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*Journal of Mammalogy*, Vol. 74, No. 3. (Aug., 1993), pp. 594-600.

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*Journal of Mammalogy* is currently published by American Society of Mammalogists.

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# FLIGHT SPEEDS AND MECHANICAL POWER OUTPUTS OF THE NECTAR-FEEDING BAT, *LEPTONYCTERIS CURASOAE* (PHYLLOSTOMIDAE: GLOSSOPHAGINAE)

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**We measured flight speeds of the nectar-feeding bat, *Leptonycteris curasoae*, during their nightly commuting flights of 25–30 km. We estimated mechanical power outputs for the flights by using an aerodynamic model and tested predicted flight speeds generated by the model against actual flight speeds observed. Bats flew an average of 27.2 km during one-way commutes to their foraging areas at a mean air speed of 8.2 m/s. Flight speeds observed in bats making commuting flights conformed to predictions generated by aerodynamic theory, and were similar to those previously reported for birds. We suggest that certain morphological attributes exhibited by *L. curasoae*, such as a relatively large body size and high wing loading, may be adaptations for flying long distances in desert habitats.**

**Key words:** *Leptonycteris curasoae*, flight, foraging, wings, morphology

Information regarding flight strategies of bats is crucial for understanding many aspects of their ecology, behavior, and energetics. Due to their nocturnal habits, bats are notoriously difficult to observe; consequently, data on flight speeds, daily flight distances, energetic costs of flight, and their relationship to wing morphology are lacking for most species. Norberg (1987) summarized recorded flight speeds of bats, but cautioned that for many of the flights the intent of the bat was unknown, varied across trials, or occurred in artificial environments. Thomas (1975) and Carpenter (1985, 1986) provided information on energetic expenditure of bats flying at various speeds in wind tunnels; however, all of the bats used in their studies were relatively large (body masses ranging 0.1–1 kg), and extrapolation of their results to smaller species is difficult. Smith and Starrett (1979) and Findley et al. (1972) reviewed wing morphology of several families of bats, while Norberg and Rayner (1987) analyzed wing morphology from an aerodynamic perspective to inte-

grate aspects of both wing morphology and flight modes in bats. Few studies, however, have investigated relationships between morphology, energetic costs of flight, and actual behavior of bats in nature. Jones and Rayner (1989) and Baagøe (1987) provide estimates of flight speeds of bats in nature under specified conditions, but flight speeds previously have not been obtained for bats engaging in long-distance commuting flights.

Pennycuik (1975, 1989) developed an aerodynamic model of avian flight that can be used to estimate mechanical output of flight muscles and flight speeds by using easily obtained values for morphological variables such as wingspan and body mass. This model yields a U-shaped power curve when the components of power required for flight are added together and plotted as a function of speed. Two points on the curve are of particular interest; the point at which the power required to fly is lowest ( $P_{min}$ ), and the point where the ratio of power to speed is lowest (maximum range power, or  $P_{mr}$ ). Flying at minimum power velocity ( $V_{mp}$ ),

an animal will minimize its energy consumption per unit time, whereas flying at maximum range velocity ( $V_{mr}$ ), an animal will minimize energy consumption per unit distance. At  $V_{mrs}$  cost of transport (defined as  $P/Vmg$ , where  $P$  = power,  $V$  = velocity,  $m$  = mass, and  $g$  = acceleration due to gravity) is minimal and is the velocity at which a bird or bat would be predicted to fly during long foraging or migrating flights to minimize the cost of transport.

Physiological measurements of birds flying in wind tunnels have yielded estimates of energy consumption that agree closely with predictions generated by the model (Tucker, 1975), and measurements of flight speed of cruising birds generally fall between  $V_{mp}$  and  $V_{mr}$  (Pennycuick, 1987; Schnell and Hellack, 1979). The only previous estimates of prolonged flight in bats (measured in a wind tunnel) indicate that bats are unable to maintain prolonged flight at speeds above  $V_{mp}$  (Carpenter, 1985). If true for bats under natural conditions, this finding would have significant implications for the many species of bats that are known to commute long distances or are migratory. In addition, these findings would suggest that bats and birds differ significantly in their flight capabilities. However, no information on actual flight speeds during prolonged flight in free-ranging bats presently is available.

Here we present data on wing morphology, flight speeds, flight distances, and estimates of mechanical-power output during commuting flights in the nectar-feeding bat, *Leptonycteris curasoae* (Phyllostomidae: Glossophaginae). Morphological data were used to predict flight speeds during commuting flights and to estimate power outputs by using the aerodynamic model developed by Pennycuick (1975, 1989). Predictions of the model were tested in the field by radiotracking bats as they flew from day roosts ca. 25 km to their foraging areas. Because their flight paths were over water, we could safely assume that the bats were not searching for food while flying.

## MATERIALS AND METHODS

*Leptonycteris curasoae* is a flower-visiting bat that migrates from central and southern Mexico to the southwestern United States during late spring and early summer (Cockrum and Petryszyn, 1991). Bats that we radiotracked roosted during the day on Isla Tiburon, located 20–30 km from foraging areas on the mainland, and commuted nightly to the mainland to forage.

The study site was located at Bahia Kino, Sonora, Mexico (29°N, 110°W) along the Gulf of California. At this site, bats feed at flowers and fruits of three species of columnar cacti; *Pachycereus pringlei* (cardon), *Carnegie gigantea* (saguaro), and *Stenocereus thurberi* (organ pipe).

Morphological measurements including body mass ( $m$ ), wing span ( $b$ ), wing area ( $S$ ), and body frontal area were obtained for 27 live bats. Wing span and wing areas were measured by using methods described in Norberg and Rayner (1987). Body frontal areas were determined by measuring the width and depth of the widest point of the chest of each bat and calculating the area of the ellipse generated from these measurements. Radiotransmitters weighing ca. 1.4 g (including adhesive) were affixed to five females that were used in this study. We radiotracked the bats as they left their day roost, using triangulation to improve accuracy (M. A. Horner, T. H. Fleming, and M. D. Tuttle, in litt.). Wind speed and direction were recorded from the mainland using a hand-held anemometer at the time each bat left its roost and began its commute to the mainland. Ground speed was determined by recording the time required to arrive at the foraging site and dividing by the distance traveled. Air speed was determined using the triangle of velocities (Blackburn, 1944) and the law of cosines, as follows:

$$V_a = \sqrt{V_g^2 + V_w^2 - 2V_gV_w\cos\theta} \quad (1)$$

where  $V_a$  is air speed,  $V_g$  ground speed,  $V_w$  wind speed, and  $\theta$  is the angle between the wind direction and the direction the bat was flying.

Mechanical power outputs and flight speeds during forward flight were estimated by using Pennycuick's (1989) program 1; this program includes basal-metabolic rate and power requirements for respiration and circulation in calculation of mechanical power. We entered the following variables into the program: wing span; body mass; body frontal area; metabolic rate (estimate from McNab, 1989).

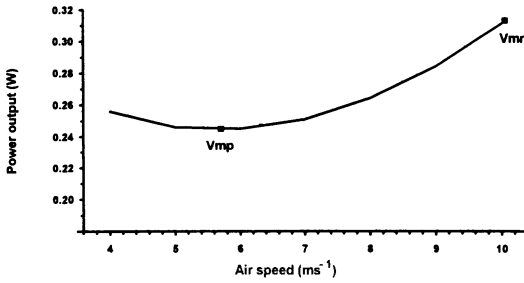


FIG. 1.—Estimated mechanical-power outputs as a function of speed for an adult female *Leptonycteris curasoae* with average morphological measurements and an attached radiotransmitter. Mechanical-power outputs were calculated using Pennycuik's (1989) program 1.  $V_{mp}$ , the minimum power velocity, and  $V_{mr}$ , the maximum range velocity as estimated by the program, are indicated on the graph.

## RESULTS

Average morphological measurements obtained for 24 adult, non-reproductive, female *L. curasoae* are as follows: mass, 0.023 kg ( $SD = 0.001$ ); wingspan, 0.34 m ( $SD = 0.01$ ); wing area, 0.0175 m<sup>2</sup> ( $SD = 0.001$ ); wing loading, 12.8 N m<sup>-2</sup> ( $SD = 1.8$ ); aspect ratio, 6.61 ( $SD = 0.45$ ); frontal area of body, 0.000418 m<sup>2</sup> ( $SD = 0.00009$ ).

Mean flight time for a one-way commute from Isla Tiburon to the mainland foraging areas was 54.3 min ( $n = 17$ ,  $SD = 12.7$ ), and the average distance flown was 27.2 km ( $n = 17$ ,  $SD = 3.4$ ). Mean air speed during commuting flight was 8.2 m/s ( $n = 17$ ,  $SD = 1.4$ ) while mean ground speed was 8.7 m/s ( $n = 17$ ,  $SD = 1.3$ ). Minimum air speed recorded was 5.7 m/s, and the maximum was 10.3 m/s. Recall that ground speed is the velocity that the bat flies with respect to the ground, while air speed is the velocity the bat flies with respect to the wind. Thus, ground speed is a measure of time taken to fly a certain distance, while air speed can be used to estimate the actual power output during flight. Distributions for ground and airspeeds, however, did not differ significantly (Kolmogorov-Smirnov test,  $P = 0.930$ ; Fig. 2). A power curve generated for an average, non-reproductive adult female

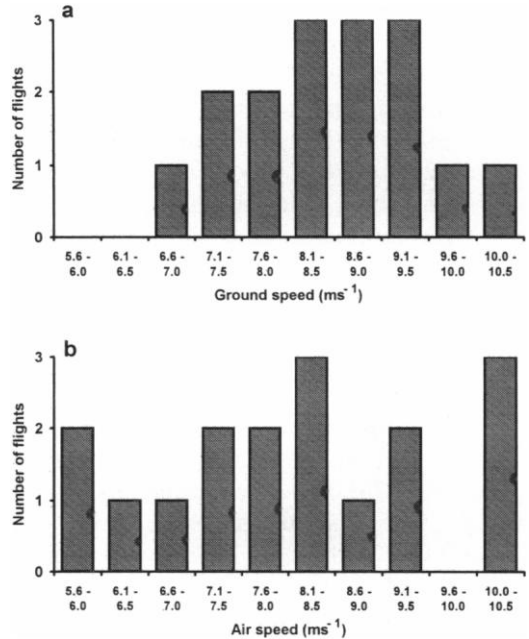


FIG. 2.—a) Frequency distribution depicting actual ground speeds during nightly commutes in five radiotracked *Leptonycteris curasoae*. b) Frequency distribution depicting actual air speeds in five radiotracked *L. curasoae*.

bat and a payload of 0.0014 kg (mass of the radiotransmitter) results in a predicted minimum power velocity of 5.7 m/s and a maximum range velocity of 10.2 m/s (Fig. 1). Comparing the air-speed distributions with these theoretical predictions, almost all flights speeds fall between  $V_{mp}$  and  $V_{mr}$ , which is predicted for cruising flight (Fig. 2b). No bats flew at speeds less than  $V_{mp}$ , while one flight was slightly above  $V_{mr}$ .

Power curves also were generated for females at different reproductive stages. Near-term pregnant females are ca. 0.0085 kg heavier than non-reproductive adults. This mass difference results in an estimated 40% increase in mechanical power required for forward flight during late pregnancy (Table 1). The additional mass of the transmitter on non-reproductive females results in a slight increase in predicted flight speeds and a 6% increase in power required for forward flight.

## DISCUSSION

*Flight speeds.*—Average flight speeds for long-distance commuting flight in *L. curasoae* fell within the range of speeds predicted by Pennycuick's (1975, 1989) aerodynamic theory for cruising flight. Recorded speeds are higher than previously reported for *L. nivalis*, for which a maximum speed of 6.17 m/s was reported (Hayward and Davis, 1964). Most flights we recorded were at speeds between  $V_{mp}$  and  $V_{mr}$ , although one was slightly above  $V_{mr}$ . The observed flight speed pattern (Fig. 2b) is similar to that found in studies of bird flight (Pennycuick, 1987; Schaffner, 1988; Schnell and Hellack, 1979). Jones and Rayner (1989) found that pipistrelles (*Pipistrellus pipistrellus*) flew faster than  $V_{mr}$  when commuting, although they did not specify over what distances bats flew at such speeds. There are no comparable estimates of flight speeds for long-distance commutes of free-flying bats. Carpenter (1985, 1986) investigated effects of flight speed on endurance in four species of pteropodid bats flying in a wind tunnel and found that bats exhibited marked reductions in endurance at speeds above  $V_{mp}$ . Our results with *L. curasoae* indicate that small bats are able to fly long distances at speeds close to or even exceeding  $V_{mr}$ . Because power required for flight varies with mass<sup>7/6</sup> while that available scales as mass<sup>-1/3</sup> (Pennycuick, 1975), large bats such as those used in Carpenter's study may have a reduced power margin, and may be limited to flying at speeds in the vicinity of  $P_{min}$ . Because many pteropodid bats are known to commute 20–40 km to reach their foraging grounds (Marshall, 1983), determining their flight speeds in nature would be valuable for understanding their flight energetics and foraging strategies.

For *L. curasoae*, flight speeds at  $V_{mr}$  not only reduce the cost of transport over long distances, but also reduce the amount of time needed to reach the foraging area. Norberg (1981) hypothesized that birds with young at a roost (or nest) might select flight

TABLE 1.—Predicted flight speeds and mechanical power outputs for non-reproductive adults ( $n = 24$ ), juveniles (2 months of age,  $n = 3$ ), and full-term pregnant females ( $n = 21$ ) of *Leptonycteris curasoae* individuals.

Size class	Mass (kg)	$V_{mp}$ (m/s)	$V_{mr}$ (m/s)	$P_{min}$ (W)	$P_{mr}$ (W)
Non-reproductive adults	0.023	5.6	9.2	0.230	0.299
Non-reproductive adults with transmitter	0.024	5.7	10.2	0.245	0.317
Full-term pregnant females	0.031	6.4	11.1	0.321	0.410
Juveniles	0.018	4.9	9.2	0.180	0.237

speeds that optimize delivery rate of food to young and would therefore fly faster than  $V_{mr}$ . Since bats generally separate lactating and foraging into diurnal and nocturnal activities respectively, this postulated scenario may not apply to them. To a female bat, the energetic cost of flying long distances and its effect on her ability to produce sufficient milk for her offspring may be more important. Our sample size precludes testing differences in flight strategies between lactating and non-reproductive females of *L. curasoae*.

We did observe significant variation in air speeds, both within and among individuals, as bats flew at speeds that spanned the range from  $V_{mp}$  to  $V_{mr}$ . Owing to their small size, bats probably are not constrained in their choice of flight speeds by available muscle power. If flying at  $V_{mr}$  is advantageous for both energetic and time-related reasons, why didn't all bats fly at  $V_{mr}$ ? Three possibilities could explain our results. First, if the bats were not limited by time or energy, there would be no reason for them to exert themselves by flying at  $V_{mr}$ . Second, it is possible that the bats we radiotracked may have been flying in a flock (Howell, 1979), and flocks may have contained juveniles that flew more slowly. Finally, be-

cause we were 25 km from where the bats began their flights, measured wind conditions may have differed from those experienced by the bats, thus affecting speed calculations.

*Morphology.*—For bats such as *L. curasoae* that migrate and fly relatively long distances between flowering plants, morphological attributes that result in a low cost of transport and relatively high flight speeds would be advantageous. Because an increase in body size reduces the cost of transport (Tucker, 1970), it is not surprising that bats of the genus *Leptonycteris* have the heaviest body mass within the subfamily Glossophaginae. The second and third largest genera of glossophagine bats are *Platalina* and *Choeronycteris*; these bats also live in arid habitats and might have to fly long distances between sparsely distributed desert plants when foraging. Because a high wing loading leads to an increase in flight speeds (Norberg, 1990), this might also be advantageous for bats that need to cover a certain distance in a given amount of time. Our data indicates that *L. curasoae* has a high wing loading relative to other glossophagine bats ( $12.8 \text{ N m}^{-2}$ ; Table 1; Norberg and Rayner, 1987). Although a high wing loading results in a higher power output for forward and hovering flight, the advantage of faster flight during long-distance travel may outweigh this potential disadvantage. Large body size and relatively high wing loadings in nectar-feeding bats might therefore be adaptations for long-distance foraging flights in desert habitats.

*Mass changes and power output.*—Mass increases during pregnancy in female *L. curasoae* result in estimated mechanical-power outputs that are 40% higher than those of non-reproductive females. Several authors (Myers, 1978; Williams and Findley, 1978) have speculated that sexual dimorphism in body size and wing area in certain bats may be a response to the increased energetic demands of flight in pregnant females. Williams and Findley (1978), however, suggested that factors such as

thermoregulation and fat storage might be more important determinants of body size of females than adaptations for flight. Arita and Humphrey (1988) have conducted a detailed morphological analysis of the genus *Leptonycteris* and reported that the only significant sexual dimorphism in *L. curasoae* was the presence of a longer second phalange in males than in females. If this difference translates into greater wing area, then males might have lower wing loadings than females. This finding would not support the hypothesis that sexual differences in wing morphology between the sexes represent adaptations for reducing power output in pregnant females. Since we did not capture any adult males we were unable to make any intersexual comparisons regarding body size or wing morphology in *L. curasoae*. Thus, whether the 40% difference in mechanical-power output between non-reproductive and pregnant individuals has led to selection for greater wing area in females relative to males is unknown. Possibly, sexual differences in flight performance and energetics between male and female bats might be an important factor influencing the migratory strategies of the sexes. Further data on wing-span and wing-area measurements (obtained by methods described in Norberg and Rayner, 1987) for male and female bats would be extremely useful for evaluating hypotheses put forth to explain sexual dimorphism in size of bats.

*Conclusion.*—Our results indicate that *L. curasoae* makes relatively long-distance commuting flights at speeds that are predicted by an aerodynamic model. Patterns observed for bats are similar to those reported for birds. Aspects of the morphology of *L. curasoae*, such as a relatively large body size and high wing loading, may be adaptations for flying long distances in arid habitats. To adequately assess this hypothesis, however, investigation of the foraging strategies and behavior of *L. curasoae* in other parts of its range, analysis of its hovering flight, and comparable data on other species of glossophagine bats are needed.

To completely evaluate the robustness of aerodynamic models and their utility in predicting flight speeds and power outputs, field studies such as the one we conducted should be combined with data obtained on flight speeds and energy consumption in a carefully controlled setting such as a wind tunnel, as has been done with birds. Also, additional data on a variety of bat species encompassing a broad size range and variable wing morphologies are needed. With additional data, aerodynamic models might prove to be a convenient and valuable tool for analyzing flight strategies of bats in the field.

#### ACKNOWLEDGMENTS

S. J. Kirkpatrick, C. J. Pennycuik, and D. Janos reviewed this manuscript and provided valuable discussion, assistance, and comments. M. D. Tuttle of Bat Conservation International, T. May, T. and L. Seckbach-Finn, as well as numerous volunteers working with Bat Conservation International, kindly assisted the authors with the field work and logistics. Funds for this research were provided by a National Geographic Society grant (awarded to T. H. Fleming and M. D. Tuttle), a National Fish and Wildlife Foundation grant (awarded to T. H. Fleming), and a Maytag Graduate Fellowship from the University of Miami (awarded to C. T. Sahley). This is contribution no. 399 from the Program in Tropical Biology, Ecology, and Behavior of the Department of Biology, University of Miami.

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*Submitted 21 April 1992. Accepted 24 September 1992.*

*Associate Editor was Kenneth T. Wilkins.*