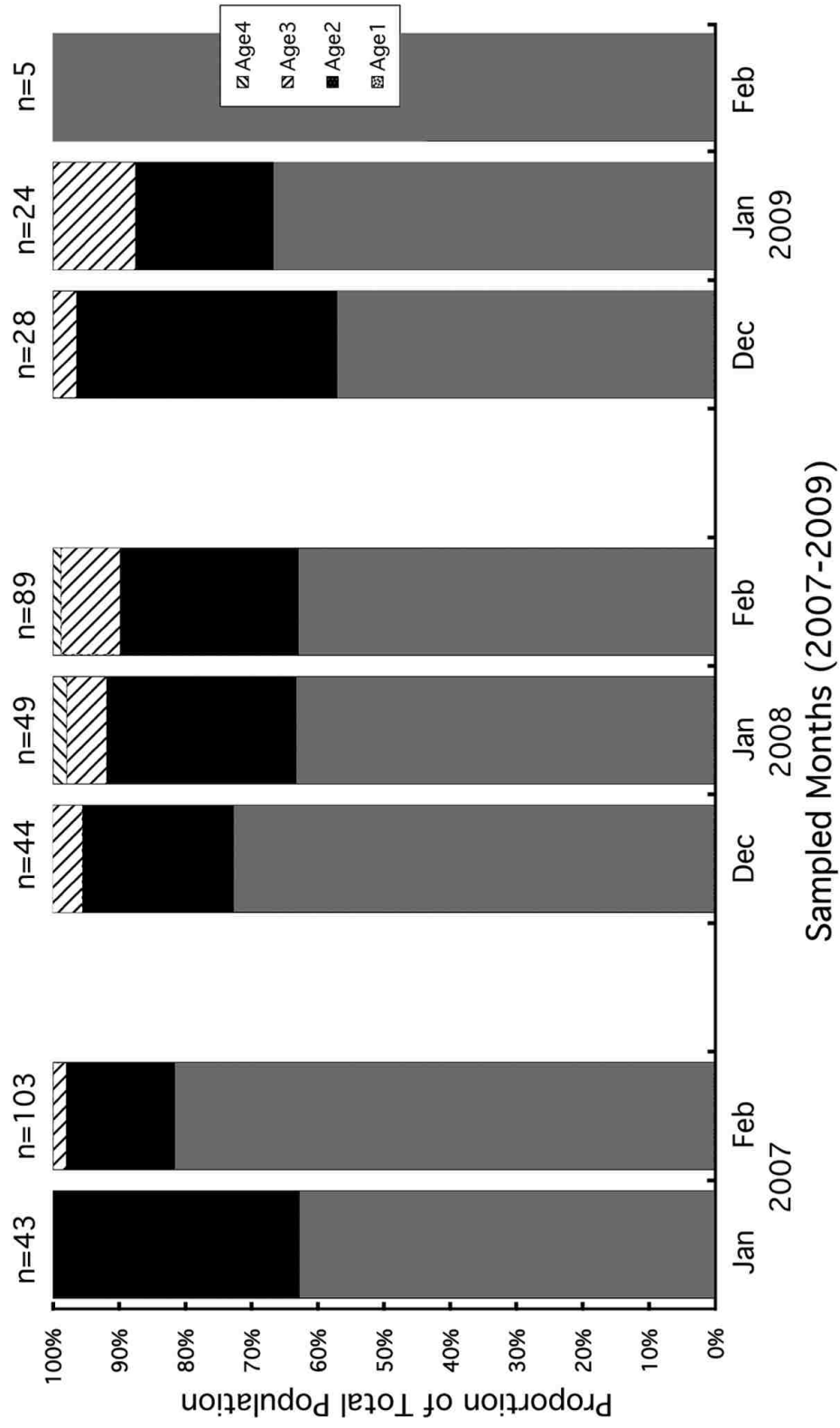
Figure 7. Age structures of *Tadarida brasiliensis* captured during winter months 2007-2009 in Kenedy County, Texas (*n* = 389).
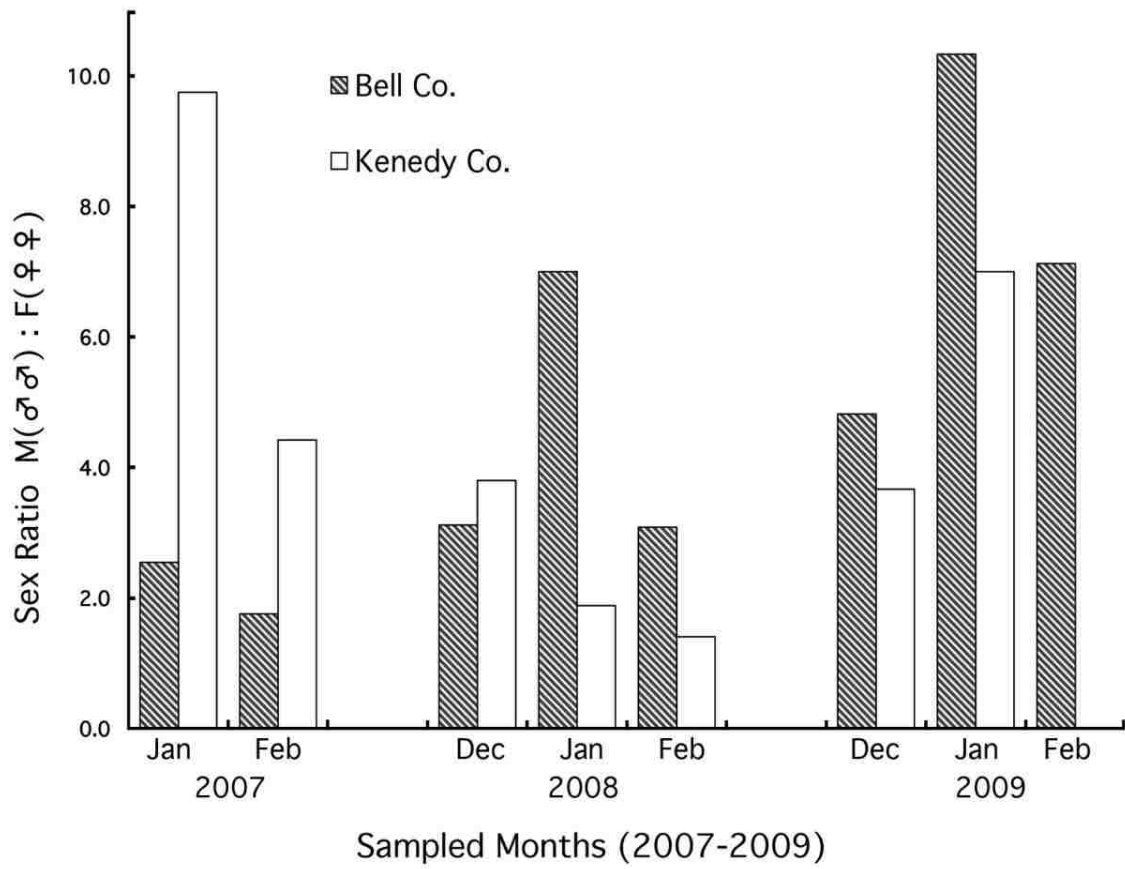
Figure 8. Winter sex ratios (M:F) of *Tadarida brasiliensis* captured during winter months of 2007-2009 in Bell and Kenedy Cos., Texas ($n = 975$).
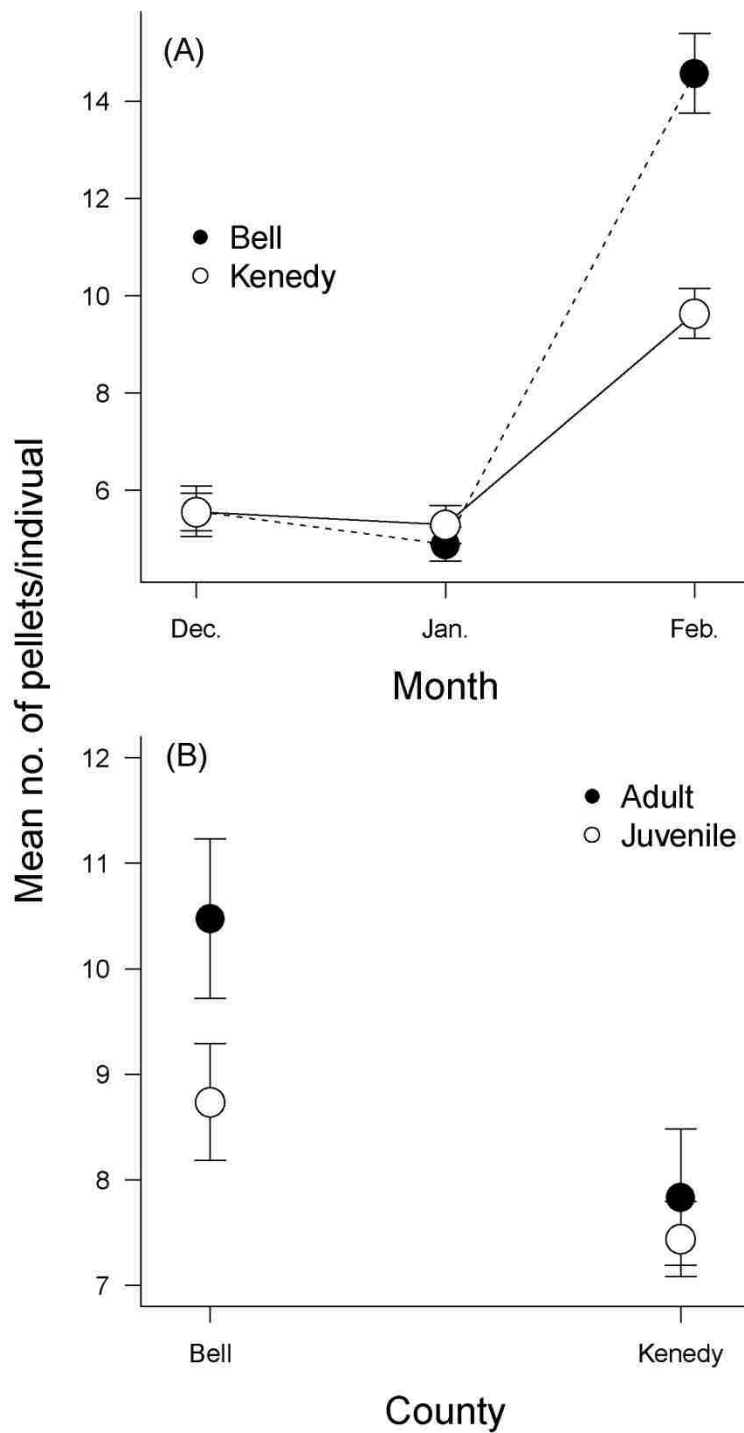
Figure 9. Comparisons of *Tadarida brasiliensis* feeding activity by (A) county vs. month, (B) age vs. county. Error bars indicate ($\bar{x} \pm 1.0$SE).
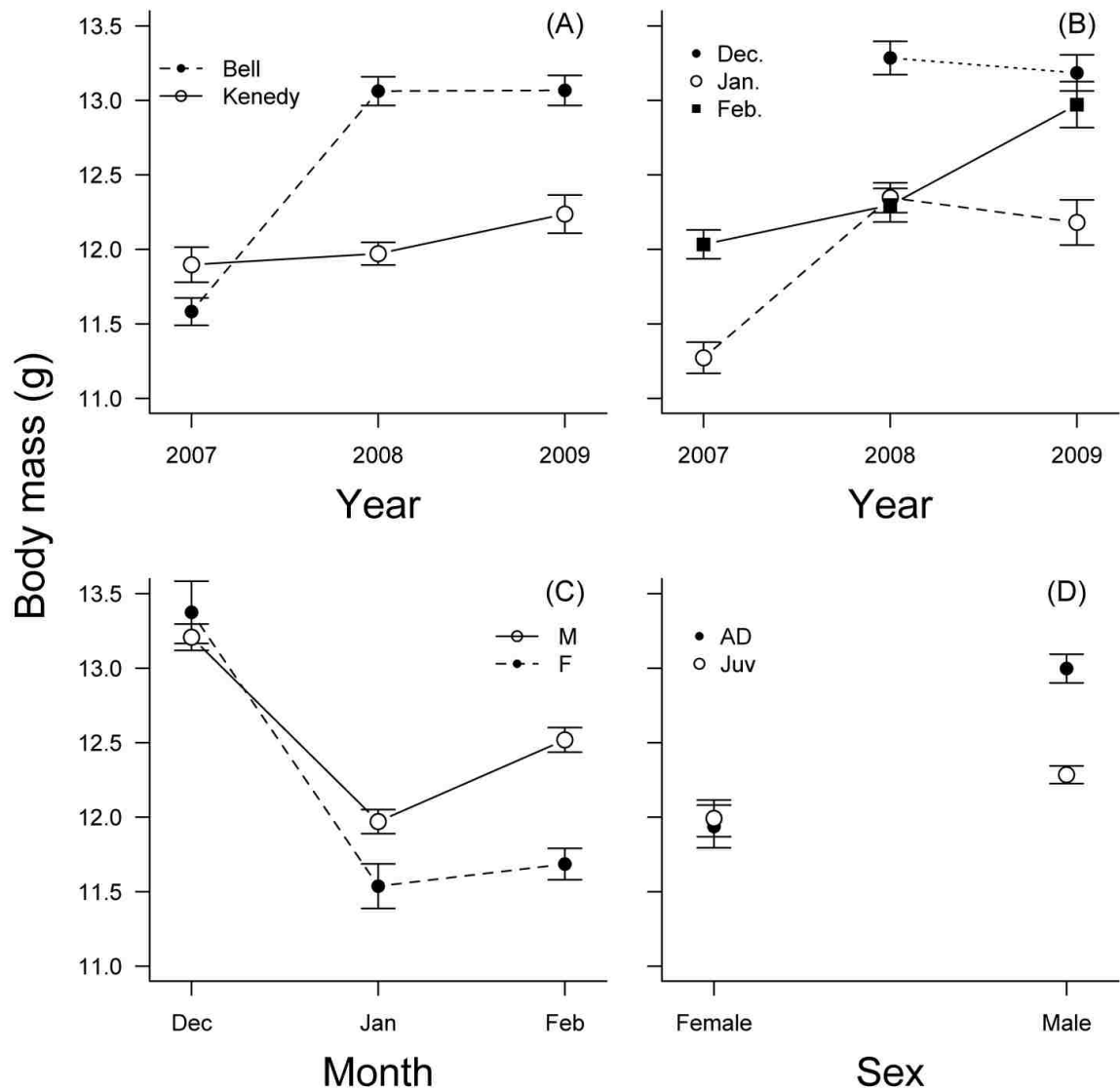
Figure 10. Comparisons of *Tadarida brasiliensis* mean winter mass between: (A) county vs. year, (B) winter months vs. year, (C) sex and winter months, and (D) age vs. sex. Error bars indicate ($\bar{x} \pm 1.0$SE).
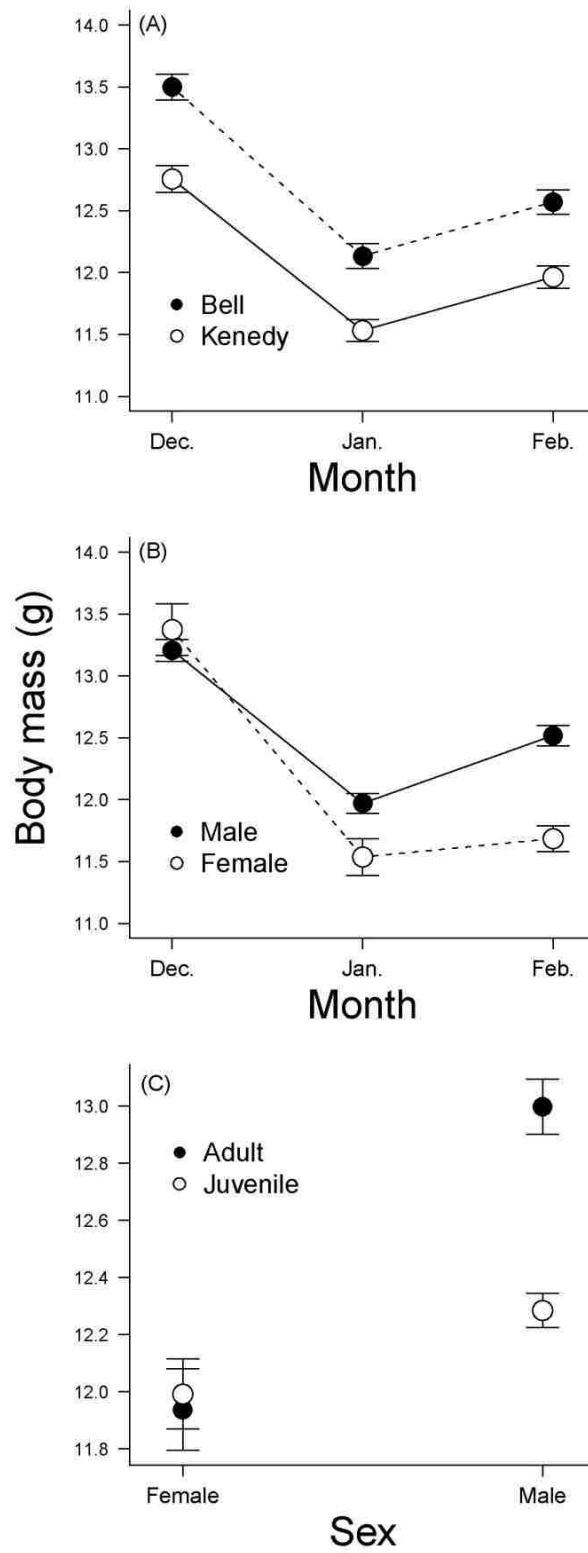
Figure 11. Comparisons of *Tadarida brasiliensis* mean winter mass between: (A) county vs. winter month, (B) sex vs. winter month, (C) age vs. sex. Error bars indicate ($\bar{x} \pm$ 1.0SE).

CHAPTER FOUR

Winter diet of Brazilian free-tailed bats (*Tadarida brasiliensis*) in Texas
Journal of Mammalogy

Abstract

Patterns of micropteran prey selection are varied, and have been aptly described for many species, species-specific behaviors, habitat influences, foraging strategies, and reproductive conditions but rarely for bats foraging in winter. During a three-year study, we documented nine insect orders and 21 families in the winter diet of migratory Brazilian free-tailed bats (*Tadarida brasiliensis*) in Texas. From 28 nights of sampling central Texas (Bell County) bats (*n*=586) and south Texas (Kenedy County) bats (*n*=389), 176 bats were sub-sampled (*n*=1,461 fecal pellets) for diet analysis. Lepidoptera and Coleoptera co-dominanted the diet with consumption frequencies of (93.8%) and (85.2%) respectively across winter months. Other food taxa included Diptera (52.3%), Hemiptera (47.2%), Hymenoptera (35.2%), Neuroptera (16.5%), Trichoptera (8.5%), Isoptera (4.6%), and Mecoptera (2.3%) with 21 inclusive insect families. Winter benthic hatches of Diptera: Chironomidae were occasionally dominant food taxa (*n*=14; 90-100% diet volume) suggesting the importance of intermittent dietary bulk food taxa during winter foraging by *Tadarida brasiliensis*. Diet varied significantly between sites, sexes, and among winter months for most insect orders, but lepidopterans and coleopterans were the most abundant and frequent food taxa. However, for several orders of insects negligible dietary differences between sites and sexes imply broad dietary overlap during most winter months. Winter diet of *Tadarida brasiliensis* in Texas

reveals a flexible, opportunistic insectivore. The association of consistent winter feeding

activity and winter residency of bridge populations of *Tadarida brasiliensis* may support

a sustainable and selectively advantageous alternative to migration.

Introduction

Bats are significant predators in a broad range of ecosystems because of their

remarkable consumption of insects, flexibility in foraging strategies (Barbour and Davis

1969; Kunz 1974; Wilson 1997), breadth of prey taxa (Black 1972; O'Neill and Taylor

1989), and potential reduction of insects of agricultural concern (Lee and McCracken

2005; Cleveland et al. 2006; McCracken et al. 2008). Prey availability, predator

behavior, foraging strategies, land-use patterns, and diet preferences all influence prey

selection (Griffin 1970; Hill and Smith 1984; Fenton et al. 1990), but the magnitude of

seasonal shifts and reduction in prey availability during winter has been largely

overlooked.

Three studies in the United States have confirmed winter feeding by six

insectivorous bat species. Whitaker et al. (1997) documented that *Lasiurus borealis*

(eastern red bat) fed in winter in North Carolina and Virginia. Dunbar et al. (2007) found

insect remnants in feces of *L. borealis*, *Lasionycteris noctivagans* (silver-haired bat), and

Eptecius fuscus (big brown bat) during winter months of December-February in Missouri.

Geluso (2008) found that four species [*Pipistrellus* (*Perimyotis*) *hesperus* (eastern

pipistrelle or tri-colored bat), *L. noctivagans*, *Myotis californicus* (California myotis), and

T. brasiliensis] commonly fed in winter months of December-February in New Mexico.

Bats from these studies consisted of both hibernating species and migrating species,

suggesting that adaptive and efficient feeding behaviors may promote physiologically flexible life histories. Despite the broad range, dispersal capabilities and high abundance of *T. brasiliensis* across North America (Christensen 1947; Constantine 1967; Cockrum 1969; Hall 1981; Jones et al. 1983; Dalquest and Horner 1984; Findley 1987;), the winter diet of this bat has not been previously described nor investigated.

Tadarida brasiliensis consume a wide variety of insects in summer nocturnal foraging bouts, (e.g., Whitaker and Kunz 1996; Lee and McCracken 2005; McWilliams 2005; McCracken et al. 2008). McWilliams (2005) found great variation across orders of insects eaten by *T. brasiliensis* from spring through summer into fall at Carlsbad Caverns, Eddy County, New Mexico. Typical food taxa included moths (Lepidoptera), beetles (Coleoptera), flies (Diptera), wasps (Hymenoptera), true bugs (Hemiptera) and flying ants (Hymenoptera).

Behavior of *Tadarida brasiliensis*, as a migratory, non-hibernating bat, demands high energy and results in low selectivity, or diet obligation to specific food taxa. Analysis of warm-season diets reveals *T. brasiliensis* as a generalist insectivore (Kunz et al. 1995, Whitaker and Rodriquez-Duran 1999) that utilizes up to 4000 km^3 for non-selective foraging (Williams et al 1973; Best and Geluso 2003; McWilliams 2005) in summer months. In other words, available insects and other arthropods (acarian mites and spiderlings) were consumed in foraging bouts.

The warm-weather diet of Brazilian free-tailed bats varies greatly among nights (Kunz et al. 1995), among localities (Lee and McCracken 2005), through time (e.g. diel (Whitaker et al. 1996)), among seasons (Whitaker and Rodriquez-Duran 1999, McWilliams 2005), among reproductive conditions (e.g. pregnancy or lactation (Kunz et

al., 1995)) and among cave populations (McWilliams 2005). However, the winter diet of

Tadarida brasiliensis populations has not been studied. Several authors have suggested

feeding activity during winter residency (Geluso 2008; Geluso and Mink 2009), based

upon guano production, buccal cavity condition, abdominal distention or flight masses.

But no study has established and quantified frequencies of occurrence and relative prey

abundances of a baseline winter diet.

Examination of *Tadarida brasiliensis* diet during winter months, especially in

south-temperate and subtropical regions, reflects the potential economic value of

Tadarida brasiliensis as a consumer of important agricultural pest populations during

times outside of summer months and insect immigration (e.g. Wolf et al. 1990; Cleveland

et al. 2006; McCracken et al. 2008). This study describes the winter diet of *T.*

brasiliensis ascertained from fecal pellets (guano) and compares populations across space

(563-km north-south gradient), habitat (south-temperate and sub-tropical), winter

monthly variations, and sex-specific foraging selections. These comparisons offer

opportunities to further understand of winter *T. brasiliensis* ecology and seasonal

influences on both diet abundances and selectivity. Selectivity of winter diet may

promote niche separation between sexes (Selander 1966) or reflect seasonal shifts in

energy content of available insect prey (Cummins and Wuycheck 1971).

Materials and Methods

Study Area Descriptions

Fieldwork was conducted at study sites in two counties in Texas, U.S.A. during

three years from January 2007 to February 2009 during the months of December, January

and February herein defined as winter months. The south-temperate site (Bell County) included two central Texas bridges near the Lampasas River and Interstate 35; Belton, Hwy 386 bridge at Interstate 35 intersection (31° 02´N, 97° 28´W; elev. 581 ft) and 6.4 km south of Highway 190 and Interstate 35, Lampasas River bridge on Interstate 35 (31° 00´N, 97° 29.31'W; elev. 503 ft.). The subtropical, more southernly site (Kenedy County) included two bridge spans across the Los Olmos River, 5.6 km south of Riviera, Texas, on Hwy 77 at Los Olmos Creek (northbound 27° 16´N, 97° 48´W and southbound spans; 27° 15´N, 97° 48´W; elev. 3-5 ft.). The study sites were separated north to south by 563 km, and each site maintained lotic stream conditions year-round (Figure 12). The foraging area of the northern site includes part of the central blackland prairie and cross timbers and prairies vegetational regions (see map in Correll and Johnston 1970) adjacent to the eastern boundary of the Edwards plateau as delineated by relief of the Balcones Escarpment. These foraging areas surrounding the Bell County, Texas sites are mainly urban with much anthropogenically modified habitat, e.g. asphalt roads, service stations, channelized storm sewers, and agricultural acreage. The Lampasas River flows within 4 km of the Bell County fieldwork site, adjacent to the Farm-to-Market road-317 bridge. Prominent plant species at this site included box elder (*Acer negundo),* bois d' arc (*Maclura pomifera)*, red mulberry (*Morus rubra*), black willow (S*alix nigra*), cottonwood (*Populus deltoides*), Texas sugarberry (*Celtis laevigatus*), rough-leaf dogwood (*Cornus drummondii*), green ash (*Fraxinus pennsylvanica*), possumhaw (*Ilex decidua*), yaupon (*I. vomitoria*), Osage orange (*Maclura pomifera*), sycamore (*Plantanus occidentalis*), wafer ash (*Ptelea trifoliata*), American elm (*Ulmus americana*), tree-of-heaven (*Ailanthus altissimus*), Chinaberry (*Melia azedarach*), glossy privet (*Ligustrum*

lucidum), chinese privet (*L. sinense*), smooth sumac (*Rhus glabra*), Alabama supple-jack (*Berchemia scandens*), Virginia creeper (*Parthenocissus quinquifolia*), Green brier (*Smilax bona-nox*), cat-brier (*S. tamnoides*), poison ivy (*Toxicodendron radicans*), pecan (*Carya illinoensis*), black walnut (*Juglans nigra)* and eastern red cedar (*Juniperus virginiana*). Dominant vegetation species, away from riparian influence, occurred on Cretaceous limestone and Blackland Prairie areas included little bluestem (*Schizachyrium scoparium*), white tridens (*Tridens albescens*), seep muhly (*Muhlenbergia reverchonii*), mesquite (*Prosopis grandulosa*), Texas persimmon (*Diospyros texana*), cedar elm (*Ulmus crassifolia*), prickly-pear (*Opuntia engelmanii*), ashe juniper (*Juniperus ashei*), Mexican buckeye (*Ungnadia speciosus*), Mexican plum (*Prunus mexicana*), woollybucket bumelia (*Sideroxylon lanuginosum*), plateau live oak (*Quercus virginiana*) and Hercules thorn-club (*Zanthoxylum clava-herculis*).

The area surrounding the southern site (Kenedy County) is part of the Tamaulipan brushland biotic province of Texas (biotic province map in Gould 1962; 1969) and transected beneath bridge spans by Los Olmos Creek, a brackish water stream. This Kenedy County site is transected under bridge spans by Los Olmos Creek, a brackish water stream, varying in widths influenced by tide and supports coastal saltgrass (*Distichus spicata*), sea oxeye daisy (*Borrichia frutescens*), saladillo (*Varilla texana*), Texas bluebells (*Eustoma russellianum* [*E. grandiflorum*]) and vidrillos (*Batis maritimas*) along a sandy littoral zone. Other vascular plants in the surrounding foraging area include Rhodes grass (*Chloris gayana*), Sarita rosette-grass (*Dichanthelium nodatum*), giant panic grass (*Panicum antidotale*), sand dropseed (*Sporobolus cryptandrus*), Bailey's ball moss (*Tillandsia baileyi*), stemless spiderwort (*Tradescantia subacaulis*), velvetleaf

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(*Abutilon theophrasti*), bee-brush (*Aloysia gratissima*), Texas lantana (*Lantana urticoides*), Texas verbena (*Verbena halei*), cenizo (*Leucophyllum frutescens*), Texas rabbit-tobacco (*Pseudognaphalium austrotexanum*), fetid marigold (*Dyssodia papposa*), Caribbean purple everlasting (*Gamochaeta antillana*), smallflower groundcherry (*Physalis cinerascens* var.*spathulifolia*), beaked mock vervain (*Glandularia quadrangulata*), prairie vervain (*Glandularia bipinnatifida* var. *bipinnatifida*) American snoutbean (*Rhynchosia americana*), Texas ragwort (*Senecio ampullaceus*), barbas de chivato (*Clematis drummondii*), Brasil (*Condalia hookeri*), desert hackberry (*Celtis pallida*), anaqua (*Ehretia anacua*), retama (*Parkinsonia aculeate)*, desert yaupon (*Schaefferia cuneifolia*), lotebush (*Ziziphus obtusifolia*), blackbrush acacia-chaparro prieto (*Acacia rigidula*), huisache (*A. farnesiana*), prickly-pear (*O. engelmanii*), Spanish dagger (*Yucca treculeana*), cenizo (*Leucophyllum frutescens*), amargosa (*Castela erecta*), mesquite (*Prosopis grandulosa*), coastal live oak (*Quercus virginiana*) and colima (*Zanthoxylum fagara*) occur in the surrounding site area.

Bat Sampling and Guano Analysis

Bats were mist-net captured from December through February (hereafter referred to as winter), from 2007-2009, regardless of lunar cycle, to minimize potential bias inherent in ambient lunar light variation. These captures employed four-shelved, 12-m length, 2-m depth, 38-mm mesh, 50-veneer mist nets (Avinet, Inc. Dryden, New York, U.S.A.. and Taiyo Tsusho Trading Co., Ltd. Kobe, Japan) placed near bridge roosts. We netted bats a total of 28 nights; 12 nights in Kenedy County and 16 in Bell County during 2007-2009, for a winter total of 975 captured *T. brasiliensis*. Captured bats were immediately placed in labeled 16-oz paper cups with plastic lids, for at least one hour to

acquire fecal pellets. One hour is a reasonable gut transit expectation of active bats, regardless of sex (Buchler 1975) and allows bats to void most, if not all, feces from a feeding bout (Whittaker 1988). Fecal pellet uniformity in color and size indicate recent feeding based on Whitaker and Rissler (1993). Time of capture, sex, body mass and number of fecal pellets (guano) was recorded for each bat. Bats were released after fecal-pellet collection. Pellets from each bat were air-dried in their respective paper cups in the field, and then stored in labeled plastic 950-ml Ziploc® bags prior to laboratory analyses.

Fecal pellet analyses followed published protocols and methods by Kunz and Whitaker (1983), Whitaker (1988), Whitaker et al. (1996) and Sparks and Valdez (2003), to reliably estimate abundance and frequency of dietary taxa. Fecal pellet examination began with random selection of fecal pellets regardless of capture time ($n = 1,461$ pellets). Fecal pellets of visible integrity were analyzed regardless of pellet count or nightly bat capture totals. Pellets from eight to 24 bats were selected as representative samples for each of the nine winter months of the study. These fecal pellet samples (one to 24 per bat; $\bar{x} = 8.3$ pellets; $n = 176$ observations) came from bats randomly subsampled from captures of 61-74 bats per winter month over three years of sampling sessions. Selected fecal pellets were placed in a 15-mm x 110-mm Kimex™ glass Petri dish and visually examined at 30x -75x magnification using a stereomicroscope as per Sparks and Valdez (2003). The fecal pellets were soaked in 70-90% ethanol for at least ten minutes and teased apart with forceps.

We identified each diet item to the most exclusive taxonomic level possible (Ordinal or Familial level) and visually estimated the percent volume (i.e., abundance) of each food taxon. Insect parts were identified based on several entomological reference

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texts (e.g. Borror and White 1970, Borror and DeLong 1971, White 1983, Borror et al., 1989, Arnett 2000, Cranshaw 2004) and comparisons to Whittaker's key (1988). In most instances, insect taxonomy followed Triplehorn and Johnson (2005), e.g. combining both hemipterans and homopterans within the order Hemiptera, as recommended by similar bat diet taxonomy protocols (see Valdez and Bogan 2009). Thereby we conserved the traditional usage of Lygaeidae in Hemiptera (Borror and DeLong 1971; Borror et al., 1989). Processed fecal samples were vouchered for future reference in 70-90% ethanol and stored in 2-ml screw cap microtube storage vials (Sarstedt®, Aktiengesellschaft & Co., Inc., Newton, North Carolina, U.S.A. 28658-0468).   Our study was approved and endorsed by the Baylor University Animal Care and Use Committee (Permit 06-05) and all bats were captured and sampled in accordance with the guidelines and protocols of the American Society of Mammalogists (Gannon et al. 2007).

Statistical Analysis

Variations of diet taxa between months, sites, and sexes were based on volume comparisons of each taxon. Dietary taxa were classified in ordinal level unknown categories if family level discrimination was not possible, however, non-food items, e.g. mist-net fibers, one instance of acarian mite instar exuviae or unidentified fine-grained particulate material were not included in analyses. Variations in bat dietary composition were calculated and compared for ordinal categories using ANOVA analyses using Type III sum of squares with unequal sample size between sites and between sexes. Comparisons of prey taxa across winter months between sites and sexes were calculated by the Tukey Honest Significant Differences test (Tukey HSD) calculating post-hoc comparisons on each factor in the model adjusted for multiple comparisons to ensure no

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autocorrelation or pseudoreplication bias (R version 2.11; R Development Core Team, Vienna, Austria).

Each diet taxon was recorded as present for a taxonomic category (order and family) and as a percent of sample volume. Frequency (%) of each taxon was calculated as number of bats consuming a particular taxon divided by total number of bats examined, multiplied by 100. Frequencies of consumed food taxa were calculated for each sampling night, each month, and total winter captures in a similar manner. The mean percent volume of each food taxon was calculated for fecal samples from all sampling nights, i.e. both sexes, each month, and all winter captures combined. Relative importance of food taxa was calculated as the product of frequency and percent volume. Therefore, utilization of each diet taxon was evaluated as frequency, percent volume and relative importance.

Results

Of all bats captured during winter months 90.9% were actively feeding as evidenced by three or more fecal pellets produced after capture ($\bar{x}$ = 8.91 fecal pellets). Nine insect orders and 21 representative families were cataloged in the winter diet of *T. brasiliensis* (Table 9). Lepidoptera (moth) and Coleoptera (beetle) were the most common dietary prey taxa identified in fecal pellets (*n*= 176 bats; *n*=1,461 fecal pellets). They collectively comprised the largest volume of ingested prey for both sexes and all winter months regardless of site (Table 9; Figure 13). The next three most common taxa recovered, in decreasing order of frequency, were Diptera, Hemiptera, and Hymenoptera. These five orders represented 98.75% of the total volume of an average fecal sample. Notable exceptions to this pattern were sampling dates when Chironomidae was the most

frequent and most abundant food taxon (four nights in January; three nights in February).

Foraging bouts with exceptionally high (>90%) chironomid abundances in the diet

occurred in both sexes and both sites only in January and February 2007-2009.

Occurrence of novel food taxa (<10% frequency) declined with multiple sampling efforts

on several dates. In other words, eight insect orders and 15 families were identified in the

first 15 bats (93 fecal pellets) processed from this study. However, only one new insect

order and six new insect families were found in the subsequent 161 bats (1,368 guano

pellets) analyzed.

Dietary composition varied significantly among winter months for certain insect

orders at both sites (Figure 14). Sexual bias in consumption of prey taxa occurred across

orders and sites (Figure 13). At the south-temperate site (Bell County) percent volume

abundances of coleopteran ($F_{2,82}$ = 5.95, $P < 0.01$), dipteran ($F_{2,82}$ = 4.32, $P < 0.05$),

hemipteran ($F_{2,82}$ =5.59, $P < 0.01$), hymenopteran ($F_{2,82}$ = 6.66, $P < 0.01$), and

neuropteran ($F_{2,82}$ = 5.83, $P < 0.01$) diet taxa varied significantly between months of *T.*

brasiliensis during winter. Whereas at the more southern site (Kenedy County) bat

dietary taxa volumes varied significantly between months for dipteran ($F_{2,86}$ = 15.53, $P <$

0.001), hymenopteran ($F_{2,86}$ = 3.43, $P < 0.05$), lepidopteran ($F_{2,86}$ = 11.01, $P < 0.001$),

mecopteran ($F_{2,86}$ = 3.43, $P < 0.05$), and neuropteran ($F_{2,86}$ = 5.28, $P < 0.01$) but also by

sex for coleopteran ($F_{1,86}$ = 4.58, $P < 0.01$) and hemipteran ($F_{1,86}$ = 7.88, $P < 0.01$)

(Table 9; Figure 13). Hymenoptera had significant differences by month and sex for both

Kenedy ($F_{2,86}$ = 4.60, $P < 0.05$) and Bell ($F_{2,82}$ = 9.89, $P < 0.001$) Counties; however,

with log-transformed data an ANOVA based on Type III sum of squares, without

interaction term, this significance was not detected (Table 10). Other insect orders were not selected preferentially based on percent volume (Tables 9 & 10; Figures 13 & 14).

Dietary composition of insect orders as a function of feeding activity (fecal pellets per bat) was negatively correlated for Coleoptera, Diptera, Hemiptera and Hymenoptera but not significantly (Figure 15). For example, with sustained feeding, based on fecal pellet production, coleopterans were selected less frequently with higher consumption rates. In contrast, dipterans, hemipterans and lepidopterans were selected regardless of feeding level intensity based on fecal pellet production (Figure 15).

Discussion

We evaluated the winter diet of *T. brasiliensis* in Texas. Analysis of fecal pellets collected from mist-netted bats reveals Brazilian free-tailed bats are opportunistic foragers that likely encounter markedly varied qualities and quantities of prey in the winter season of lower ambient temperatures and relative dearth of insect activity. The winter diet shifts included variation between counties, sexes, and months in percent volume of certain ordinal categories, but frequency of ordinal presence was consistent through winter. This dietary breadth suggests that *T. brasiliensis* is an opportunistic winter predator, with discrete periods of selection probably based on exploiting heavy abundances of acceptable food taxa, e.g. chironomids, or lepidopterans, on occasional nights. Despite date-specific feeding bouts on a single food taxon the spectrum of insect prey detected in *T. brasiliensis* in this study is similar to those of other seasons (Kunz et al. 1995; Whitaker et al. 1996; McWilliams 2005) and confirms a wide dietary breadth for *T. brasiliensis* in winter.

Disparate study sites (563 km), separate biogeographic regions and their climatic differences of mean minimum temperature in winter (USDA 2012) did not radically alter the relative composition of diet taxa in *T. brasiliensis*. Despite the temperature differences between Bell and Kenedy Cos. in winter (minimum mean at least 8.3 C colder at the northern site) similar food items occurred in the winter diet across sites. The relative abundances of dietary taxa varied between sites, sexes and ordinal taxa but the frequencies of food items were consistent except for minor occurrences and abundance of specific orders e.g. Isoptera, Mecoptera and Trichoptera. Sporadic differences between sites, and sexes did occur with Diptera, and significant diet variation between bat sexes, locations and months indicated opportunistic feeding centered around irregular episodes of novel bulkfood taxa (i.e. chironomid emergences).

Weather patterns of temperature and wind likely influence *T. brasiliensis* foraging activity, flight times and space. Additionally, weather may influence distribution and performance of flying insects as interpreted by dietary similarity in food taxa consumed. Whittaker et al. (1996) suggested that bats with overlapping foraging areas feed on similar insects, which tentatively explains the similarity of diet taxa frequency among individuals, regardless of sex, on a given night at a particular field site. However, insect abundance and activity, influenced by cold fronts, likely vary across foraging area, and large scale dietary shifts may only occur as a result of insect emergences, e.g. chironomid hatches (current study), or emigrating lepidopterans (Dickison et al. 1982; Wolf et al. 1990; Drake 1994), and not necessarily as a function of low insect diversity because of winter weather. As a consequence, samples collected on a single night during a particular

winter month are unlikely to adequately reflect the dietary breadth of *T. brasiliensis* in winter.

Our study introduces evidence that winter foraging of *T. brasiliensis* varies by month, sex, and location. This apparent lack of dietary dependence and episodic selection may offer *T. brasiliensis* an advantage during periods of insect dearth, e.g. winter. Distributions and abundances of flying insects may be sporadic in winter as indicated by the variation of dietary content among bats. Hoffmeister (1986) discussed the lack of actively feeding *T. brasiliensis* during late fall-early winter in Arizona based upon O'Sheas (1976) fat mass comparisons of bats migrating in fall versus spring in central Arizona. Incomplete partitioning of prey taxa (Whitaker 1994) may reflect a winter diet as a factor of evolutionary adaptations to general, or available, insect resources, and thereby advantageous for generalist bats. Molossids and vespertilionids that feed on coleopterans reflect more robust jaw morphology than related bat species that feed on lepidopterans and dipterans (Freeman 1979, 1981; Valdez and Bogan 2009). These evolutionary adaptations are likely further differentiated by echolocation strategies (Neuweiler 1983; Aldridge and Rautenback 1987) and flight performance (Norberg and Rayner 1987; Barclay and Bingham1991). When incomplete partitioning occurs, and our data suggests it has, then these behaviors and morphology may dictate where and when *T. brasiliensis* forages but not necessarily what *T. brasiliensis* feeds upon.

The occurrence and abundance of dietary taxa consumed in winter were consistent with previous publications on diet of *T. brasiliensis*, as a generalist with broad dietary breadth (Whittaker et al. 1996; McWilliams 2005). The sporadic importance of single food taxa, e.g. chironomid hatches (this study) or migratory lepidopteran species

(McCracken et al. 2008) reflects dietary flexibity and an exploitation of insect activity. Although sex-specific and site-specific prey selection differences were found to be significant, we are hesitant to consider these occurrences as evidence for winter specialization of feeding. Behavioral opportunism, or behavioral character displacement is known to occur interspecifically with sympatric bats (Husar 1973), perhaps this occurs intraspecifically in winter *T. brasiliensis*. Recent investigation in another wide-ranging western hemisphere insectivorous bat provides an alternative explanation. Population-level variation may suggest opportunistic habitat use, prey selection or a combination of individual habitat preferences or dietary specialists between or among bat populations (Cryan et al.2012).

We are hesitant to suggest that specialization on winter prey taxa occurs in *T. brasiliensis* based on a few dietary taxa differences detected between sexes and sites. Apparent differences may be temporarily inflated by what appears to be strong selection of particular prey, but is actually the result of intense feeding bouts on highly sporadic swarm densities of taxa such as chironomids, hemipterans and neuropterans. Previous researchers have termed bat 'specialization' on patchy resources of coleopterans, hymenopterans, isopterans and trichopterans (Ross 1967; Brigham and Saunders 1990; Agosta et al. 2003). In contrast, other researchers found no correlation or exploitation of emergence in cicadas (*Magacicada* spp.) with big brown bats (*E. fuscus*) (Storm and Whitaker 2008), but this lack of emergence influence on diet may reflect prey unavailability based on diurnal life history of the cicada (Heath 1967) and not bat avoidance. Bat diet may be determined by encounter frequency and capture success (Sih and Christensen 2001), consequently candidate prey taxa may vary in foraging bouts.

Patchy or stochastic availability of prey taxa may suggest that particular prey taxa are not always available and thus as taxa become available on a particular time or space *T. brasiliensis* may concentrate feeding efforts on those taxa. Assuming prey discrimination occurs in *T. brasiliensis* foraging bouts, then optimal foraging theory (Stephens and Krebs 1986) predicts prey choice on absolute abundance regardless of the abundance of alternative prey. Therefore, if coleopterans and lepidopterans are co-dominant prey taxa in winter, then other ordinal prey availability should not influence foraging bouts and diet unless beetles and moths are unavailable.

Life history traits of *T. brasiliensis* describe an insectivore that contends well with low temperatures (Ruffner et al. 1979; Geluso 2007), occupies a breadth of roost habitats, (e.g. caves, bridges, and timber railroad trestles (Davis and Cockrum 1963; Geluso and Mink 2009)), and remains opportunistic in feeding (Whitaker et al., 1996, McWilliams 2005) especially in winter. The portrayal of *T. brasiliensis* as an obligate migratory bat that is transient through central Texas and subsequently resides in caverns of the Mexican plateau (Villa 1956; Davis et al. 1962; Villa and Cockrum 1962; Cockrum 1969; Glass 1982; Davis and Schmidly 1984; Findley 1987; Lopez-Gonzalez and Best 2006) is suspect. Suitable winter food availability (dietary breadth) and the frequency of fecal pellet production ($\bar{x} = 8.3$ pellets per bat) indicate that Texas is a sustainable feeding ground in winter. Consistent winter capture and active feeding described in this study suggest that sufficient food (O'Farrell and Bradley 1970), water (O'Farrell and Bradley 1977) and roost (Geluso and Mink 2009) availability compensate for low temperatures (O'Farrell et al. 1967; Bradley and O'Farrell 1969; Spenrath and LaVal 1974) and support persistent bat populations in winter. Several tropical African bats migrate

seasonally following rains (Thomas 1983; Fenton and Thomas 1985) and likely the

subsequent abundance of insect prey and seasonal recruitment, suggesting migration is a

general, food-dependent phenomenon regardless of temperature. Given the considerable

energy costs (Dingle 1996) and risks associated with hazards encountered during

migration (Mink 2003), winters in the southwestern U.S. appear to be hospitable with

available food for *T. brasiliensis*. The dietary breadth, behavioral flexibility and

heterothermic abilities of *Tadarida brasiliensis* likely offer selective advantages during

Texas winters and provide alternatives to migration.

Resumen

Los modelos de la selección de la presa del micropteran se varían, y se han

descrito conveniente para mucha especie, comportamientos propios de cada especie,

influencias del hábitat, estrategias del forraje, y condiciones reproductivas pero raramente

para los murciélagos que forrajean en invierno. Durante un estudio de tres años,

documentamos nueve órdenes del insecto y 21 familias en la dieta del invierno del

Brasileño migratorio los murciélagos (*Tadarida brasiliensis*) en Tejas. A partir de 28

noches de muestrear los murciélagos centrales de Tejas (el condado de Bell) ($n = 586$) y

los murciélagos del sur de Tejas (el condado de Kenedy) ($n = 389$), 176 murciélagos sub-

fueron muestreados (las pelotillas fecales $n = 1,461$) para el análisis de la dieta.

Lepidópteros y coleóptero co-dominanted la dieta con frecuencias del consumo (93,8%) y

(85,2%) respectivamente a través de los meses de invierno. Otras taxus de la comida

incluyeron el díptero (52,3%), los hemípteros (47,2%), los himenópteros (35,2%),

Neuroptera (16,5%), el Trichoptera (8,5%), la isóptera (4,6%), y Mecoptera (2,3%) con

21 familias inclusivas del insecto. Portillas bénticas del invierno del díptero: El

Chironomidae era de vez en cuando las taxus dominantes de la comida ($n = 14$; 90-100% volumen de la dieta) que sugiere la importancia de las taxus a granel dietéticas intermitentes de la comida durante el invierno que forrajea por *Tadarida brasiliensis*. La dieta variada perceptiblemente entre los sitios, sexos, y entre los meses de invierno para la mayoría de las órdenes del insecto, pero los lepidopterans y los coleopterans era las taxus más abundantes y más frecuentes de la comida. Sin embargo, porque varias órdenes de las diferencias dietéticas insignificantes de los insectos entre los sitios y los sexos implique la coincidencia dietética amplia durante la mayoría de los meses de invierno o de la especialización individual secreta. La dieta del invierno del *Tadarida brasiliensis* en Tejas revela un insectívoro flexible, oportunista. La asociación de la residencia constante de la actividad y del invierno de la alimentación de invierno de las poblaciones del puente de *Tadarida brasiliensis* puede apoyar una alternativa sostenible y selectivamente ventajosa a la migración.

Table 9: Winter diet of Brazilian free-tailed bat, *Tadarida brasiliensis*, (105 ♂♂bats, *n* = 861 pellets; 71 ♀♀ bats, *n* = 600 pellets) based on frequency of occurrence, percent volume and relative importance of food taxa in 1,461 total fecal pellets taken in December, January and February 2007-2009 from Bell (central) and Kenedy (south) Cos., Texas.

Taxon	Frequency	%Volume	Relative Importance
ARTHROPODA	100.0	100.0	100.0
INSECTA	100.0	100.0	100.0
LEPIDOPTERA	**93.8**	**49.9**	**46.8**
COLEOPTERA	**85.2**	**21.4**	**25.1**
Carabidae	26.1	2.7	0.7
Chrysomelidae	17.1	1.4	0.2
Bupestridae	13.1	0.5	0.1
Scarabaeidae	11.4	0.7	0.1
Hydrophilidae	8.5	0.4	<0.1
Curculionidae	7.4	0.5	<0.1
Cerambycidae	4.6	0.2	<0.1
Dytiscidae	3.4	0.5	<0.1
DIPTERA	**52.3**	**16.3**	**8.5**
Chironomidae	18.2	13.9	2.5
Culicidae	3.4	0.5	<0.1
Dolichopodidae	1.7	0.1	<0.1
Psychodidae	1.1	0.2	<0.1

Table 9 continued. Winter diet of Brazilian free-tailed bat, *Tadarida brasiliensis*, (105 ♂♂bats, *n* = 861 pellets; 71 ♀♀ bats, *n* = 600 pellets) based on frequency of occurrence, percent volume and relative importance of food taxa in 1,461 total fecal pellets taken in December, January and February 2007-2009 from Bell (central) and Kenedy (south) Cos., Texas.

Taxon	Frequency	%Volume	Relative Importance
Empididae	0.6	<0.1	<0.1
Stratiomyidae	0.6	<0.1	<0.1
Tipulidae	0.6	<0.1	<0.1
Mycetophilidae	0.6	<0.1	<0.1
HEMIPTERA	**47.2**	**4.9**	**2.2**
Lygaeidae	37.5	3.8	1.4
Cicadellidae	15.9	0.6	0.1
Corixidae	11.3	0.6	0.1
Pentatomidae	1.1	0.1	<0.1
HYMENOPTERA	**35.2**	**2.5**	**0.9**
NEUROPTERA	**16.5**	**0.9**	**0.2**
Myrmeleontidae	0.6	<0.1	<0.1
TRICHOPTERA	**8.5**	**0.2**	**<0.1**
ISOPTERA	**4.6**	**0.1**	**<0.1**
MECOPTERA	**2.3**	**0.1**	**<0.1**

Table 10: Tukey's HSD test F-statistics on winter diet of Brazilian free-tailed bat, *Tadarida brasiliensis*, (105 ♂♂bats, $n = 861$ pellets; 71 ♀♀ bats, $n = 600$ pellets) based on percent volumes of food taxa in 1,461 total fecal pellets taken in December, January and February 2007-2009 from Bell (central) and Kenedy (south) Cos., Texas. Asterisks indicate significant differences as *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$, italics = $P< 0.1$.

Order	Kennedy		Bell	
	Month $_{2, 86}$	Sex $_{1, 86}$	Month $_{2, 82}$	Sex $_{1, 82}$
Coleoptera	0.10	4.58*	5.06**	0.18
Hempiptera	0.53	7.88**	5.53**	0.00
Diptera	15.53***	1.33	4.42*	0.55
Lepidoptera	11.01***	0.59	1.18	*3.89*
Neuroptera	1.90	0.02	8.60***	*3.45*
Hymenoptera	0.65	0.07	6.92**	*3.20*
Trichoptera	--	--	0.51	*3.34*
Isoptera	--	--	1.15	0.08
Mecoptera	*3.03*	0.31	--	--
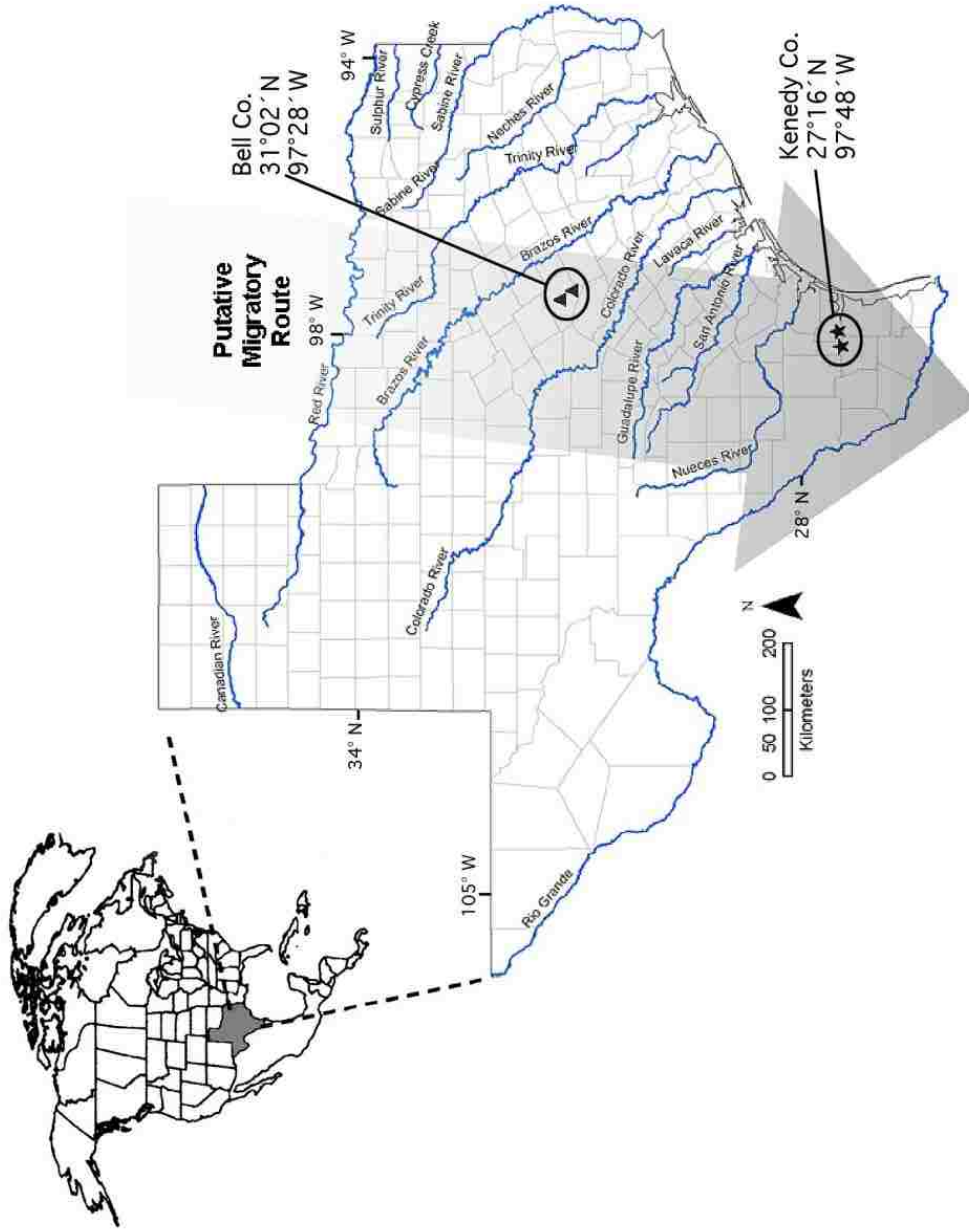
Figure 12.- Map showing study sites in Kenedy Co., south Texas and Bell Co., north-central Texas and putative migration route through Texas, highlighted by shaded arrow, modified from Cockrum's 1969 distribution of *Tadarida brasiliensis* in the United States.

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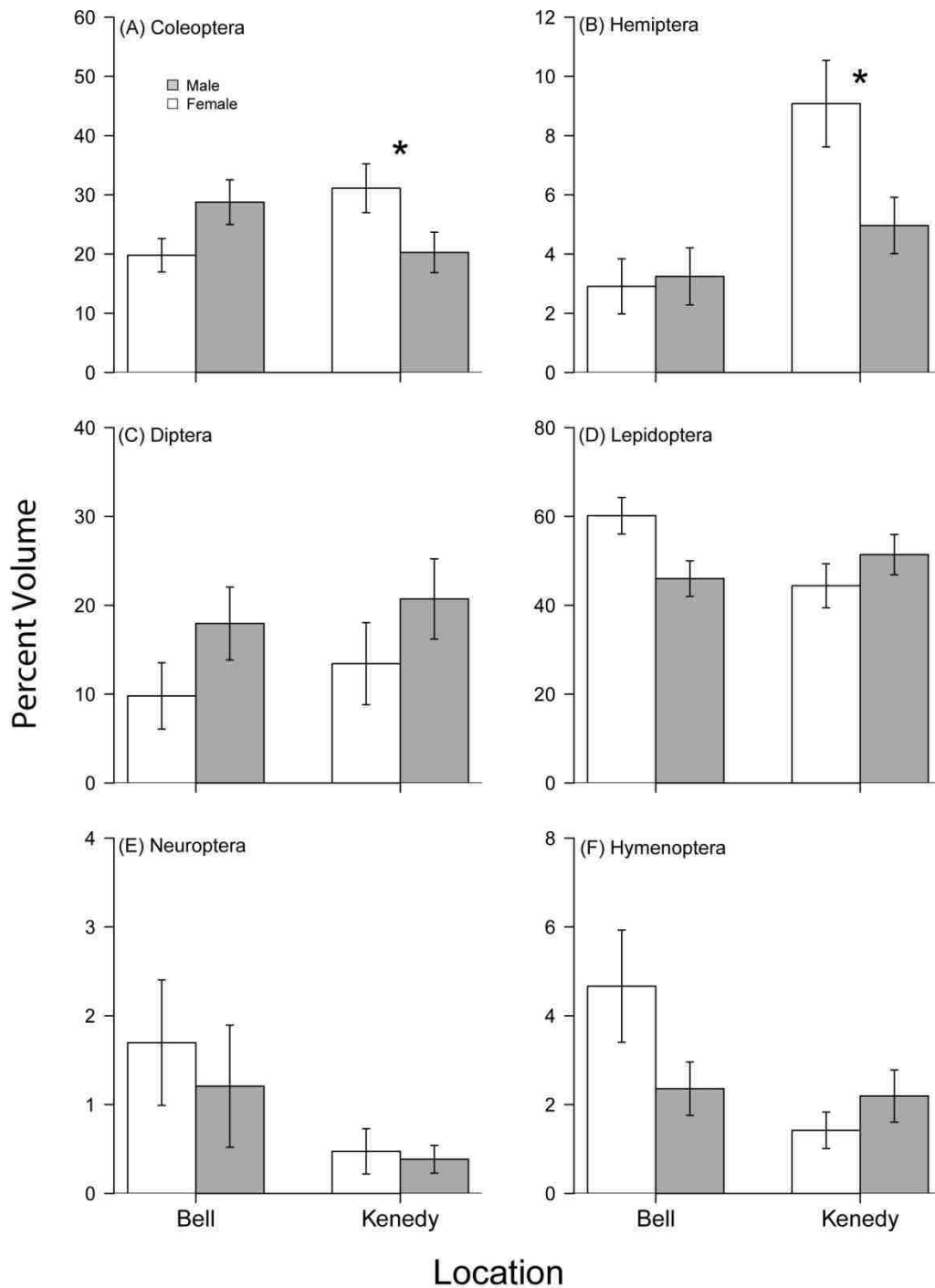
Figure 13. Winter dietary taxa volume comparison between sexes (105 ♂♂bats, $n = 861$ pellets; 71 ♀♀ bats, $n=600$ pellets) and locations (86 north-central bats, $n = 753$ pellets; 90 south bats, $n = 708$ pellets) in Texas *Tadarida brasiliensis* based on fecal pellet composition. Error bars are ±1.0SE. [*asterisks represent significant differences between months (Tukey's HSD test, $P < 0.05$)]
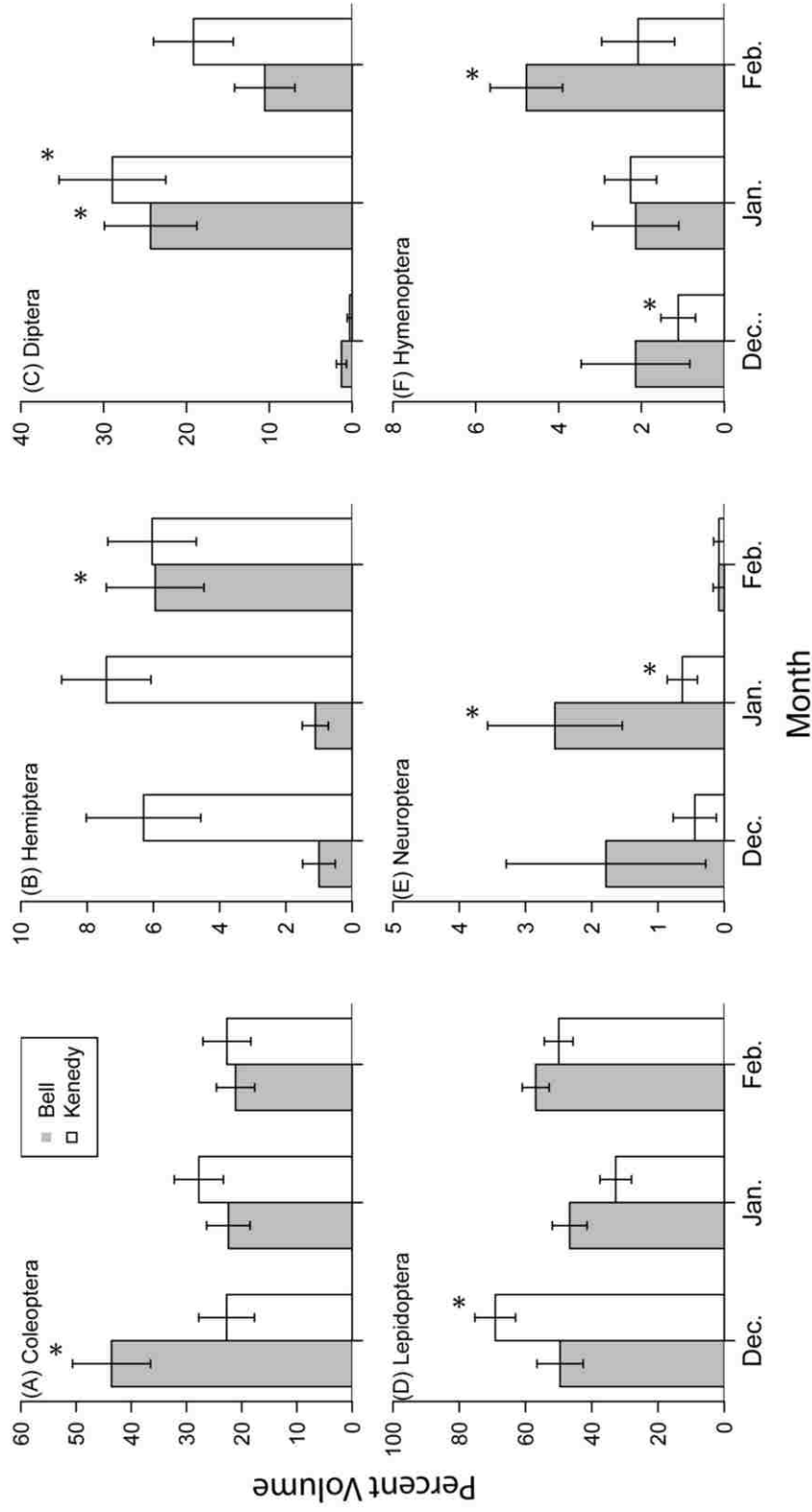
Figure 14. Comparison of volumes of major food taxa in winter diets of *Tadarida brasiliensis* in Kenedy Co., south Texas (white bar) versus in Bell Co., north-central Texas (gray bar) (*n* = 176 bats). Error bars are ± 1.0 SE. [*asterisks represent significant differences between months (Tukey's HSD test,*P* < 0.05)]

Figure 15. Winter dietary taxon frequency as a function of fecal pellet count in *Tadarida brasiliensis* in Texas across winter months (n = 1,461).

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CHAPTER FIVE

Conclusions

This research program investigated three aspects of winter ecology of *Tadarida brasiliensis* and assessment of bridges as alternative roosts for other bat species in New Mexico and Texas. Bats roost 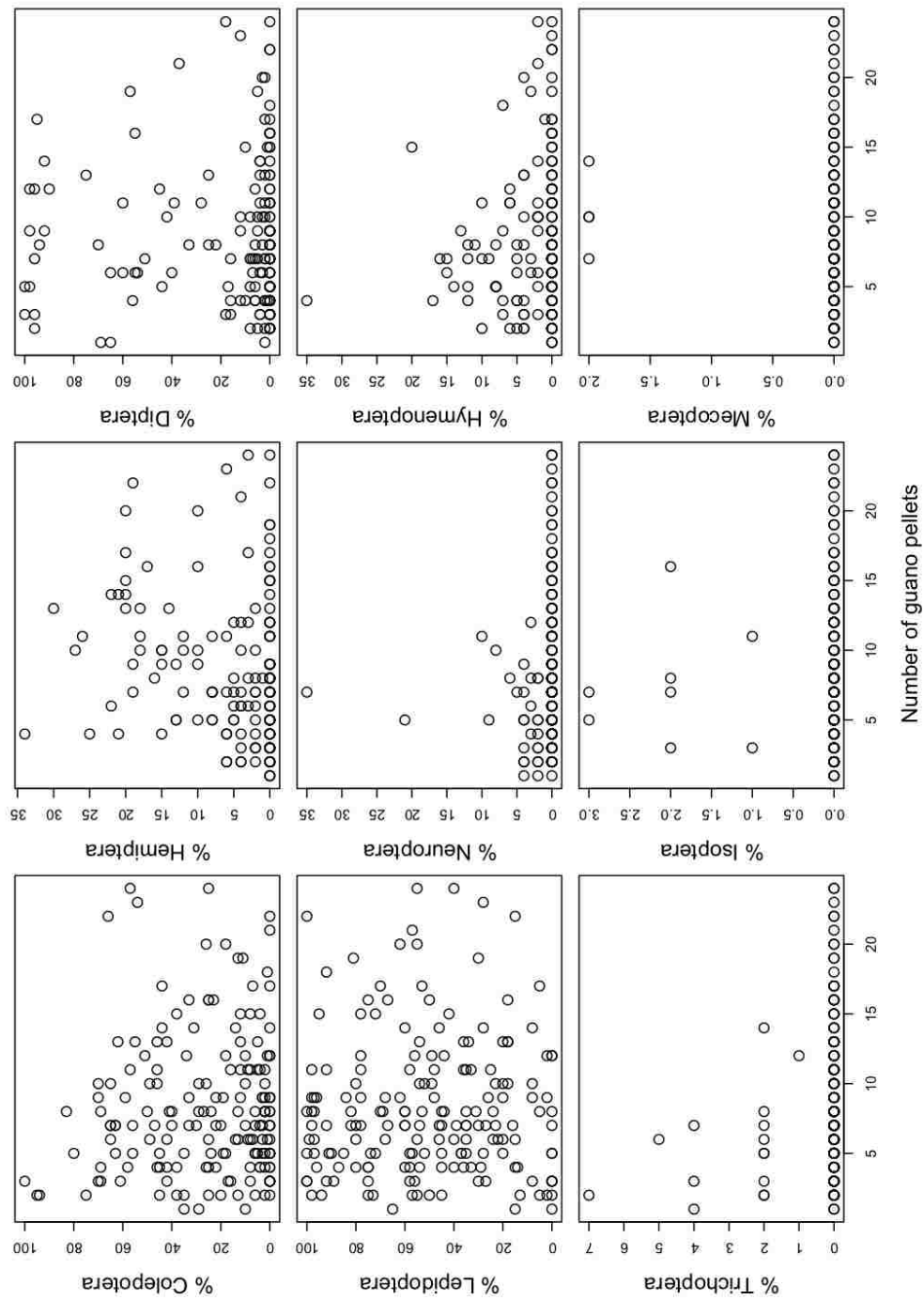in bridges for various life-history functions, but little is known about use of bridges in the southwestern United States. The Yuma myotis (*Myotis yumanensis*), Arizona myotis (*M. occultus*), and Brazilian free-tailed bat (*Tadarida brasiliensis*) formed maternity colonies in bridges in the lower Rio Grande valley of New Mexico. The California myotis (*M. californicus*), fringed myotis (*M. thysanodes*), silver-haired bat (*Lasionycteris noctivagans*), big brown bat (*Eptesicus fuscus*), and pallid bat (*Antrozous pallidus*) only roosted infrequently in bridges. Use of bridges by day-roosting bats differed seasonally, with most individuals occupying bridges April-October. From November to March, relatively few individuals of *T. brasiliensis* occupied bridges; however populations persisted throughout winter months. Bridges throughout the southwestern United States likely serve similar life-history functions for bats, and should be managed as a resource, especially those occupied by maternity colonies or large numbers of individuals.

Investigation into the demography of wintering *Tadarida brasiliensis* produced information reflecting energetically robust, healthy, viable populations. This study of winter *Tadarida brasiliensis* populations occupying bridges in Texas offers insight into variation in migratory patterns, and describes demographics of previously undescribed winter populations found midway along an expected U.S. to Mexico migration route.

Bridge populations of day-roosting bats were censused at two sites in central and south Texas, 563 km apart, through six winters (2005-2011). Mean counts during winter months were consistently several thousand (Bell County x̄ = 3,132; Kenedy County x̄ = 2,699). Mist-net sampling of *Tadarida brasiliensis* through three winters from 2007-2009 yielded consistent captures ($n = 975$) at bridge sites. Roosting behaviors by *Tadarida brasiliensis* in natural caverns and bridges, and continuous occupation during winter have important implications for migrating populations of these insectivorous bats and for winter ecosystems. We described winter-month fluctuations in *Tadarida brasiliensis* populations at four bridges and two locations separated geographically north-south by 563 km. Demography, sex ratio, age class, feeding activity and mass over winter months was evaluated and dynamic shifts were found in these categories. Juvenile *Tadarida brasiliensis* comprised 58% of sampled bats, however, all four age classes and both sexes were captured in all winter sampling sessions. Feeding activity was high and consistently detected in captured bats throughout winter. Representation of all age categories throughout winter suggests adaptation or acclimatization to bridge roosts as a viable winter strategy for *Tadarida brasiliensis* bats. Bridge occupation is advantageous as an alternate winter strategy to migration. This winter roost behavior is likely a result of behavioral plasticity or a predisposition to a commensal relationship with humans rather than unrelenting habitat loss.

Examination into the winter diet of *Tadarida brasiliensis* revealed significant variation and bouts of feeding activity across sexes, months and locations in Texas. Analysis of fecal pellets collected from mist-netted bats reveals Brazilian free-tailed bats are opportunistic foragers that likely encounter markedly varied qualities and quantities

of prey in the winter season of lower ambient temperatures and relative dearth of insect activity. The winter diet shifts included variation between counties, sexes, and months in percent volume of certain ordinal categories, but frequency of ordinal presence was consistent through winter. This dietary breadth suggests that *T. brasiliensis* is an opportunistic winter predator, with discrete periods of selection probably based on exploiting heavy abundances of acceptable food taxa, e.g. chironomids, or lepidopterans, on occasional nights.

Patterns of micropteran prey selection are varied, and have been aptly described for many species, species-specific behaviors, habitat influences, foraging strategies, and reproductive conditions but rarely for bats foraging in winter. During a three-year study, we documented nine insect orders and 21 families in the winter diet of migratory Brazilian free-tailed bats (*Tadarida brasiliensis*) in Texas. From 28 nights of sampling central Texas (Bell County) bats (*n*=586) and south Texas (Kenedy County) bats (*n*=389), 176 bats were sub-sampled (*n*=1,461 fecal pellets) for diet analysis. Lepidoptera and Coleoptera co-dominanted the diet with consumption frequencies of (93.8%) and (85.2%) respectively across winter months. Other food taxa included Diptera (52.3%), Hemiptera (47.2%), Hymenoptera (35.2%), Neuroptera (16.5%), Trichoptera (8.5%), Isoptera (4.6%), and Mecoptera (2.3%) with 21 inclusive insect families. Winter benthic hatches of Diptera: Chironomidae were occasionally dominant food taxa (*n*=14; 90-100% diet volume) suggesting the importance of intermittent dietary bulk food taxa during winter foraging by *Tadarida brasiliensis*. Diet varied significantly between sites, sexes, and among winter months for most insect orders, but lepidopterans and coleopterans were the most abundant and frequent food taxa. However, for several

orders of insects negligible dietary differences between sites and sexes imply broad

dietary overlap during most winter months. Winter diet of *Tadarida brasiliensis* in Texas

reveals a flexible, opportunistic insectivore. The association of consistent winter feeding

activity and winter residency of bridge populations of *Tadarida brasiliensis* may support

a sustainable and selectively advantageous alternative to migration.

APPENDICES

APPENDIX A

Future Research Considerations

1) In future research, determine the winter abundance of *T. brasiliensis* at various caverns with known summer occupancy and compare to other roosts, such as bridges, during an extremely cold winter. Why do some individuals remain in these northern areas rather than migrate farther south where temperatures are warmer and insects are more abundant?

2) Applied research on retrofitting existing bridge structures throughout the southwest would be relevant to the economic value of *T. brasiliensis* consuming important agricultural pests in summer as well as other seasons. The beneficial economic impact of foraging insectivorous bats on the farming community could be increased if bridge architecture promoting bat occupancy could be assessed and determined to be feasible.

3) Future experimental studies could measure calorimetric value of known insect food items, from this study, to determine an economic caloric value to those food items, are those items selected based on caloric value, or do bats simply forage on any available insect prey they can?

4) Additional studies on the natural history of wintering *T. brasiliensis* are warranted in temperate regions of North America. Compilation of similar studies with Old world migratory insectivorous bats, and corroboration with migratory insectivorous birds might reveal emerging global migration patterns in volant vertebrates.

APPENDIX B

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