

Flight speeds of three species of Neotropical bats: *Glossophaga soricina*, *Natalus stramineus*, and *Carollia subrufa*

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Flight speeds of Pallas's long-tongued bat (*Glossophaga soricina*), the Mexican funnel-eared bat (*Natalus stramineus*), and the gray short-tailed bat (*Carollia subrufa*) were measured in Colima, Mexico, during January 2006. Bats from an abandoned mine tunnel were transported to a nearby simulated flyway, where speeds were determined over a known distance. For *G. soricina*, average speeds for 26 males and 14 females were 4.85 and 4.80 m/s, respectively ($P > 0.05$), which are similar to those reported by other investigators. Averages for *N. stramineus* were 2.84 m/s for 40 males and 2.39 m/s for 23 females, values that were statistically different ($P < 0.05$) despite the fact that body masses for the sexes were similar. For *C. subrufa*, three males and three females averaged 3.67 and 3.52 m/s, respectively. Speeds were unrelated to body mass for any of the species. Speeds for *N. stramineus* and *C. subrufa* are the first reported, whereas those for *G. soricina* are the first recorded under near-field conditions.

Key words: *Glossophaga*, *Natalus*, *Carollia*, flight speed, Mexico, Neotropics

INTRODUCTION

All aspects of the biology and natural history of bats are integrally related to their ability to fly (Feldhamer *et al.*, 2004). Bats generally are characterized as slow and highly maneuverable in flight when compared to birds, but the manner of flight of bats varies. Knowledge of flight speed helps with respect to our understanding of feeding habits, homing ability, home range, and

seasonal movements (Kennedy and Best, 1972). Previous investigators (e.g., Norberg, 1987; Sahley *et al.*, 1993; Winter, 1999; Hopkins *et al.*, 2003) have summarized much of the available literature relating to flight speeds for bats, but many species remain unstudied. Hopkins *et al.* (2003) noted the limited accounts of flight speeds of bats in the Neotropics of Mexico. Because much of the habitat in this region is diverse and threatened by high rates of deforestation

associated with a multitude of human activities (Ceballos and Garcia, 1995), and there is a paucity of information relating to the speed in flight of many species of bats in the region, we investigated three species — Pallas's long-tongued bat (*Glossophaga soricina*), the Mexican funnel-eared bat (*Natalus stramineus*), and the gray short-tailed bat (*Carollia subrufa*) — that have not been investigated or have been little studied with regard to flight speed in the field.

Winter (1999) reported speeds for six *G. soricina*, not differentiating between sexes, and Lindhe Norbert and Winter (2006) studied in detail its flight characteristics, including speeds of two females. Sahley *et al.* (1993) noted the need for additional information relating to flight habits of glossophagine bats. Our investigation provides new information relating to flight speed for three species. Specifically, we obtained additional flights speeds for *G. soricina* (differentiating between males and females) under near-field conditions in a habitat where this species had not been previously tested. We also report the first speeds in flight for *N. stramineus* and *C. subrufa*.

MATERIALS AND METHODS

On 5 January 2006, individuals of *G. soricina*, *N. stramineus*, and *C. subrufa* were captured in an abandoned mine tunnel (túnel de mina Paredón Alto) about 1 km NE Cardona, Colima, Mexico (19°13'N, 103°39'W, elevation 438 m). These bats were captured, handled, and examined following methods described by Kennedy *et al.* (1977) and Sánchez-Hernández *et al.* (2006). They were obtained during a 1.5 h period following the end of civil twilight (17:55) from the wall of the tunnel by hand or with a small hand-held net. On capture the bats were placed in cloth bags (5 to 10 per bag) and transported 75 m to a simulated cave passage or flyway located beneath the forest canopy in an area clear of understory shrubbery. The flyway was a tunnel comprised of plastic tarps that was 20 m long, 1.5 m wide, and 1.5 m high. Gas lanterns and a 12-volt light were placed at the beginning of the flyway and provided light that made bats visible during flight. As suggested by Kennedy *et al.* (1977), the lights probably

encouraged them to fly toward the darkened end of the passage, which was open.

We identified each bat to species, determined its sex and age, and recorded body mass with a Pesola scale just before release, which occurred between 20:00 and 23:00 h. After release at the beginning of the tunnel, individuals were given a distance of 15 m within the flyway to attain normal flight. Elapsed times from release to 15 m and to 20 m were recorded with stopwatches, thus enabling us to determine the time required for the bat to traverse the final 5-m section of the tunnel. Only results of more-or-less direct and level flights of adults were recorded. Individual bats were tested only once and were not recaptured after release.

Statistical differences for variables between sexes were tested using a single-classification ANOVA. Associations of body mass to flight speed were examined using Pearson's product-moment correlation coefficient. A few observations that were greater than 3 SDs from the mean were considered outliers and possibly mismeasurements (Burt and Barber, 1996); they were removed from the data set.

RESULTS

Speeds for 109 bats were recorded (Table 1). Intraspecifically, none of the species exhibited significant associations of flight speed with body mass ($r = 0.18, 0.60$, and -0.15 for *G. soricina*, *N. stramineus*, and *C. subrufa*, respectively; all $P > 0.05$).

No difference in flight speed or body mass between males and females was detected for *G. soricina*. For *N. stramineus*, there was no statistical difference in body mass between males and females. However, sexes differed significantly in flight speed, with males averaging 2.84 m/s and females 2.39 m/s ($F_{1, 61} = 6.07$, $P = 0.02$). Small sample sizes for *C. subrufa* precluded meaningful assessment of possible differences in flight speeds of males and females.

DISCUSSION

Wilson (1997) reported that flight speeds of bats under captive conditions usually are within the range of 2.2 to 4.4 m/s. For each

TABLE 1. Flight speed (m/s) and body mass (g) of *G. soricina*, *N. stramineus*, and *C. subrufa* recorded in Colima, Mexico

<i>n</i>	Sex	Flight speed			Body mass	
		$\bar{x}$	SD	Range	$\bar{x}$	SD
<i>G. soricina</i>						
26	♂♂	4.85	1.43	2.7–7.6	10.3	1.0
14	♀♀	4.80	1.57	3.2–7.9	10.8	1.8
<i>N. stramineus</i>						
40	♂♂	2.84	0.79	1.3–4.7	5.6	0.8
23	♀♀	2.39	0.53	0.9–3.3	5.6	0.7
<i>C. subrufa</i>						
3	♂♂	3.67	0.46	3.2–4.1	14.3	1.2
3	♀♀	3.52	0.85	2.8–4.5	14.3	1.5

of the three species reported herein, some individuals flew faster than represented by this range (Table 1). For *N. stramineus* and *C. subrufa*, the fastest speeds recorded were slightly greater than the 4.4 m/s, and average flight speeds for these two species were well within the range indicated by Wilson (1997). Several of the flight speeds of *N. stramineus* were slower than 2.2 m/s. Many speeds of *G. soricina* were considerably higher than the high-end value of 4.4 m/s, with even the averages of both males and females being higher (i.e., 4.85 and 4.80 m/s, respectively).

Bats in level flight will fly slower than those in the open with a tail wind or diving (Yalden and Morris, 1975; Norberg, 1987). Thus, it is not surprising that much faster speeds have been reported for bats in the open (e.g., 17.8 m/s, *Lasiurus borealis* — Tuttle, 2005); 26.5 m/s, *Tadarida brasiliensis* — Davis *et al.*, 1962). Furthermore, bats in our study were not familiar with the flight path, so likely flew somewhat slower than if it had been along a flight corridor known to them.

Considerable work has been done with *G. soricina* concerning flight aerodynamics and physiology (Norberg *et al.*, 1993; Winter and von Helversen, 1998; Winter *et al.*, 1998; Voigt, 2000, 2004; Lindhe Norberg and Winter, 2006; Hedenström *et al.*, 2007). Winter (1999) tested six individuals

in several different-sized and shaped flight enclosures. Average flight speed was 3.39 m/s in a simulated passage for bats moving between two feeders at opposite ends of a U-shaped flyway 14 m long; average instantaneous speeds at midsections of flyways of several lengths ranged from 4.63 to 8.29 m/s, with some variation attributed to differences among enclosures, among individuals, and between nights for individual bats. He recorded average speeds of 3.12 and 3.31 m/s for *Glossophaga commissari-si* and *G. longirostris*, respectively, flying from feeder to feeder in the U-shaped flyway; instantaneous average speeds were 4.38 and 4.72 m/s, respectively. Lindhe Norberg and Winter (2006) recorded speeds of 1.23 to 7.52 m/s for two *G. soricina*. Speeds we recorded for *G. soricina* (Table 1) are similar to those recorded for *Glossophaga* by these authors.

Winter (1999) demonstrated that enclosure size affects speeds of *G. soricina*. Mean speeds ranged from 4.6 m/s in a 7-m half-section of the 14-m U-turn tunnel (2 m high $\times$ 1 m wide) to 7.3 m/s in a 50-m flight tunnel (2 m high $\times$ 2 m wide); bats flying in narrower tunnels (rhombic in cross-section with 0.7-m side lengths) 33 and 42 m long flew at intermediate speeds. Lindhe Norberg and Winter (2006) also noted mean speeds of *G. soricina* increased with tunnel length and width; mean speed in a 35-m tunnel was 6.6 m/s. Average speeds we recorded in a 20-m tunnel fit well in the pattern outlined in these studies, being higher than reported in the 7-m tunnel section but lower than in tunnels 33 to 50 m long.

We did not find an association of flight speed with body mass. However, significant positive correlations have been demonstrated between flight speed and body mass for *G. soricina* and other species of *Glossophaga* (Winter, 1999; Lindhe Norberg and Winter, 2006). In fact, Winter (1999) noted

that individuals increased flight speeds in response to gains in body mass during foraging.

Lindhe Norberg and Winter (2006) calculated theoretical values for optimal flight speeds based on equations by Pennycuik (2001) and Rayner (1986). For a non-pregnant *G. soricina*, the Pennycuik estimates for minimum power speed (V_{mp}) and for the maximum-range speed (V_{mr}) were 6.0 m/s and 11.5 m/s, respectively. Comparable values based on Rayner's equations were considerably lower at about 3.4 and 4.6 m/s. Average speeds we recorded for males and females of this species were below V_{mp} of Pennycuik, but the ranges encompassed it. Intuitively, estimates from Rayner's equations seem low; our average speeds for *G. soricina* were higher than V_{mp} or V_{mr} based on those equations, while the range of speeds we recorded encompass both values.

Because bats we tested were in a straight simulated passage during their normal activity time and had not yet fed, we think our findings represent typical speeds in flight for these species in a short passage, although speeds probably were somewhat slower than would have been the case if bats had been flying in a passage familiar to them. Differences in flight speeds of the three species studied reflect in part their feeding strategies, as well as their wing morphology. Because *G. soricina* is a feeding generalist known to feed on insects, fruit, pollen, nectar, and flowering parts (Gardner, 1977), faster speeds would be advantageous in many situations. Also, the species often hovers while feeding (Lemke, 1984). As is the case for other glossophagines, *G. soricina* has a high wing loading and below-average aspect ratio relative to other bats; these are characteristics of species that fly relatively fast and exhibit relatively great agility (Norberg and Rayner, 1987).

Natalus stramineus is an insectivore; speeds were slower than reported for other insectivorous species (Kennedy *et al.*, 1977; Hopkins *et al.*, 2003). The fluttering (moth-like) flight of funnel-eared bats (i.e., species in the family Natalidae; Nowak, 1994) is slower and may be an adaptation related to maneuverability needed for feeding on insects in forested habitat or thick vegetation. *Natalus* has wings with about average aspect ratio, but extremely low wing loading (Norberg, 1987; Norberg and Rayner, 1987). Given these characteristics, Norberg and Rayner (1987) predicted that flight of *Natalus* would be extremely slow and maneuverable; speeds we recorded for *N. stramineus* certainly confirm their flight-speed prediction.

Carollia subrufa is considered, as are other species of the genus, to be an understory frugivore (Bonaccorso, 1979; Fleming 1988). While aspect ratio and wing loading have not been recorded for *C. subrufa*, *C. perspicillata*, and *C. brevicauda* both have low aspect ratios, with wing loading for the former being average and for the latter somewhat higher than average (Norberg and Rayner, 1987). Heithaus and Fleming (1978) obtained flight speeds of foraging *C. perspicillata* of 4.5 to 6.7 m/s, which as pointed out by Norberg and Rayner (1987) are relatively high flight speeds for forest bats; speeds we recorded for *C. subrufa* in a simulated passage are somewhat slower.

Our results for *G. soricina* support previous investigations (Hopkins *et al.*, 2003) that suggest no difference between flight speed of males and females. However, our observations do indicate that male *N. stramineus* fly faster than females. In a few studies (e.g., Haywood and Davis, 1964; Kennedy and Engbretson, 1974) females have been reported to fly faster than males, although the biological significance of these findings is unclear.

Kennedy *et al.* (1977) attempted to record flight speeds of bats in a simulated flyway where the top was a forest canopy and the sides were of thick vegetation. While their flyway was used successfully for recording flight speed of some insectivorous species, the setup did not work for *G. soricina*. Individuals of this species are agile fliers adapted for movement through dense vegetation; they made no attempt to fly the length of the flyway (Kennedy *et al.*, 1977). Rather, they usually flew a short distance and then escaped through a small opening in the vegetation. Success in recording flight speeds of this species and probably *N. stramineus* in the present study likely is related to no openings being available along the flyway, with the nearest escape being at the dark end of the tunnel. Thus, most flights were direct from the light end of the flyway to the dark end.

About 20% of all mammals are bats and, with the exception of swimming, flying is the most energetically efficient means of moving a given body mass (Norberg, 1994). Given that flight speeds have not been measured for many of the species, additional studies are needed to assess flight speeds and relate them to characteristics of wing morphology and aspects of natural history.

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