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Biological Sciences

Sexual dimorphism in the endangered Florida bonneted bat, *Eumops floridanus* (Chiroptera: Molossidae)

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Abstract Interest in the Florida bonneted bat (*Eumops floridanus*) has risen dramatically since the species was listed as federally endangered in 2013. However, understanding of many aspects of the species' biology is limited, due in part to the fairly recent recognition of *E. floridanus* as a distinct species rather than a subspecies of *E. glaucinus*. Through a two-year mark-recapture study of *E. floridanus* roosting in a group of bat houses, we obtained morphological measurements on >200 individuals. We documented modest male-biased sexual size dimorphism (forearm length, wing width, and wing length were larger in adult males than adult females) and found gular glands exclusively among males. If these morphological differences lead to niche partitioning between sexes, conservation planning may need to consider the foraging habitat use of males and females independently. Relative to other species in the genus *Eumops*, *E. floridanus* had a moderate aspect ratio index, low wing shape index, and low wing tip index, suggesting the species may not be capable of flying at speeds as fast as other closely related species, but may be more maneuverable and more efficient when flying in cluttered space.

Keywords: Body condition, *Eumops floridanus*, Florida bonneted bat, morphology, sexual dimorphism, wing shape

Introduction

The Florida bonneted bat (*Eumops floridanus*) is a rare species endemic to South Florida, designated as federally endangered in 2013 (USFWS 2013). *Eumops floridanus* is one of only eight species of the family Molossidae (free-tailed bats; Norberg and Rayner 1987) found within the United States, and the only with federal conservation status. Due to its rarity, small geographic range, and fairly recent recognition as a distinct species (Timm and Genoways 2004), extremely little is known about the basic biology of *E. floridanus*. A single species, *E. glaucinus*, was previously believed to range across the northern one-third of South America, Central America, Jamaica, Cuba, and south Florida (Barbour and Davis 1969). In recognition of significant morphological differences, *Eumops* occurring in

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Florida were designated a distinct subspecies in 1971 (*E. g. floridanus*; Koopman 1971), and then a distinct species in 2004 (*E. floridanus*; Timm and Genoways 2004). The recent classification of *E. floridanus* as an endangered species greatly increases the need to understand its ecology (FWC 2011, USFWS 2013). Establishment of baseline morphological data for *E. floridanus* is needed to provide a foundation for future comparative studies and for developing appropriate conservation strategies.

Although male-biased sexual dimorphism in body mass or size is relatively common among many species of mammals (i.e., males are heavier or larger than females; Isaac 2005), female-biased sexual dimorphism tends to be more pervasive within Chiroptera (Ralls 1977, Williams and Findley 1979). For example, female-biased sexual dimorphism is widespread among many species in the family Vespertilionidae (Myers 1978, Williams and Findley 1979), particularly in forearm length (Stevens and Platt 2015). In contrast, Molossidae commonly exhibit male-biased sexual dimorphism (Freeman 1981). Male-biased sexual dimorphism has been reported in several species of *Eumops* (Eger 1977), with more pronounced differences in larger species within the genus. *Eumops floridanus* is intermediate in overall size among these species, and the occurrence of sexual dimorphism in *E. floridanus* is uncertain. The few studies that have investigated sexual dimorphism in the closely related *E. glaucinus* have reached mixed conclusions regarding dimorphism in mass and forearm length (Gardner et al. 1970, Eger 1977, Silva Taboada 1979, Myers and Wetzel 1983, Bowles et al. 1990). Understanding patterns of sexual dimorphism can be critical to development of species-specific conservation strategies if differences in morphology result in differential habitat selection or movement patterns between sexes (Blanckenhorn 2005, Isaac 2005).

Wing morphology is the primary determinant of flight capabilities of bats, affecting foraging strategies, extent of foraging area, and migratory capacity (Fenton 1972, Findley et al. 1972, Norberg 1972). Wing shapes vary among species and also between sexes within species, resulting in differential habitat selection, movement patterns, time budgets, diet, thermoregulatory requirements, metabolic rates, and susceptibility to predation (Ralls 1977, Blanckenhorn 2005, Isaac 2005). Wing length, wing tip length, aspect ratio, and speed are high among species in Molossidae (Findley et al. 1972), whereas wing area is relatively small (Norberg and Rayner 1987). Bats with long, narrow wings generally have rapid, efficient flight, whereas bats with short broad wings have high turning performance (i.e., high maneuverability, meaning a small minimum space is required to change flight directions at a given speed, and high agility, meaning a turn can be initiated at a rapid rate; Findley et al. 1972, Norberg 1972). Molossids use swift, direct flight trajectories to pursue prey through aerial hawking in open habitats or at high altitudes, and to fly long distances when commuting between roosts and foraging areas or migrating (Findley et al. 1972, Freeman 1981, Aldridge and Rautenbach 1987, Norberg and Rayner 1987). High metabolic costs are incurred when these bats attempt to fly at slower speeds in confined spaces relative to faster speeds in straight flight, which may constrain many molossids to forage exclusively in open environments (Voigt and Holderied 2012). Gradation in flight capabilities among

species within Molossidae can be predicted on the basis of wing morphology (Freeman 1981). To date, few live *E. floridanus* individuals have been captured, and morphological measurements of *E. floridanus* specimens are extremely scarce. Nothing is known about sexual dimorphism in wing morphology, or about wing shape relative to that of closely-related species, constraining our understanding of flight capabilities of these bats.

Due to a lack of data on basic morphology and flight capacity in *E. floridanus*, our goal was to obtain a robust dataset of morphological measurements that would enable interspecific and intraspecific comparisons. Given the presence of male-biased sexual dimorphism in other *Eumops* and the ecological implications of variation in wing morphology, our objectives were to compare mass, size, body condition and wing morphology in *E. floridanus* of different sexes and ages, and contrast wing morphology with that of other *Eumops* species.

Materials and Methods

We conducted this study at Fred C. Babcock - Cecil M. Webb Wildlife Management Area (BWWMA) in southwest Florida. The vegetation communities were a mix of mesic and hydric pine flatwoods with embedded freshwater marshes, ponds, and hardwood hammocks. Average annual temperature was 23.4°C, and average rainfall was 128.8 cm per year, most of which fell during summer months (http://www.usclimatedata.com). BWWMA was owned and managed by the Florida Fish and Wildlife Conservation Commission (FWC).

Eumops floridanus was observed in Punta Gorda, FL (5 km from BWWMA) in 1979 (Belwood 1981), and was first detected on BWWMA in 2006. To augment roosting habitat for the species, the FWC erected matched pairs of one- or three-chamber bat houses on poles at eight sites in 2007-2008, and at five additional sites in 2012. Each pair of bat houses sharing a pole is considered a single roost. To date, *E. floridanus* have been observed in nine of these 13 roosts.

We conducted seven multi-day capture sessions spaced four months apart: 22-25 April 2014, 27-30 August 2014, 15-17 December 2014, 20-24 April 2015, 24-26 August 2015, 14-16 December 2015, and 19-21 April 2016. During each session, we used triple-high mist nets in an attempt to catch every *E. floridanus* roosting in each of the occupied roosts. Mist nets were opened at sunset and remained open for a maximum of three hours.

Each captured bat was placed individually in a numbered cotton bag, and examined to determine age (adult/sub-adult), sex, body mass, forearm length, reproductive status, and the presence or absence of gular-thoracic glands. Sub-adults were distinguished from adults by examining the degree of fusion of phalangeal cartilage; when that was ambiguous, we used status of genitals and mammae as secondary indicators of age. Adult females were classified as non-reproductive, pregnant, lactating, or post-lactating. Adult males were classified as non-reproductive (testes abdominal) or reproductive (testes descended). We calculated body condition index (BCI = mass/forearm length; Reynolds et al. 2009, Jonasson and Willis 2011, Lisón et al. 2014) to generate a relative metric of each bat's overall condition and to facilitate future comparisons of mass relative to body size when making inferences about wing loading and fat reserves among individuals of different ages, sexes, and reproductive status.

During the December 2015 and April 2016 capture sessions, we took four additional wing measurements from a subset of individuals. We fully extended the right wing of each bat and measured the following lengths using dial calipers (precision ± 0.1mm): the distance from the wrist to the tip of the 5th finger excluding the wrist (D5), distance from the wrist to the tip of the 3rd finger excluding the wrist (D3), and length of the 1st and 2nd phalanx of the 4th finger (Figure 1). These are considered simple descriptions of wing width (D5), wing length (D3), and wingtip width (1st and 2nd phalanx of the 4th finger; features that vary greatly in length among Molossidae; Freeman 1981). Each measurement was repeated three times by the same observer and averaged. From these measurements we calculated three indices: *aspect ratio index* ([D3+forearm]/D5; Findley et al. 1972), *wing shape index* (D3/D5; Fenton
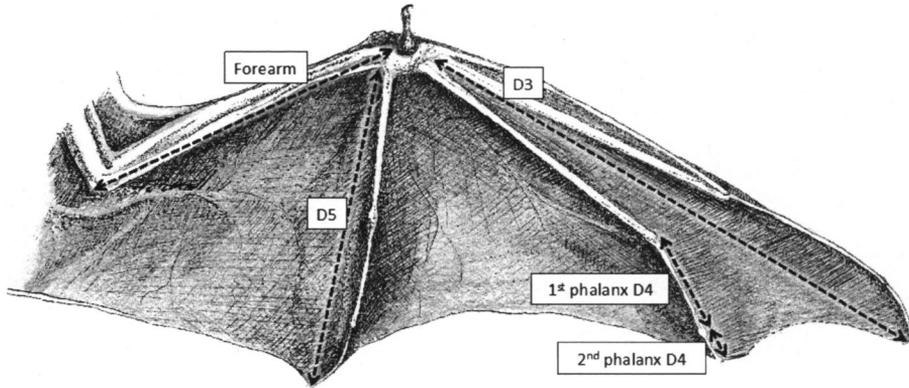
Figure 1. Diagram showing measurements used to reflect *Eumops floridanus* wing size and shape.

1972), and *tip index* (100*D3/[D3+forearm]; adapted by Freeman 1981), to facilitate comparisons with wing shapes of other *Eumops* species.

All bats were uniquely marked with passive integrated transponders (PIT-tag; 12 mm, 134.2 kHz FDXB tags (Biomark Inc., Boise, ID)) to enable identification of recaptured individuals. Tags were implanted subcutaneously in the lower lumbar region near the plagiopatagium. After processing, each bat was released near the site of capture. All capture and handling processes followed American Society of Mammalogists guidelines (Sikes et al. 2011), were approved by the University of Florida IACUC (#201308070 and 201408587), and were in accordance with U.S. Fish and Wildlife Service permit #TE 23583B-1 and Florida Fish and Wildlife Conservation Commission permit #SUO-49616.

After examining all data to determine whether assumptions of normality and homogeneity of variance were met with Shapiro-Wilks and Levene's tests, we tested for differences in morphometric measurements between sexes (mass and forearm length) using student's t-tests (when data met assumptions of normality and homogeneity of variance), Welch's t-tests (when data had unequal variance), or Mann-Whitney U tests (when data were not normally distributed). We tested for differences in wing metrics (D5, D3, 1st and 2nd phalanx of the 4th finger) using MANOVA. Lastly, we compared measurements among individuals of different reproductive status categories using ANOVA followed by Tukey HSD tests for multiple comparisons. For all morphometric comparisons involving individuals captured more than once, we used a single mean value to represent each characteristic for each individual that was reported in the same reproductive category during more than one capture session. Throughout, we define sexual size dimorphism as any statistically significant difference in morphometric measurements of different sexes within the same age or reproductive category (Lovich and Gibbons 1992). All statistical analyses were conducted with SPSS version 23.0 (IBM Corp. 2015).

Results

During each of the seven capture sessions we captured 50, 61, 42, 56, 63, 79, and 89 individual *Eumops floridanus* respectively. In total we captured 201 unique individuals: 36% were males and 64% were females. Gular glands were apparent on all adult males and most sub-adult males, but absent from all females of both age groups.

Mass ranged greatly among individuals (from 27 to 59 g), but we did not find sexual dimorphism in mass (Table 1). Mass of all adult males ($n = 65$) did not differ from mass of adult females that were not pregnant (i.e., non-reproductive or post-lactating, $n = 109$) ($t_{172} = 0.090$, $p = 0.928$). Similarly, mass of non-reproductively

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Table 1. Mean (± SD) mass, forearm length, and body condition index (BCI; mass/forearm length) of 201 *Eumops floridanus* at Fred C. Babcock - Cecil M. Webb Wildlife Management Area, FL. Total sample size exceeds the number of unique individuals captured because some individuals captured multiple times exhibited different reproductive status during different capture events.

Sex	Status	n	Mass (g)	Forearm (mm)	BCI
Male	reproductively active adult	31	43.77 ± 4.38	63.72 ± 1.49	0.686 ± 0.062
	non-reproductive adult	16	40.68 ± 5.79	63.37 ± 1.80	0.642 ± 0.088
	non-reproductive sub-adult	35	38.46 ± 3.82	63.19 ± 1.81	0.608 ± 0.053
Female	pregnant adult	56	47.13 ± 4.10	62.75 ± 1.30	0.750 ± 0.063
	post-lactating adult	59	45.29 ± 2.96	62.79 ± 1.26	0.722 ± 0.046
	non-reproductive adult	46	40.47 ± 3.32	62.70 ± 1.23	0.645 ± 0.053
	non-reproductive sub-adult	35	38.03 ± 4.03	62.39 ± 1.26	0.609 ± 0.059

active adult males ($n = 16$) did not differ from mass of non-reproductively active adult females ($n = 50$) ($t_{18.26} = 0.137$, $p = 0.893$).

We detected male-biased sexual dimorphism in forearm length, a characteristic typically used to reflect overall body size in bats (Table 1). Forearm length ranged from 60.0 to 69.1 mm. Forearm length of all adult males ($\bar{x} = 63.74 \pm 1.44$ mm, $n = 54$) was significantly greater than that of all adult females ($\bar{x} = 62.74 \pm 1.23$ mm, $n = 111$) ($t_{163} = 4.642$, $p<0.001$). Similarly, forearm length of sub-adult males (median $= 63.3$ mm, $n = 35$) was significantly greater than that of sub-adult females (median $= 62.5$ mm, $n = 35$) ($U = 374.5$, $p = 0.005$).

We found differences between adult males ($n = 29$) and females ($n = 38$) in wing morphology ($F_{4,62} = 4.07$, $p = 0.005$, Wilk's $\Lambda = 0.792$, partial $n^2 = 0.208$). Two of the four wing measurements differed between sexes, after Bonferroni corrections to account for multiple comparisons (Table 2). Wing width (D5) was greater in males than females ($F_{1,65} = 45.32$, $p<0.005$; $\bar{x}$ difference $= 1.56$ mm, 95% CI from 0.76 to 2.35 mm larger). Wing length (D3) was also greater in males than females ($F_{1,65} = 8.447$, $p = 0.005$; $\bar{x}$ difference $= 2.09$ mm, 95% CI from 0.65 to 3.52 mm larger). In contrast, there were no differences in wingtip width (1st and 2nd phalanx of the 4th finger). Length of the first phalanx was similar in males and females ($F_{1,65} = 4.1$, $p = 0.047$; $\bar{x}$ difference $= 0.44$ mm, 95% CI from 0.01 to 0.87mm larger), as was length of the 2nd phalanx ($F_{1,65} = 0.007$, $p = 0.936$; $\bar{x}$ difference $= 0.01$ mm, 95% CI from -0.02 mm smaller to 0.23 mm larger).

Body condition index (BCI) ranged from 0.460 to 0.952 (Table 1, Figure 2). We found differences in BCI among bats of different reproductive categories [$F_{6,\ 274} = 40.238$, $p<0.001$]. There were no significant differences in BCI for *post-hoc* pair-wise comparisons between male sub-adults, female sub-adults, male non-reproductive adults, and female non-reproductive adults; however, there were significant differences in BCI for pair-wise comparisons between these categories and BCI of reproductively active adult males, post-lactating females, and pregnant females.

Relative to seven other species in the genus *Eumops*, *E. floridanus* wing morphology was typical in some respects but unusual in others. *Eumops floridanus* had a moderate *aspect ratio index*, the second lowest *wing shape index*, and the lowest *tip index* (Table 2).

Table 2. Comparisons of selected wing characteristics among *Eumops floridanus* (mean ± SD, derived from this study) and those reported for other species in the genus *Eumops* (from Freeman 1981).

| Species	n	D3	D5	1st Phalanx of D4	2nd Phalanx of D4	Aspect Ratio Index	Wing Shape Index	Tip Index
E. floridanus	**67**	**112.56±3.07**	**61.13±1.78**	**21.79±0.90**	**5.00±0.45**	**2.88±0.06**	**1.84±0.04**	**63.96±0.46**
(adult females)	**38**	**111.65±2.92**	**60.46±1.67**	**21.60±0.95**	**5.01±0.49**	**2.89±0.07**	**1.85±0.04**	**63.98±0.43**
(adult males)	**29**	**113.73±2.89**	**62.02±1.54**	**22.04±0.79**	**5.00±0.41**	**2.87±0.05**	**1.83±0.03**	**63.94±0.51**
E. auripendulus		·	·	·	·	3.04	2.05	67.43
E. bonariensis		·	·	·	·	2.70	1.81	66.90
E. glaucinus		·	·	·	·	2.94	1.95	66.43
E. hansae		·	·	·	·	3.01	1.96	65.11
E. maurus		·	·	·	·	2.93	1.95	66.54
E. perotis		·	·	·	·	2.88	1.92	68.41
E. underwoodi		·	·	·	·	2.87	1.95	67.79
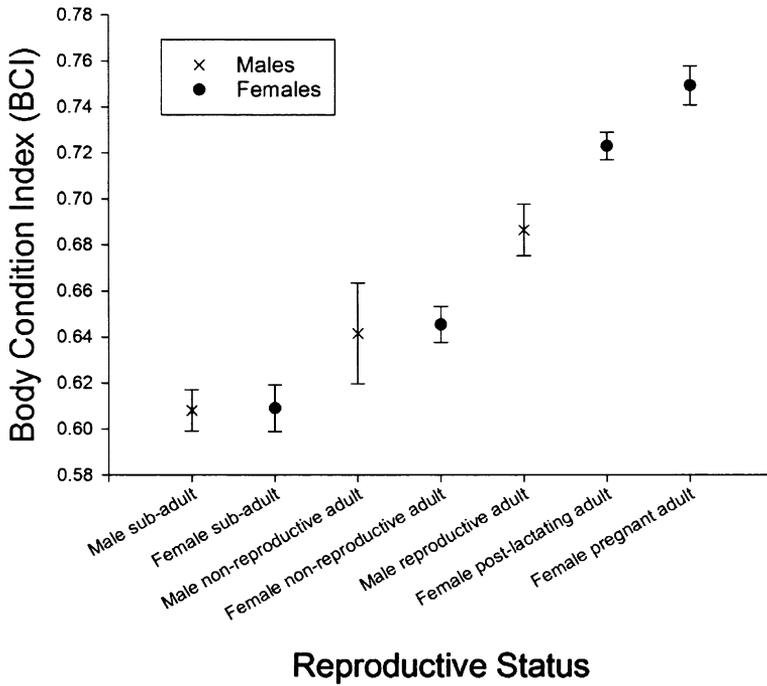
Figure 2. Mean ± SE in body condition index (BCI) among *Eumops floridanus* of different sexes and reproductive categories.

Discussion

We found modest male-biased sexual dimorphism in *Eumops floridanus*. Forearm length (often used as a surrogate for overall body size in bats) was larger for males than females, in both adults and sub-adults. In addition, two of the four measures of wing structure were larger in adult males than females, suggesting that wings of males are both longer and wider than those of females. The degree of difference we observed in forearm length between sexes was 1.5%, which is similar to the degree of sexual dimorphism found in other bat species (Williams and Findley 1979, Lindenfors et al. 2007, Lu et al. 2014, Wu et al. 2014).

We are aware of little previous investigation into the occurrence of sexual dimorphism in *E. floridanus*. Only two publications report data on forearm length of *E. floridanus*. Eger (1977) describes only males and does not speculate on sexual dimorphism. Timm and Genoways (2004) reported greater average forearm lengths than we found, 63.9 mm for males (*n*=23), and 64.7 mm for females (*n*=4), and concluded that the species was not sexually dimorphic. The differences between our findings and those of Timm and Genoways (2004) may be because: 1) we measured live specimens while they measured preserved museum specimens, which can produce discrepancies (Bininda-Emonds and Russell 1994, Simmons and Voss 2009, Stephens et al. 2015), 2) their sample size was not large enough to accurately capture the variation in forearm length within and between sexes, and/or

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3) their small sample size resulted in analyses that lacked adequate power to detect differences between sexes. Regardless, potential differences in measurements from live and preserved specimens do not influence the comparisons between sexes we report, as all our measurements were on live animals.

Sexual dimorphism is often explained by sexual selection. It has been argued that sexual selection in males is the primary evolutionary force selecting for larger body size (Ralls 1977, Blanckenhorn 2005). Further, it is common for males to be slightly larger in size than females among mammal species that have a harem social structure due in part to male - male competition (Racey 2009). There is evidence that *E. floridanus* use a harem social structure (Ober et al. 2016) and our finding of gular glands in males but not females provides additional evidence to support the potential role of sexual selection. These glands are present in several species of Molossids (Horst 1966, Gutierrez and Aoki 1973, Gustin and McCracken 1987, Scully et al. 2000), and had been noted previously for *Eumops* in general (Eger 1977), and more specifically in *E. glaucinus* (Silva Taboada 1979, Bowles et al. 1990) and *E. floridanus* (Belwood 1992). In most species these gular glands are well developed in males and rudimentary or lacking in females (Horst 1966, Scully et al. 2000), as we found in the present study. In other species, these glands undergo seasonal fluctuations in size, becoming swollen with sebaceous oils during breeding seasons (Gutierrez and Aoki 1973, Krutzsch 2000), but understanding of their exact function is limited. It has been proposed that these glands may be used in harem defense and roost site marking (Belwood 1992).

Sexual size dimorphism may result in sex-specific niche utilization (Selander 1966, Williams and Findley 1979). Individuals with high wing loadings (defined as body mass/wing area) tend to have fast flight speeds but low maneuverability (Aldridge and Rautenbach 1987, Norberg and Rayner 1987). The larger wing size of adult males relative to females results in lower wing loading for males, which may slightly lessen niche overlap during the energetically demanding phase of pregnancy. As the only species known to form harems in the U.S., niche differentiation may be especially important for *E. floridanus* because individuals are not sexually segregated during the maternity season, as is the case with the majority of temperate species (Bradbury 1977, Senior et al. 2005). Future investigations of whether males and females forage in different habitats or at different distances from roosts would better inform recovery plans for the species.

The two better-known *Eumops* species that occur in the U.S. (*E. perotis* and *E. underwoodi*) are considered to be among the fastest flying species in the country. (Vaughan 1966, Findley et al. 1972). *Eumops perotis* and *E. underwoodi* are found in dry regions at high elevation in the western U.S., Mexico, and Central and South America where they forage in open habitat. They roost in shallow caves and crevices in cliffs and rock walls that provide a substantial vertical drop to enable launch into flight after roosting (Kiser 1995, Best et al. 1996), as well as in cavities in tall plants with minimal foliage to impede the bats' approach (i.e., royal palms (*Roystonea*; Hellebuyck et al. 1985) and saguaro cacti (*Carnegia gigantea*; Tibbitts et al. 2002). Our results indicate that although *E. floridanus* has an aspect ratio index similar to these species, it has a lower wing shape index (the second lowest

among all eight *Eumops* species for which this has been reported), and a lower tip index (the lowest among all species in the genus). Collectively, this suggests *E. floridanus* has shorter or wider wings with shorter wing tips than most other *Eumops*. While *E. floridanus* may not be capable of flight speeds as fast as some of the other species in the genus, it may not need to fly as fast to generate enough lift to remain airborne (Findley et al. 1972). When commuting through open space, *E. floridanus* may incur slightly higher metabolic costs than other species in the genus, but this may be compensated for with lower metabolic costs when maneuvering in more confined air space (Voigt and Holderied 2012). *Eumops floridanus* may encounter more clutter than other species in the genus, roosting in pines (*Pinus palustris* and *P. elliottii*; Angell and Thompson 2016, Braun de Torrez et al. 2016) located in pine flatwoods and scrubby flatwoods, which are more cluttered than the desert areas typically inhabited by *E. perotis* and *E. underwoodi*. Future studies of foraging habitat use and flight speeds of *E. floridanus* are recommended.

Knowledge of the ecology and physiology of *E. floridanus* is extremely limited, yet is critical due to the species designation as federally endangered. The morphological data we report serves as a foundation for our understanding of sexual dimorphism, body condition, and flight capabilities of *E. floridanus*. We found that these bats exhibit moderate sexual dimorphism in wing size, suggesting there may be niche partitioning between sexes. Thus, we may need to consider the foraging habitat use of males and females independently. The baseline body condition and mass we report can be used in future studies to examine associations between individual variation in physiological condition and environmental conditions, habitat use, and movements.

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