

Original Study

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Natural history of the fishing bat *Noctilio leporinus* (Chiroptera: Noctilionidae) in the Gulf of Mexico

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Abstract: We report feeding behaviour, dates of peak reproduction, and sexual size dimorphism of the fishing bat, *Noctilio leporinus*, in the Gulf of Mexico. For the first time we document the size of cheek pouches in *N. leporinus* and fish species consumed in the water bodies of southern Mexico and analyse differences in wing morphology and biomechanical flight descriptors between the sexes. We found sexual dimorphism in size for most of the external measurements but not in wing characters. This species can consume prey up to a third of its size. We confirmed the presence of *N. leporinus* in localities in Tabasco, Mexico 60 years after the first report.

Keywords: feeding behaviour; fishing bats; piscivory; sexual dimorphism; wing morphology.

1 Introduction

The fishing bat *Noctilio leporinus* Linnaeus, 1758 (Chiroptera: Noctilionidae) is distributed in America and the Caribbean, occurring from Mexico through Central America to northern Argentina (Hood and Jones 1984). This species is restricted to

low and middle elevations (0–1100 m a.s.l.), and is mainly found in humid coastal areas and, in South America, in large river basins (Hood and Jones 1984). The subspecies with the largest distribution is *N. l. mastivus* Vahl 1797, which is found from Central America and the Antilles to northern Argentina (Davis 1973). In Mexico, it is found in mangrove and riparian forests, along the Pacific coast (from Sonora to Chiapas) and the coast of the Gulf of Mexico (from Veracruz to the Yucatán Peninsula; Ospina-Garcés and León-Paniagua 2021).

N. leporinus presents a trawling foraging strategy, hunting prey over bodies of water by dragging its feet through the water. The fishing bat uses short-CF/FM echolocation pulses that detects water surface disturbances such as ripples or exposed fish fins (Wenstrup and Suthers 1984). It has external adaptations to piscivory, such as greatly elongated feet, large and laterally compressed claws, and cheek pouches used to store food while foraging (Altenbach 1989; Hood and Jones 1984; Kalko et al. 1998; Schnitzler et al. 1994). Morphological traits of the feet and claws have been related to trawling behaviour to capture prey, especially fish, over water (Aizpurua and Alberdi 2018), while cheek pouches may allow bats to fish continuously at their feeding sites (Hood and Jones 1984). In this species, wing morphology and flight descriptors have been also related to the trawling strategy. For example, Norberg and Rayner (1987) mentioned the high aspect ratio of *N. leporinus* as the most striking flight adaptation. This aspect ratio generates low wing loading and relatively long, pointed wings that allow slow and manoeuvrable flight, and it may also minimise energy consumption and the cost of transport while it forages above the water's surface.

This species feeds mainly on fishes and crustaceans, but sex differences in dietary preferences and foraging patterns have been documented. Males exhibit a wider diversity of prey sizes than females, and females consume more insects during lactation (Bordignon 2006). It has a polygynous social organization, where discrete and stable groups of females cluster together with a single male during reproductive seasons (Brooke 1997). Males forage alone in larger areas and away from roosting sites, while females

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and younger bachelor males forage together (Brooke 1997). Marked sexual dimorphism has been found in cranial morphology and external measurements in *N. leporinus*, with males larger than females (Davis 1973; Hood and Jones 1984; Ospina-Garcés and León-Paniagua 2021).

In addition to the morphological differences between the sexes, geographic variation among populations has been documented. In Mexico, body size differences between individuals from the west and east coast are subtle (Goldman 1915), and substantial differences in cranial morphology between these two populations have been recently reported (Ospina-Garcés and León-Paniagua 2021, Supplementary Figure S1). In the Gulf of Mexico (eastern populations), *N. leporinus* has been recorded in coastal and riparian ecosystems from Quintana Roo to Campeche in the last 20 years (GBIF.org 2020). However, there have been no record from Tabasco or Veracruz since the 1960's. The most recent specimens from these states were recorded in 1962 in Tabasco (Teapa, Río Puyacatengo) and in 1964 in Veracruz (2 km E Catemaco), the corresponding specimens are housed at the Colección Nacional de Mamíferos of Universidad Nacional Autónoma de México (available at: <http://datosabiertos.unam.mx/>). Here, we document differences in size of external measurements between the sexes of *N. leporinus* from populations of the Gulf of Mexico and report its biomechanical flight descriptors and feeding behaviour.

2 Materials and methods

2.1 Field work

Individuals of *N. leporinus* were sampled in four localities along the Gulf of Mexico, including mangrove forests within the Los Petenes Biosphere Reserve, Campeche (Ich Ha Lool Xaan, municipality of Hampolol: 19.943N-90.375E; El Remate, municipality of Tankuché: 20.507N-90.384E), and riparian vegetation along the Puyacatengo and Oxolotán Rivers in Tabasco (Balneario Las Garzas, municipality of Teapa: 17.553N-92.929E, and Arroyo Grande, municipality of Tapijulapa: 17.367N-92.717E, respectively; Supplementary Figure S1). Field-work was carried out in December 2020 in Campeche, and May 2021 in Tabasco; with a total sampling of five and six days, respectively. We sampled bats using monofilament mist nets (3 × 6 × 12 m) placed along the surface of streams and lakes in the mangrove forests (Petenes) and within the riparian vegetation. Mist nets were opened for 4 h after sunset; all bats captured were released at the sampling site within 6 h of capture. Captured individuals were identified using the description of the species (Davis 1973) and the field guide of Reid (2009). We recorded the time of capture, sex, age category, reproductive condition, and external measurements. 10 individuals were marked in El Remate and nine individuals were marked in Ich Ha Lool xaan, Campeche with metal forearm rings (Lambournes B'ham Ltd).

Additionally, three females and three males were fed *in situ* at El Remate, Campeche, and two females in Teapa, Tabasco, with fish obtained from local streams at the same site as *N. leporinus* captures, and identified using taxonomic guides (Angulo et al. 2021; Gallardo-Torres and Badillo-Alemán 2016).

2.2 Morphometric variables

To evaluate body size differences between the sexes, six external measurements were taken using a digital caliper (Mitutoyo CD-6" Mitutoyo U.S.A): Total length (TL), Tail length (T), Tibial length (Tib), Ear length (E), Forearm length (FA), and Hind Foot length (HF). Body mass (Wt) was measured using a Pesola spring balance (100 g ± 0.5) and was used to calculate biomechanical flight descriptors.

We also obtained photographs of the right wings of adult individuals of *N. leporinus* to evaluate sex differences in wing morphology and flight capacity. We took the images with a Nikon D5600 camera (Nikon, Inc.) and saved them in TIF format with 300 dpi resolution. We obtained a total of 26 photographs (15 females and 11 males). We measured wingspan (WS) and wing area (WA) from individual scaled photographs (Figure 1a), using Image J software (Schneider et al. 2012). We used these measurements to calculate the wing aspect ratio (AR) and relative wing loading (WL), two biomechanical variables that have been widely used to characterise foraging strategies and dispersion patterns (Luo et al. 2019; Norberg and Rayner 1987; Tholleson and Norberg 1991). The calculations were performed following Norberg and Rayner (1987): $AR = WS (m)^2/WA (m^2)$, $WL = Wt (N)/WA (m^2)$.

We also used the images to quantify variance in wing shape and size using a 2-dimensional (2D) geometric morphometrics protocol. For this, we designed a 2D configuration of 10 landmarks to describe individual wing configurations. We defined landmarks based on anatomical characters visible in all the specimens, such as the fusion of the phalanges of the wing bones and the wing tip (Figure 1b). Configurations of landmarks were digitized in the program TpsDig 2.32 (Rohlf 2018).

We performed a Procrustes superimposition of configurations to eliminate the effect of scale, position and rotation of all configurations. Prior to superimposition, we obtained the size descriptor "Centroid Size" (CS) for each configuration (Zelditch et al. 2012). From these procedures, we obtained aligned configurations and CS that were used in statistical comparisons of wing shape and size using the package geomorph 3.3.2 (Adams et al. 2021).

2.3 Statistical analyses

To test for sex differences in external measurements, biomechanical variables (AR, WL and wing area) and body weight, we performed Analysis of Variance (ANOVA). We excluded the single specimen from Arroyo Grande, Tabasco from the statistical analyses for the absence of variance. We tested the normality of model residuals using the Shapiro-Wilks test. All analyses were done in R 4.3.1 (R Core Team 2022).

We analysed wing shape and size variance in relation to sex. First, we explored the morphospace of wing configurations among sexes and sites using a Principal Component Analysis (PCA) (Zelditch et al. 2012). Then, to evaluate sexual dimorphism in wing shape we used a Procrustes ANOVA model to test the effects of CS, sex and the interaction between CS and sex. We performed a permutation procedure on the residuals of this model, with 1000 replicates, to assign the significance

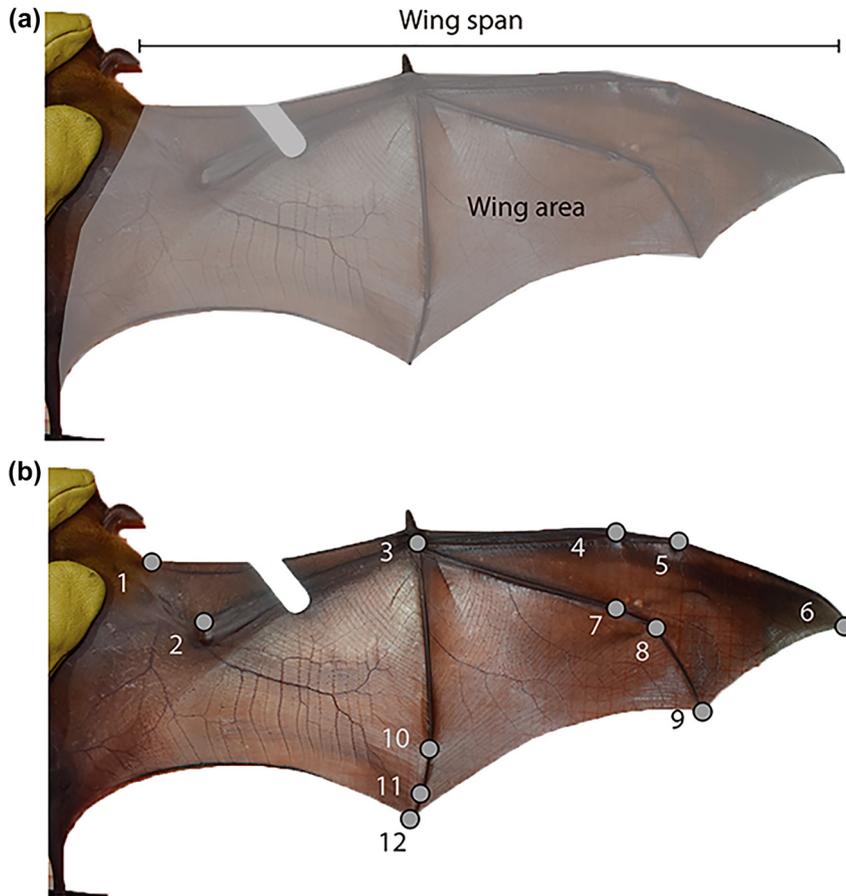


Figure 1: Wing images indicating morphometric data analyzed. (a) Wing photograph of *N. leporinus* illustrating variables (wingspan and wing areas) used to estimate aspect ratio and wing loading. (b) Landmark configuration used to describe wing shape variation between sexes in *N. leporinus*.

of the F statistic to each variable and factor included in the model, using the package RRPP 1.02 (Collyer and Adams 2018, 2020). Finally, we evaluated differences in wing CS between sexes using an ordinary linear model, and used permutations of the residuals as previously described to assign the significance of the estimated statistic.

3 Results

3.1 Feeding behaviour and reproductive activity

We captured a total of 30 individuals (Table 1) and identified the reproductive activity of all of them. In Tabasco, we captured three lactating and two postlactating females, and one male with scrotal testicles, in late May and early June at Las Garzas, Teapa; one lactating female was captured in Arroyo Grande, Tapijulapa, in early June. In Campeche, we captured two lactating and three postlactating females, and one male showing sub-axial secretions (Figure 2a), during December at El Remate, Campeche. There were no signs of

Table 1: Number of individuals of *N. leporinus* captured per site in the Gulf of Mexico.

Site	Sample	
	Females	Males
Ich Ha Lool Xaan, Campeche	4	5
El Remate, Campeche	5	9
Las Garzas, Tabasco	5	1
Arroyo Grande, Tabasco	0	1
Total	14	16

reproductive activity in the individuals from Ich Ha Lool xaan, Campeche.

We observed the same feeding behaviour in all the captured individuals when presented with potential prey (recently captured fishes, Figure 2c). The fishes were rapidly grasped with the incisors and canine teeth and transferred immediately to the mouth where it was partially masticated using the molars, then stored in cheek pouches on both sides, before being masticated a second



Figure 2: Photographs describing body secretions, prey consumption and dietary preferences of *N. leporinus*. (a) Male *N. leporinus* from El Remate, Campeche, showing sub-axial secretions. (b) Female *N. leporinus* eating a fish (*A. altior*). (c) Fish consumed by *N. leporinus* in Campeche, from top to bottom: *Belonesox belizanus*, *Mayaheros urophthalmum* and *A. altior*. (d) Male *N. leporinus* filling its cheek pouches during fish consumption. (e) Individual of the fish *R. guatemalensis* carried by a female in Arroyo Grande, Tabasco.

time and then swallowed. The first male consumed 8 g of the Yucatan tetra *Astyanax altior* (Caracidae), with a total weight of 17 g (Figure 2b), that was carried by the bat. The same individual was recaptured the second night of sampling and consumed 7.5 g of fish. In general, males consumed 12.87 ± 3.56 g (average \pm standard deviation) of fish, filling their cheek pouches to a maximum diameter of 12.23 ± 1.27 mm (left side) and 14.25 ± 0.76 mm (right side), before discarding the remnants of the prey. Females consumed a similar quantity of fish (10.75 ± 3.5 g) and showed similar diameters of cheek pouches (left side: 13.43 ± 0.67 mm, right side: 11.68 ± 1.02 mm).

Both males and females were able to consume large fishes (Figure 2d and e). The female fed at Teapa consumed three fishes from the family Characidae, and the female from Arroyo Grande (81 g), was captured carrying an individual of the Pale catfish, *Rhamdia guatemalensis* (Heptateridae) that

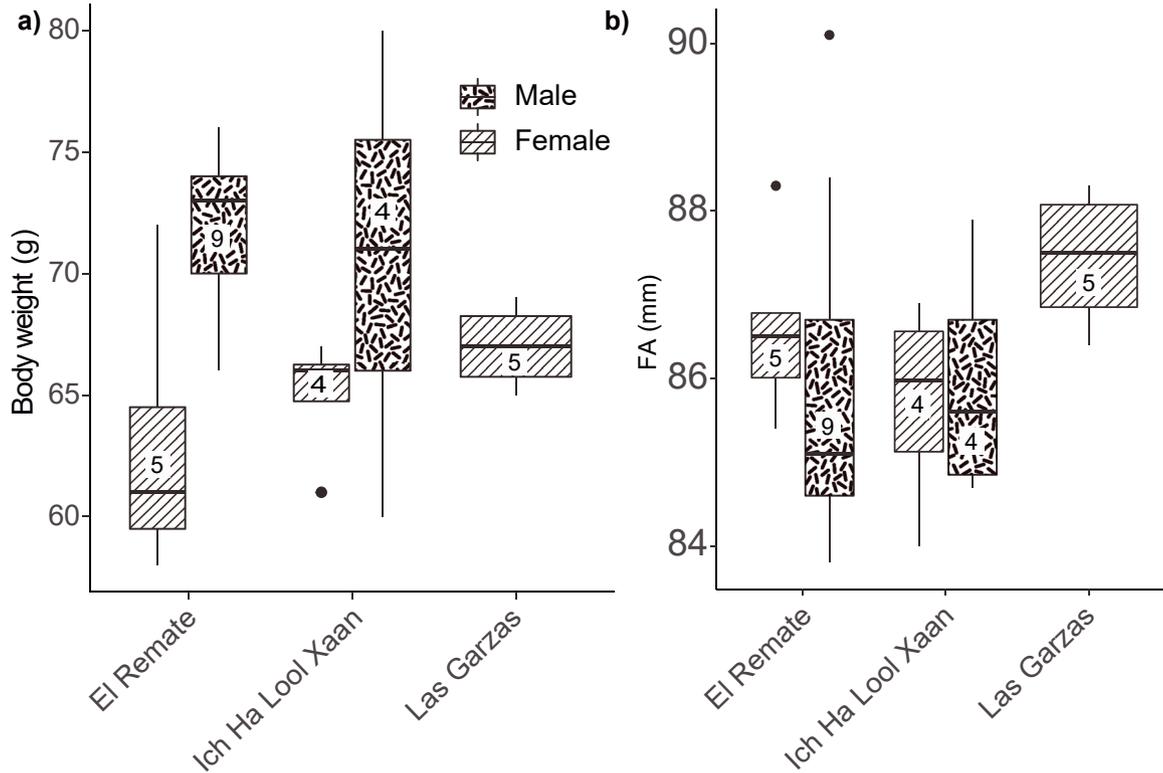
measured 19 cm in length and weighed 59 g (Aguilar-Rodriguez pers. obs).

3.2 Morphometric differences between the sexes

The results of the ANOVA models indicated significant differences between sexes in TL, Tib and T ($F_{1,26} > 5.70$, $P < 0.04$), and in body weight ($F_{1,26} = 14.28$, $P < 0.01$). In opposite, no significant differences were observed in FA ($F_{1,26} = 0.55$, $P = 0.46$), HF ($F_{1,26} = 0.11$, $P = 0.75$) or E ($F_{1,26} = 2.83$, $P = 0.10$), averages and standard deviations are presented in Table 2. Males were larger than females in most of the dimorphic variables (Figure 3a). However, FA was slightly larger in females than in males (Figure 3b). In the case of the biomechanical variables, we did not find significant differences

Table 2: Mean \pm SD of morphometric variables of each sex of *N. leporinus* individuals captured.

Sex	Total length (mm)	Tail length (mm)	Tibial length (mm)	Ear length (mm)	Forearm (mm)	Foot length (mm)	Body mass (g)	Aspect ratio	Wing loading (N/m ²)
Males	88.02 \pm 4.26	26.96 \pm 3.24	42.37 \pm 1.44	19.14 \pm 2.49	85.97 \pm 1.88	34.78 \pm 3.17	71.89 \pm 5.03	6.99 \pm 0.71	19.30 \pm 2.42
Females	84.14 \pm 2.44	24.64 \pm 1.68	41.24 \pm 0.95	17.84 \pm 1.47	86.51 \pm 1.20	35.14 \pm 2.93	65.43 \pm 3.96	6.96 \pm 1.086	17.56 \pm 3.20

**Figure 3:** Boxplot showing a. body mass and b. forearm length (FA) of *N. leporinus* between sexes and sites. Boxes show the median with upper and lower quartiles, and the number within the box indicates the number of individuals measured.

between the sexes in any of the variables considered ($F_{1,24} < 2.27$, $P > 0.14$), except for Wt, which was higher in males than females (Table 2 and Figure 4). The residuals of all the models presented a normal distribution ($W > 0.93$, $P > 0.06$).

3.3 Wing shape and size

The wing morphospace showed greater variance in females than males, however there was strong overlap in shape between sexes and sites (Figure 5). There was no significant effect of sex on CS ($F_{1,25} = 1.73$, $P = 0.203$). Deformation grids derived from the first PC illustrate changes in the position of the forearm with respect to the body (landmarks 1 and 2). The Procrustes ANOVA model for

shape indicated no significant effect of wing CS ($F_{1,25} = 1.92$, $P = 0.096$), sex ($F_{1,25} = 2.09$, $P = 0.092$) or the interaction between sex and CS ($F_{1,25} = 1.37$, $P = 0.205$) on shape variance. Thus, our results suggest that there is no sexual dimorphism in wing shape or size.

4 Discussion

4.1 Reproductive activity and feeding behaviour

The breeding season for *N. leporinus* has been reported from November to December, followed by five months of gestation during the winter and early spring, and births from late

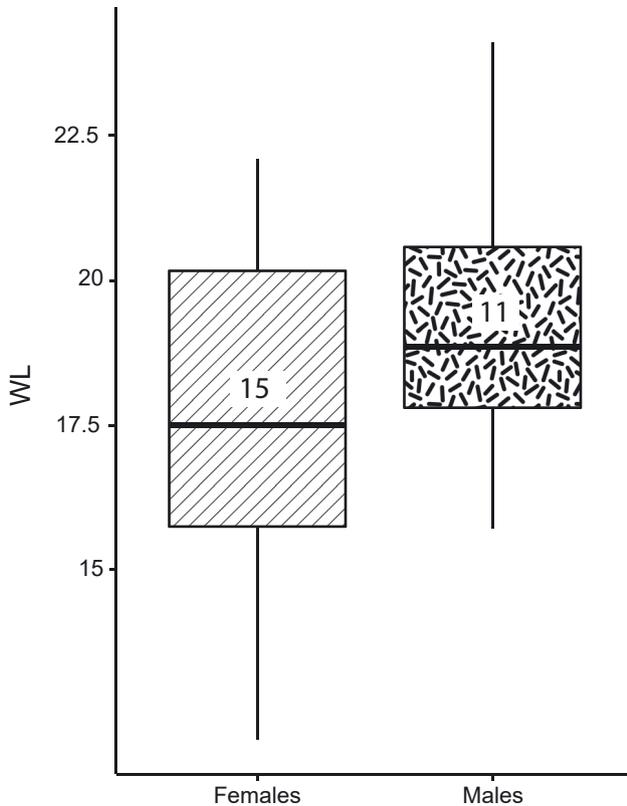


Figure 4: Boxplot comparing wing loading values (WL) between sexes in sampled individuals of *N. leporinus*. Boxes show the median with upper and lower quartiles, and the number of individuals is indicated by the number within the box.

April to July (Bordignon and Oliveira França 2012; Brooke 1997; Hood and Jones 1984). A secondary reproductive peak has been suggested during the summer, from June to September, followed by parturition from October to December (Carter 1970; Carter et al. 1966; Davis et al. 1964). The presence of lactating females in Tabasco in December is consistent with previously recorded data of one pregnant and three lactating females between May and June 2017 in Campeche (C. MacSwiney pers. obs.), and with the proposed parturition between late April and July (Hood and Jones 1984). Moreover, the presence of one male with scrotal testes in May from Tabasco, a previous finding of a male with scrotal testes in March 2017 from Campeche (C. MacSwiney pers. obs.), and lactating females in Campeche during December, support the idea of a second reproductive peak soon after parturition, resulting in pregnancies during the summer and birthing in winter (Carter 1970; Hood and Jones 1984). Additionally, we confirmed the presence of this species in Tabasco, 60 years after it was last reported there.

During the first reproductive peak we identified additional signs of mating. We captured one male showing sub-axial secretions in Campeche. Individuals presenting sub-axial secretions have been observed during reproductive seasons in individuals of both sexes from Puerto Rico (Brooke 1997). These secretions have been related to the recognition between females from the same group (Brooke 1997), and as marking of foraging territories and roosting

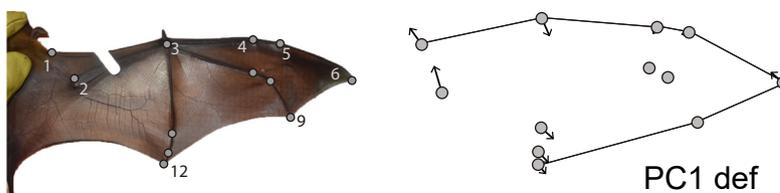
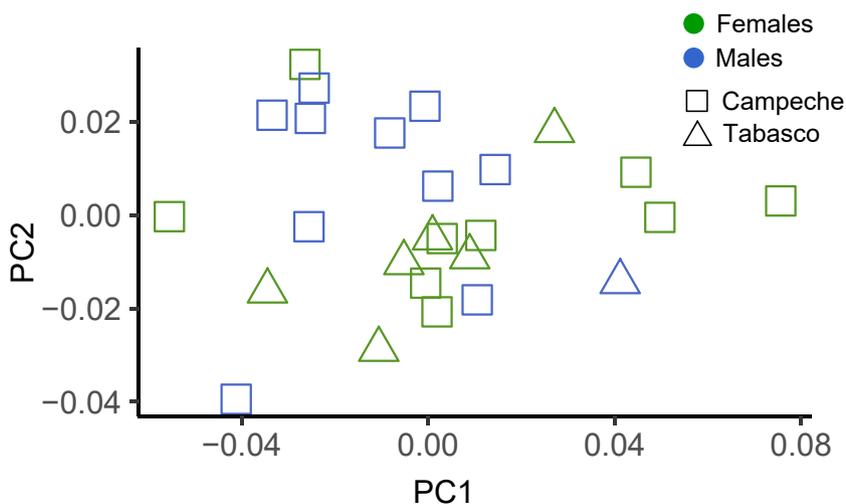


Figure 5: Morphospace of the first two principal components of wing shape in *N. leporinus*. Wing configuration of landmarks and deformations grids derived from minimum (grey dots) to maximum (arrows) PC1 score are illustrated.

sites among males, due to it being more noticeable and with stronger odour in adult males (Brooke and Decker 1996).

We recaptured three males during the second night and one male during the third night of sampling at El Remate, Campeche. Recaptures support the previously proposed stability of foraging groups and their fidelity to feeding sites, as well as the small home range size reported in *N. leporinus* (<5 km², Brooke 1997). This small home range could also be related to the alternation of dietary items between fish and insects throughout the year in aquatic ecosystems (Zortéa and Aguiar 2001), that allows bats to find food without the need to move to farther foraging sites.

In both reproductive seasons, we observed individuals preying on fish. Fishing behaviour has evolved multiple times in bats, though *N. leporinus* consumes more fish than other “fishing bat” species, with fish constituting up to 90% of its diet (Bordignon 2006; Hooper and Brown 1968). Feeding behaviour was similar between the sexes, as observed previously by Hood and Jones (1984) and Norberg and Fenton (1998), and males and females had similar cheek pouch size during fish consumption. Cheek pouches in *N. leporinus* are formed from posterolateral expansions of the buccinator muscle, which forms a sac-like expansion over the buccal side of the mandible, occupying up to 1/3 of the mandible length (Murray and Strickler 1975). These pouches could help store food while flying, while allowing the airway to remain clear during echolocation (Murray and Strickler 1975).

Meanwhile, a prolonged period of time to masticate prey remnants more finely is reported in some fishing bats (Altenbach 1989; Bloedel 1955), and might be important to prevent internal wounds caused by the consumption of bones or other hard parts (Aizpurua and Alberdi 2018), or to improve nutrient assimilation. In this sense, longer retention times theoretically improve digestion efficiency (Sibly 1981). However, bats have reduced intestines (as an adaptation to flight; Bishop 2008; Price et al. 2015), and larger bats (>20 g) may assimilate less food by enzymatic action than smaller species (at least for Vespertilionidae; Cabrera-Campos et al. 2021). Thus, chewing the food into fine pieces (in addition to other mechanisms; Caviedes-Vidal et al. 2007; Price et al. 2014) could improve digestive efficiency, metabolic activity, and therefore nutrient absorption, while reducing digestion time, which could reduce overall daily food demand (Clauss and Hummel 2005; Clauss et al. 2009; Viot et al. 2017). This hypothesis may help to explain also the short foraging time recorded for this species (1.2–2.30 h; Brooke 1997).

Although males consumed a larger amount of food than females, a larger sample size is required to statistically test differences between the sexes in total food consumption and size of individual prey items. In general, individuals fed *in situ* consumed about 16% of their weight. However, one female captured in Arroyo Grande was carrying a fish weighing more than half her own weight, suggesting that *N. leporinus* might be able to consume a greater amount of prey by night than previously considered (Aguilar-Rodríguez, pers. obs). This finding suggests that the fishing bat *N. l. mastivus* could consume prey half its body weight (ranging from 65 to 72 g). Additionally, opportunistic carnivory has been recently documented in populations of *N. l. mastivus* from Puerto Rico (Rodríguez-Durán and Rosas 2020), where this subspecies preys on young individuals of *Brachyphylla cavernarum*, a phyllostomid bat species whose body weight ranges from 34.4 to 49.2 g and length ranges from 80 to 98 mm (Swanepoel and Genoways 1983) and other smaller bat species (*Molossus molossus* and *Pteronotus quadridens*, Rodríguez-Durán and Rosas 2020). Large carnivorous bats can depredate animals almost as heavy as themselves (Santana and Cheung 2016; Vehrencamp et al. 1977), even larger than predicted by their size (Gual-Suárez and Medellín 2021). With its relatively large body mass, *N. leporinus* has considerable carrying capability (Norberg and Fenton 1998) and thus can hunt large prey.

4.2 Sexual dimorphism

In accordance with the sexual dimorphism previously documented for this species (Brooke 1997; Davis 1973; Hood and Jones 1984; Ospina-Garcés and León-Paniagua 2021), males were larger than females in most of the morphometric variables and body mass (Figure 3a). However, forearms of females are slightly larger than males, with the largest forearm length recorded at Las Garzas in Tabasco (Figure 3b). Sexual dimorphism in body size has been related to mating access by males in species presenting highly polygynous mating systems, such as the case of *N. leporinus* (McCracken and Wilkinson 2000). Additionally, morphological differences in cranial size and morphological characters related to masticatory muscle volume (greater in males than females) could be related to functional differences in masticatory performance (Ospina-Garcés and León-Paniagua 2021). The expression of sexual dimorphism in this species seems to reflect different aspects of its natural history, including polygynous organization and sex differences in dietary and foraging behaviour.

Wing shape and biomechanical flight descriptors do not support sexual dimorphism in flight capacity, but size differences could have an influence on prey capture. In both sexes, wing morphology generally concords with the characteristics previously described in this trawling species (Norberg and Rayner 1987), such as long, pointed wings. However, our calculations of aspect ratio (6.9) and wing loading (males: 19.5, females: 17.2) differed from previously reported values (9 and 15.2, respectively) due to the wing area estimation method since we could not include the uropatagium in our calculations.

Our results did not show significant differences between the sexes in wing loading, but males had a higher average value than females because of larger body size. Consequently, males may carry more weight than females per unit area. This observation agrees with previous studies documenting smaller prey size and higher insect consumption in females than males (Bordignon 2006). Additionally, it has been documented that males forage at greater distances than females (Brooke 1997). This could also be due to the fact that females forage while carrying pups while males do not. Therefore, males could carry prey over greater distances than females. The results presented here provide new information about the diet preferences and the expression of sexual dimorphism in external characteristics relevant to foraging strategies of *N. leporinus* populations in the Gulf of Mexico.

Research ethics: The authors used a collecting permit (SGPA/DGVS/003071/18) issued by the Secretaría del Medio Ambiente y Recursos Naturales.

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Author contributions: SMOG and MCMG designed this study; SMOG, LLP, MCMG, PAAR collected the data; SMOG performed the analysis and wrote the first draft of the manuscript. All authors have read, contributed, edited, and agreed to the final draft of the manuscript.

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Conflict of interest statement: The authors declare that they have no conflicts of interest regarding this article.

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