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Hydrodynamics of the Feet of Fish-Catching Bats: Influence of the Water Surface on Drag and Morphological Design

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ABSTRACT The bats, *Noctilio leporinus* and *Pizonyx uiuesi*, display similar hind foot morphologies specialized for their fish-catching habits. The hydrodynamic drag force of isolated hind feet from fishing and closely related non-fishing bats was measured in a water channel at velocities up to 0.74 ms^{-1}. Drag force increased curvilinearly with increasing water velocity. The highest values of drag force for a given velocity were measured for the fishing bats, which have hind feet **1.8–3.9** times larger than related non-fishing bats. However at high Froude Numbers, the dimensionless drag coefficient (C_D) was **23–39%** lower for fishing bats compared to non-fishing bats. Cross-sections of the laterally compressed toes of *N. leporinus* and *P. vivesi* conformed to hydrofoil designs with minimum drag capabilities, indicated by Fineness Ratio and shoulder position. Moving at high Froude Numbers at the water surface results in the addition of spray drag to the other components of the total drag force (i.e., frictional, pressure, and wave). Spray drag is suppressed by a foil shape with a long pointed leading edge with a short rounded trailing edge. The configuration of the fishing bat toe with a sharp leading edge and relatively long forebody region compared to the maximum thickness provided a measurable drag reduction at the air-water interface. It was concluded that hydrodynamic drag considerations at the water surface were important in the design of hind feet for fish-catching bats.

Noctilio leporinus of the family Noctilionidae and *Pizonyx vivesi* of the Vespertilionidae are unique among the various species of chiroptera, because they are highly specialized in their habits for catching and eating fish (Burt, '32; Bloedel, '55; Gudger, '45; Hill and Smith, '84; Patten and Findley, '70; Suthers, '65, '67). Both species demonstrate considerable parallelism in their behaviors and morphology for piscivory (Altenbach, '89; Bloedel, '55; Blood, '87; Reeder and Norris, '54). The bats use their echolocation to detect fish by ripples or breaks in the water surface and then drag their feet 0.3 to 3.0 m through the water to gaff the fish (Bloedel, '55; Hood and Jones, '84; Suthers, '65, '67; Wenstrup and Suthers, '84).

Structurally, fishing bats are large bodied with elongate digits on the hind feet, hooklike claws are directed forward due to a 180 degree rotation of the hindlimb from the typical mammalian pattern, the plantar surfaces are smooth with a reduced number of wrinkles and hair, the claws and digits are laterally compressed, and plagiopatagium is truncated and attaches high on the tibia (Blood, '87; Gudger, '45; Reeder and Norris, '54; Vaughan, '86; Walker, '75). These morphological similarities in the hind limbs are believed to reduce the drag associated with raking the water for fish (Blood, '87).

The present examination was initiated to determine the extent of drag reduction due to morphological specializations by the fishing bats. Comparisons of fishing bats with related non-fishing species were made to determine which particular anatomical modifications were derived for fish-catching.

MATERIALS AND METHODS

Differences between the drag characteristics of fishing and non-fishing bat feet were determined from isolated hind feet of preserved specimens ob-

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tained from the Los Angeles County Museum of Natural History. Specimens were stored in 70% ethanol. The bat species examined were *Pizonyx vivesi, Myotis californicus,* and *M. velifer* of the Family Vespertilionidae (Koopman,'84), *Noctilio leporinus* and *N. albiventris* of the Family Noctilionidae (Koopman,'84), and *Pteronotus parnellii* of the Family Mormoopidae (Herd, '83; Koopman, '84). The Noctilionidae and Mormoopidae are both included within the Superfamily Phyllostomatoidea and considered to be closely related (Hill and Smith, '84).

Water channel and drag measurement

Drag represents the total force resisting forward movement due to the behavior of a fluid around a submerged body. Measurements of the hind foot drag force for the bats were made using a recirculating water channel based on a design by Vogel and LaBarbera ('78). Tests were conducted in the working section of the 2 m water channel with cross-sectional dimensions of 0.25 x 0.25 m. Turbulent flow was reduced by a grid of 0.1 m long plastic straws located in the upstream end of the working section. Water flow was produced by a variable speed electric motor connected to a propeller located in the return channel. Water velocity (U) was determined by videotaping neutrally buoyant particles in the flow under illumination from a GenRad model 1546 stroboscope operating at 60 flashes per second. Videotapes recorded with a Panasonic Camcorder displayed multiple crisp images of each particle when single video frames were played back on a video monitor. U was calculated for several particles at each flume speed as the rate of the distances between multiple images of a particle to the time between stroboscope flashes (1160 s).

Each foot was suspended in the water by the drag measurement apparatus which consisted of a plastic cantilever beam with bonded SR-4 foil strain gauges mounted on both sides. The strain gauges, one in tension and the other in compression when the cantilever was bent, were configured as two active arms of a Wheatstone bridge. After amplification, the voltage signal was low pass R-C filtered (0–0.5 Hz) and displayed on a Linear model 142 chart recorder. Data were collected at velocities in which voltage measurements as an indication of drag force were consistently above the baseline noise of the apparatus. Throughout testing, the foot was submerged so that the ankle joint was at the air-water interface, and positioned with the plantar surface normal to the water flow. Submergence of the foot to the ankle joint provided a position consistent with fish-catching by fishing bats (Altenbach, '89; Bloedel, '55; Suthers, '65). The digits of the foot were maximally abducted (spread) by inserting an insect pin (No. 0) transversely through the foot. The portion of the pin extending from the foot was cut flush to the skin.

To adjust for differences in drag force due to size, comparisons between bat species were made using the dimensionless values of drag coefficient and Froude Number. The drag coefficient (C_D) which accounts for peculiarities in the behavior of drag (Vogel, '81), was calculated according to the following standard hydrodynamic equation:

$$C_D = 2D/\rho A U^2$$

where D = drag force measured on the hind foot, p = water density, A = plantar surface area measured from photographs (see below), and U = water velocity. Froude Number (F_L) represents the ratio of inertial forces to gravitational forces experienced by a body moving at or close to a fluid/fluid interface such as the water surface (Webb, '75). Froude Number was computed from the following equation:

$$F_L = U^2/Cg$$

where C is a characteristic length, represented by the maximum chord length of the third digit, and g is the acceleration due to gravity ($9.8\,\mathrm{ms}^{-2}$).

Cross sections of bat digits

The third digit was removed from each foot for histological sectioning. Each toe was decalcified in 5% Nitric acid, dehydrated in a graded ethanol series, transferred to toluene, and then embedded in paraffin. Twenty micron cross-sections through the digital pad and mid-shaft of the second phalanx were mounted on glass slides for examination (Fig. 1).

The physical dimensions of the foot and cross-sections of the digits were measured with a GTCO digitizing tablet interfaced with an IBM PC. Plantar surface area of the foot was measured by projecting a scaled photographic slide of the foot onto the tablet. Cross-sections of the toe were projected onto the tablet for measurement with a microprojector. The dimensions of the cross-sectional profiles included the chord length, C, maximum thickness, T, and position of the maximum thickness with respect to leading edge of the chord, X (Fig. 1).

The dimensions of the digit cross-sections were

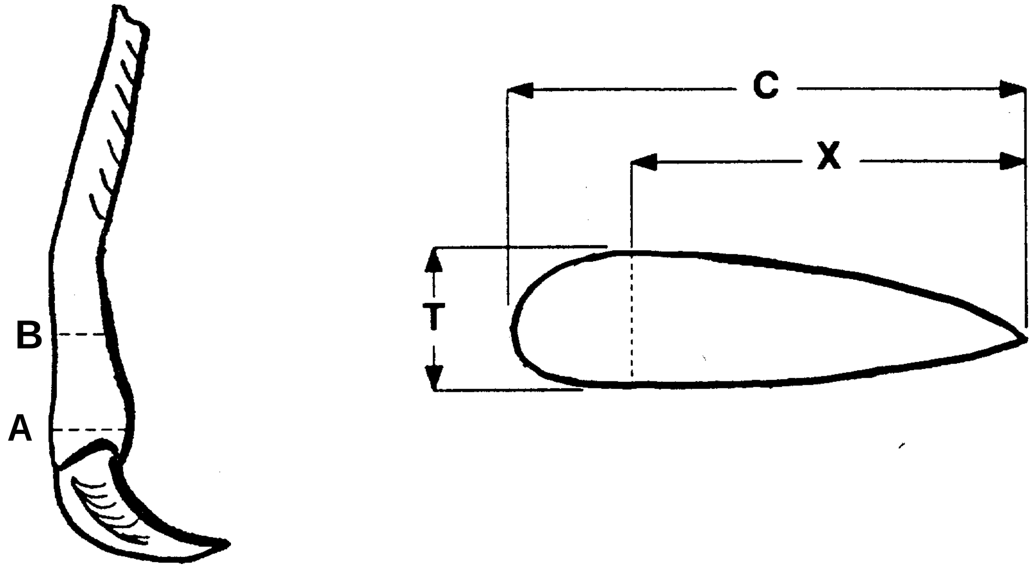

Fig. 1. Lateral view of the third digit of *Noctilio leporinus* showing position where cross-sections from the digital pad (A) and mid-shaft of the second phalanx (B) were obtained. An outline of section A is provided showing the chord length (C), maximum thickness (T), and distance of maximum thickness to leading edge (X).

used to compute the Fineness Ratio (FR) = C/T, Shoulder Position (SP) = X/C, and Forebody Thickness Ratio (FTR) = T/X (Hoerner, '65; Webb, '75). These ratios provide an indication of the design and degree of streamlining of the digits, that ultimately impact the drag experienced.

Statistical procedure

Statistical analyses of the data were performed using Minitab (Ryan et al., '76). Regression lines derived from data on drag as a function of water velocity were computed by the least-squares regression method after logarithmic (base 10) transformation. Comparisons of slopes, b, and elevations, a, were performed using analysis of covariance and Dunnett's test according to Zar ('84). Statistical examination of the ratios FR, SP, and FTR were performed using the Mann-Whitney U-test (Bruning and Kintz, '77).

RESULTS

Drag force on the hind feet of five species of fishing and non-fishing bats was determined over a range of U of 0.26 to 0.74 ms^{-1}. *Myotis californicus* was excluded from these determinations, because its small size prevented the necessary manipulation of the hind foot for drag measurements. As U increased toward maximum flow, the water was piled up on the leading surface of the foot while a trough formed immediately downstream of the foot. The depression formed posterior to the foot represented an air-filled pocket referred to as ventilation (Marchaj, '79).

At all speeds, the drag force on the feet of fishing bats was generally greater than for non-fishing bats, with *Noctilio Zeporinus* displaying the highest drag. The higher drag of fishing bats was due to the greater size of their feet which were 1.8 to 3.9 times larger than non-fishing bats. The drag force increased curvilinearly with increasing U for all specimens (Fig. 2). The best-fit equations for drag as a function of U, based on log transformed data, are presented in Table **1**. Although the slopes, b, varied from 1.58–2.05 between the different species, multiple comparisons of slopes showed no significant difference. In addition, the common slope for all species of 1.90 was not significantly different from the predicted exponent of **2** from the theoretical drag equation **(Eq. 1)**. Multiple comparisons among elevations, a, were found to be significantly different ($P < 0.05$) between all species.

Drag coefficients (C_D) calculated from individual drag force estimates and frontal surface areas are plotted as a function of Froude Number in Figure 3. Froude Numbers for the fishing bats are lower compared to non-fishing bats, despite testing over the same range of velocities, because the chord lengths of the fishing bats used in the calculation of F_L (Eq. 2) were 1.4–5.4 times larger. Compared to non-fishing bats, fishing bats have

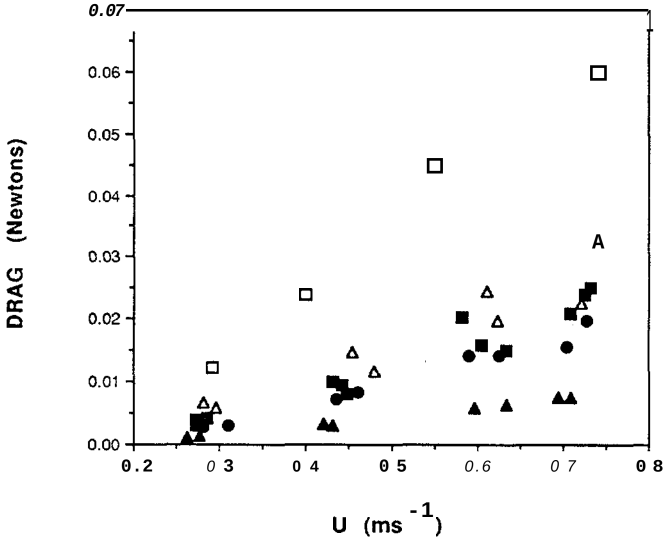

Fig. 2. Drag on isolated hind feet as a function of the water velocity, U. Open symbols represent the fishing bats, *Noctilio leporinus* (□) and *Pizonyx vivesi* (△); closed symbols represent non-fishing bats, *Myotis velifer* (▲), *Noctilio albiventris* (■), and *Pteronotus parnellii* (●).

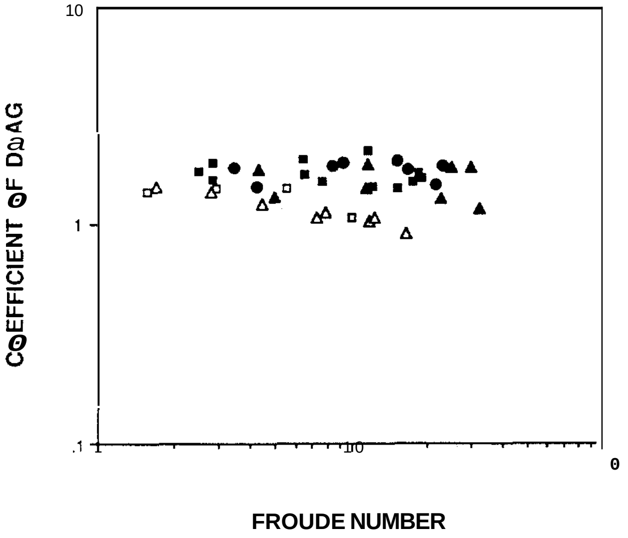

Fig. 3. Drag coefficient, C_D, plotted against Froude Number, F_L. Open symbols represent the fishing bats, *Noctilio leporinus* (□) and *Pizonyx vivesi* (△); closed symbols represent non-fishing bats *Myotis velifer* (▲), *N. albiventris* (■), and *Pteronotus parnellii* (●).

TABLE 1. Equations and correlation coefficients, r, of drag as a function of water velocity, U, for fishing bat feet. Equations are in the form of Drag = aU^b, where Drag is in Newtons and U is in ms^{-1}.

Species	b (± SE)	a	r
Myotis velifer	1.948 (0.033)	0.015	0.996
Noctilio albiventris	1.922 (0.063)	0.044	0.983
Noctilio leporinus	1.724 (0.056)	0.111	0.989
Pizonyx vivesi	1.580 (0.071)	0.046	0.969
Pteronotus parnellii	2.048 (0.048)	0.037	0.991

lower values of C_D. Values of C_D for fishing bats were 23–39% lower than non-fishing bats at the maximum equivalent F_L. Fishing bats show a trend in which C_D decreases with increasing F_L. However, non-fishing bats maintain a nearly constant C_D with increasing F_L.

Morphology of the laterally compressed digits

The feet and digits of the fishing bats were generally larger than those of non-fishing bats. The proportion of foot length represented by the third digit was maximum for **P. vivesi** at 68%, whereas the other bats examined ranged between 58–63%.

Varying degrees of lateral compression were observed from cross-sections of the third digit from the hind feet for all bats examined in this study (Fig. 4, 5). Fishing bats, particularly **P. uiuesi**, displayed the greatest lateral compression of the digits, while non-fishing bats showed the least. The general shape defined by the cross-sections approached that of an elongate tear drop or fusiform shape with the pointed end oriented anteriorly. This shape was particularly apparent at the distal end of the digit at the base of the claw. At this level, the digital pad and combined tendons of the Flexor Digitorum Plantaris and Flexor Digitorum Fibularis muscles composed the tapered leading edge. The maximum girth or shoulder of the digit's cross-section was associated with the posterior position of the phalanx within the digit (Fig. 5).

The Fineness Ratio (FR), Shoulder Position (SP), and Forebody Thickness Ratio (FTR) for sections through the digital pad and mid-shaft of the third digit for each species are presented in Table 2. Maximum FR values were found for the more distal sections. This was particularly noticeable in the digital pad of **P. vivesi**, which displayed a high degree of lateral compression and streamlining. Distal segment FR for **P. uiuesi** was at least 1.4 times greater than those of N. **leporinus** and over 1.9 times the FR values of non-fishing bats. The FR values from digital pad sections for fishing bats was significantly different ($P < 0.001$) from values for non-fishing bats, whereas proximal sections showed no significant difference.

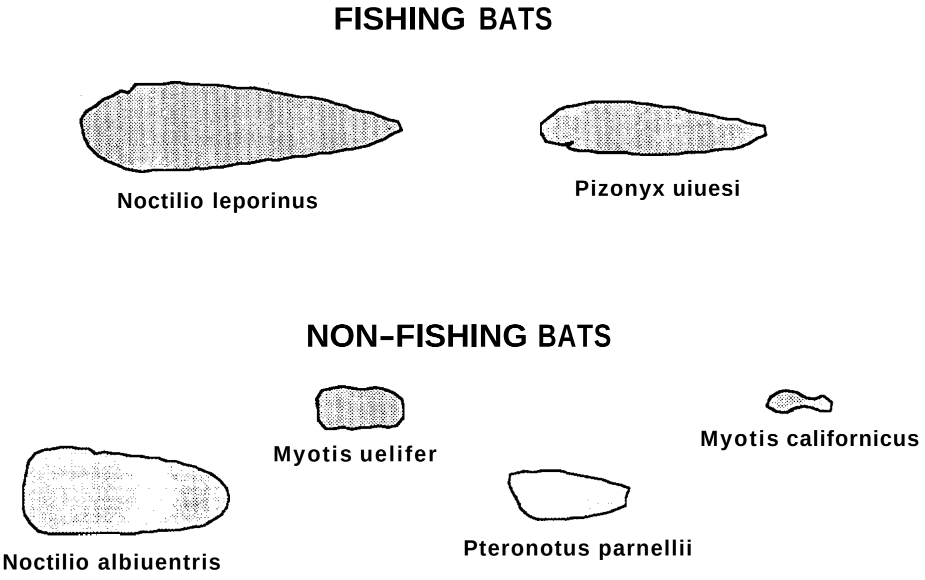

Fig. **4.** Outline of cross-section through digital pad (Fig. **1**;section **A)** from fishing and non-fishing bats. Leading edge of each section is oriented to the right.

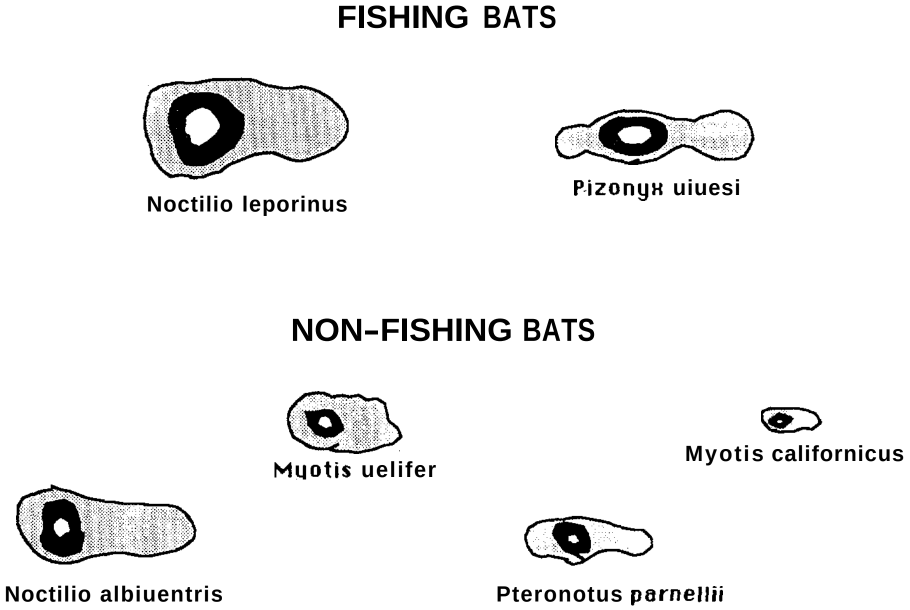

Fig. **5.** Outline of cross-section through second phalanx (Fig. **1**;section B) from fishing and non-fishing bats. Bone is indicated in black. Leading edge of each section is oriented to the right.

No significant difference was found for SP between fishing and non-fishing bats. With the exception of M. *velifer*, the maximum thickness of proximal and distal sections was displaced to the posterior half of the digit chord. Fishing bats had SP values between about 60–70% of the chord.

The posterior placement of the shoulder and compression of the digit resulted in a lower FTR of fishing bats compared to non-fishing bats. **A** significant difference in FTR between fishing and non-fishing bats was found for both proximal ($P < 0.001$) and distal ($P < 0.05$) cross sections. **Ex**treme differences were noted between distal sections of the various bat species examined. FTR for ***N. leporinus*** was at least **34%** lower than for related non-fishing species, whereas the FTR for *P.*

***TABLE** 2. Fineness Ratio (FR), Forebody Thickness Ratio (FTR), and Shoulder Position (SP) determined from bat toe cross-sections from the digital pad (A) and the middle of the second phalanx: (B)*

Species	Section	FR	FTR	SP
Myotis californicus	A	2.58	0.54	0.72
	B	2.63	0.80	0.48
Myotis velifer	A	2.44	1.22	0.34
	B	2.09	1.16	0.41
Noctilio albiventris	A	2.10	0.67	0.71
	B	1.85	1.00	0.54
Noctilio leporinus	A	3.16	0.42	0.75
	B	2.01	0.65	0.73
Pizonyx vivesi	A	5.24	0.28	0.68
	B	3.48	0.50	0.58
Pteronotus parnelli	A	2.48	0.64	0.63
	B	2.26	0.65	0.69

vivesi was 48–77% lower than for its non-fishing relatives.

DISCUSSION

The ability to catch fish while in flight is a highly derived behavior among the chiroptera and one that requires specialized morphology. Although there is evidence that a few species of bats are occasionally piscivorous (Bloedel, '55; Blood, '87; Fenton et al., '81; Robson, '84), only *Noctilio leporinus* and *Pizonyx vivesi* have been observed to drag their hind feet below the water surface and gaff fish (Altenbach, '89; Bloedel, '55; Reeder and Norris, **'54;** Suthers, '65, '67). These two species represent parallel radiations from generalized insectivorous bats. Intermediate species, such as *M. adversus* (not examined in this study) and *N. albiventris*, feed on insects over water (Hood and Pitocchelli, '83; Hooper and Brown, '68; Novick and Dale, '71; Robson, '84; Suthers and Fattu, '73). Suthers and Fattu ('73) believed that the foraging behavior of *N. albiventris* represented a relatively early step in the evolution of fish-catching, where the major hurdle was the use of the hind feet to catch food.

In the evolution of fish-catching, the major morphological change was in the development of large streamlined hind feet capable of catching and holding sizable fish. The increased size of the feet, observed in *N. albiventris* for catching insects up to 20 mm in body length (Hooper and Brown, '68) is still 57% smaller than *N. leporinus*. However, the cost of larger feet for catching fish is an increased drag force as the feet are trolled through the water. Therefore, morphological adaptations in the feet for drag reduction are beneficial. The adaptations would minimize momentum loss to the water allowing fishing bats the force necessary to impale fish on their claws and fly off with their prey. Furthermore, morphological adaptations in the feet for drag reduction would prevent excessive turbulence and noise which might be detected by potential prey.

Our results demonstrate that the design of the hind feet and compressed digits influences the hydrodynamic performance of fishing bats. Although only distantly related, both *N. leporinus* and *P. vivesi* show similar morphological specializations for fish-catching that provide increased drag reduction compared to closely related non-fishing species.

Although the results of this study indicate a reduction in C_D for the hind feet of fishing bats, drag on isolated hind feet was measured at speeds lower than recorded flight speeds. Goodwin ('28) indicated that the average speed of *N. Zeporinus* was 8.9 ms^{-1}, although this was for bats being chased by a car. Bloedel ('55) estimated the cruising speed of *N. leporinus* over water to be between 5.5–7.6 ms^{-1}. This agrees reasonably well with laboratory experiments in which typical flight speeds were determined to range from 4.5 to 6.2 ms^{-1} with a minimum flight speed of 3.7 ms^{-1} (Suthers, '65; Wenstrup and Suthers, '84). Assuming similar foot dimensions with *N. leporinus* in this study, a bat dragging its feet through the water at the minimum flight speed would have a F_L of 2.7 x 10^2. This is approximately 26 times higher than the maximum F_L calculated for *N. Zeporinus* in this study. However, examination of the drag profiles of surface-piercing struts, cylinders, and flat plates indicates that C_D gradually 'decreases to a plateau with increasing F_L (Hoerner, '65). F_L in this study is within the range of F_L in which the plateau for C_D occurs indicating that C_D for fishing bat feet is near its minimum.

Despite high absolute drag forces measured for fishing bats, C_D was lower for *N. Zeporinus* and *P. vivesi* than non-fishing bats when compared over an equivalent range of F_L. In addition, the trends observed in this study suggest that as U increases the difference in C_D between fishing and non-fishing bats will become greater. At F_L of 2.7 x 10^2, *N. Zeporinus* would have a total drag for both hind feet of 2.1 N and a C_D of 0.77, whereas the total drag and C_D for *N. albiventris* is 0.62 *N* and **1.52,** respectively. This is approximately a 2-fold difference in C_D, although *N. Zeporinus* would be trolling 1.3 times faster than *N. albiventris*.

The design of the hind foot digits of fishing bats shows a high degree of specialization for drag reduction approaching a high performance hydrodynamic shape. Cross-sections of fishing bat digits present a streamlined profile to the flow as the feet are dragged through the water. The importance of a streamlined profile is that it reduces the flow-induced pressure gradient around the body (Blake, '83; Webb, '75). This delays separation of the boundary layer to a downstream point on the body, thus maintaining a small wake and ultimately minimizing the pressure component of drag. The drag on a streamlined body is composed primarily of frictional drag, due to shear stresses in the attached portion of the boundary layer (Streeter, '66). Reduction of the pressure component of drag is more beneficial than decreasing the frictional component, because the pressure component is often larger (Webb, '75).

All fishing bat digit cross-sections were within the FR range of between 2 and 6, that characterizes a streamlined profile (Blake, '83). FR values of cross-sections from the digit pad approach the optimum of 4.5, which provides a shape that gives the minimum drag for the maximum volume (Blake, '83; Webb, '75). In addition, FR can vary between 3 and 7 with only a 10% increase in the drag force from the minimum (Webb, '75).

The position of the shoulder also influences the point of boundary layer separation and the magnitude of the drag force on a body. Adverse pressure gradients (i.e., pressure increases in the downstream direction) occur downstream of the shoulder and facilitate boundary layer separation, which in turn increases the pressure component of drag (Vogel, '81; Webb, '75). The posterior displacement of the shoulder maintains a longer favorable pressure gradient (i.e., pressure decreases in the downstream direction) upstream of the shoulder. This delays the separation of the boundary layer from the body surface. In addition, the position of the shoulder determines the percentage of the body where laminar flow occurs due to favorable pressure gradients upstream of the shoulder (Blake, '83). The presence of laminar versus turbulent flow in the boundary layer minimizes the frictional drag component (Blake, '83; Vogel, '81; Webb, '75).

Laminar flow foils, which have shoulders far posterior to the leading edge, are characterized by low drag performance (Hammitt, '75; Vogel, '81). Indeed, the SP of 60 to 75% of chord length for fishing bat digits would substantially delay boundary layer separation keeping the wake small, Similar placement of the shoulder as an adaptation for reduced drag associated with high speed swimming is observed in the body design of thunniform fish, cetaceans, and phocid seals (Aleyev, '77; Fish et al., '88; Hertel, '66; Walters, '62).

The SP and near optimal FR values for the digits would appear to benefit fishing bats by minimizing the hydrodynamic drag incurred while catching fish, However, the posterior position of the shoulder combined with a sharp leading edge and blunt trailing edge run counter to the preferred orientation for low drag hydrofoils. Minimum drag is realized by typical streamlined foils oriented with the reverse configuration (Hoerner, '65).

The typical streamlined 'shape with a blunt leading edge and an elongated, tapering trailing edge is common throughout nature; particularly, it is prevalent in macroscopic organisms subjected to flow such as swimmers and flyers (Hertel, '66; Vogel, '81, '88). The long, tapering tail of a streamlined shape allows fluid to decelerate gradually in the rear with little or no boundary layer separation and generates an anteriorly directed pressure pushing the body forward (Marchaj, '79; Vogel, '81). The effect is to minimize the drag force by maintaining a small pressure component (Prandtl and Tietjens, '34). Why then do sections from fishing bat toes have a shape exactly opposite that of streamlined bodies with minimal drag? Animals whose structure include a long, tapering tail or trailing edge (e.g., fish, dolphin, birds) are totally immersed in the fluid through which they move. These animals experience a drag composed of only frictional and pressure components. Unlike bodies with typical streamlined shapes, the toes of fishing bats act at the fluid-fluid interface of the water surface and encounter additional drag components.

Movement at the water surface incurs additional energy losses, compared to submerged bodies, due to work performed in the vertical displacement of water against the force of gravity. These energy losses are realized in the form of two additional drag components, wave and spray drag.

Wave drag represents the kinetic energy transferred from a body traveling at the water surface as water is accelerated upward (Foley and Soedel, '81; Marchaj, '64; Prandtl and Tietjens, '34). Wave drag can be 5 times the frictional drag and represents the largest component of drag for the displacement hulls of ships and yachts (Hertel, ’66; Marchaj, **'64;** Prange and Schmidt-Nielsen, ’70). Wave drag increases with increasing F_L to a maximum at the hull speed equal to $(gL/2\pi^{1/2}$, where g is the gravitational acceleration, L is the wave length (Prange and Schmidt-Nielsen, '70). At the hull speed, the wave pattern generated by the hull produces a constructive interference between the transverse bow and stern waves (Foley and Soedel, ’81). Subsequently, the hull becomes trapped in the trough between bow and stern waves. **As** speed increases, the wave drag increases dramatically (Prange and Schmidt-Nielsen, ’70), because the hull must climb up the bow wave (Foley and Soedel, '81; Kay, '71). However, wave drag decreases appreciably for a body at the surface as F_L increases above the critical hull speed (Hoerner, **'65;** Prandtl and Tietjens, **'34;** Taylor, **'33).** In this case, the body is traveling so fast that the water does not have time to respond to the disturbance. Theoretically, the wave drag will approach zero as F_L increases further (Hoerner, **'65;** Prandtl and Tietjens, **’34**).

Fishing bats, such as N. *leporinus*, drag their feet through the water at such high F_L that even when the bat is traveling at the minimum flight speed the foot speed would be at least **41** times greater than the predicted hull speed. At such speeds, wave drag would be of only minor importance in the total drag on the feet.

More important than wave drag for bats skimming the water surface at high F_L is spray drag. Spray drag or surface interference drag is caused by water piling up along the forebody of a surface-piercing strut or foil and being shot into the air (Hoerner, '65; Marchaj, '79). This effect is encouraged by ventilation, the formation of an air-filled pocket, behind the strut. At high F_L, spray drag is approximately **26%** of the total drag for a surface-piercing flat plate and **30%** for a strut with a blunt trailing edge (Hoerner, **'65).**

The best design for a foil or strut to reduce spray drag is a pointed leading edge and long forebody region relative to the maximum thickness (Fig. **6;** Hoerner, ’65). The Forebody Thickness Ratio (FTR) for fishing bats was lower than values for non-fishing bats. FTR values from distal segments for N. *leporinus* and *P. vivesi* of **0.42** and 0.28, respectively, have only 11–60% of the spray drag of non-fishing bats, based on the equations of spray drag coefficient as a function of FTR by Hoerner (**’65**). Thus it appears that the interaction of the compression of the digits and posterior displacement of the shoulder act to reduce the spray drag component and minimize the total drag for fishing bat feet.

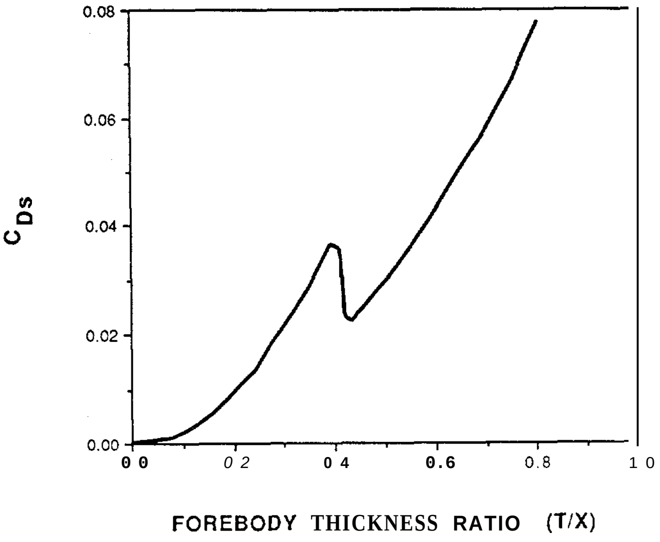

Fig. 6. **Relationship between spray component of drag, C_{Ds}, and Forebody Thickness Ratio. Modified from Hoerner, 1965.**

To verify that the design for reducing spray drag as observed for the digits of fishing bats minimizes total drag, a model was constructed with the same cross-sectional shape as the distal section of the third digit of *N. leporinus*. The model was suspended by the drag measurement apparatus in a jet of water from a nozzle of **0.45** cm radius. Drag force estimates were determined at mean water speeds of 2.8 and **4.5** ms^{-1}, representing F_L values of 7.2×10^1 and 1.8×10^2 (C = 0.012 m). Comparisons of drag estimates were made between the model oriented with the sharp leading edge upstream and with the reverse configuration. The results of this test showed that the drag on a model toe with the blunt end oriented into the flow was almost 50% greater than drag with the flow direction reversed.

A design similar to the digits of fishing bats is found in the lower mandible of the black skimmer (*Rhyncops nigra:* Rhyncopidae: Charadriformes). These birds capture prey, such as small fish and crustaceans, by flying or gliding above the water surface with the mandible extended into the water (Withers and Timko, ’77). Although fish are not gaffed, the skimmer's method of prey capture is similar to that of the fishing bats. The lower mandible is streamlined for drag reduction at the water surface (Withers and Timko, ’77). Cross-sections of the portion of the lower mandible that extends into the water exhibit lateral compression with a pointed leading edge, rounded trailing edge, and long forebody region. The presence of an analogous design in the toes of fishing bats and beaks of skimmers indicates the importance of resistance forces unique to the water surface.

In conclusion, the hind feet of *Pizonyx uiuesi* and *Noctilio leporinus* have undergone a parallel modification from a primitive insectivorous morphology. This change is associated with a reduction of the drag and thus the momentum losses associated with fish-catching. Although the absolute drag force for the fishing bats is high due to the enlarged feet necessary for fish-catching, the dimensionless coefficient of drag is lower than for unmodified feet. The design of the elongate digits provides a shape different from shapes of fully submerged bodies and thus minimizes the dominant drag components associated with the water surface. The reductions in frictional, pressure, wave, and particularly spray drag are important considerations in the evolution of form for the unique fish-catching behavior of the these bats.

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