

THE DYNAMICS OF FLIGHT-INITIATING JUMPS IN THE COMMON VAMPIRE BAT *DESMODUS ROTUNDUS*

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Summary

Desmodus rotundus, the common vampire bat (Phyllostomidae: Desmodontinae), exhibits complex and variable terrestrial movements that include flight-initiating vertical jumps. This ability is unique among bats and is related to their unusual feeding behavior. As a consequence of this behavior, the wing is expected to have design features that allow both powered flight and the generation of violent jumps. In this study, high-speed cine images were synchronized with ground reaction force recordings to evaluate the dynamics of jumping behavior in *D. rotundus* and to explore the functional characteristics of a wing operating under competing mechanical constraints.

The pectoral limbs are responsible for generating upward thrust during the jump. The hindlimbs stabilize

and orient the body over the pectoral limbs. The thumbs (pollices) stabilize the pectoral limb and contribute to extending the time over which vertical force is exerted. Peak vertical force can reach 9.5 times body weight in approximately 30 ms. Mean impulse is 0.0580 ± 0.007 N s (mean \pm s.d., $N=12$), which accelerates the animal to a mean take-off velocity of 2.38 ± 0.24 m s⁻¹. A model of the muscular activity during jumping is described that accounts for the characteristic force output shown by these animals during flight-initiating jumps.

Key words: Chiroptera vampire bats, *Desmodus rotundus*, jumping, cinematography, dynamics, locomotion.

Introduction

Chiroptera is the second most specious mammalian order, yet only three of the nearly 900 extant bat species are vampires. Although naturalists assigned generic names to a number of bats erroneously implying vampirism, true vampire bats were not studied extensively until the 1930s (De Verteuil and Urich, 1936; Pawan, 1936; Torres and de Queirox Lima, 1936). Three extant genera have been identified: *Desmodus rotundus*, the common vampire bat, *Diaemus youngi*, the white-winged vampire bat, and *Diphylla ecaudata*, the hairy-legged vampire bat. Once placed in their own family, Desmodontidae (Miller, 1907; Hall, 1981; Vaughan, 1986), vampire bats are now generally recognized as a subfamily (Desmodontinae) within the large neotropical family Phyllostomidae (Machado-Allison, 1967; Forman *et al.* 1968; Smith, 1972; Koopman, 1988).

Vampire bats are the only extant mammals whose diet consists exclusively of blood. It is not surprising, therefore, that they exhibit a number of interesting morphological and behavioral adaptations related to their unique diet (for a review, see Greenhall and Schmidt, 1988). One such aspect of

vampire bat behavior is their ability for quadrupedal locomotion, which had been little more than noted by researchers until relatively recently (Beebe, 1927; Ditmars and Greenhall, 1935; Price, 1950; Wimsatt, 1969).

The pectoral limbs of bats are highly modified for flight, while the pelvic limbs of most bats are specifically adapted for hanging. These modifications severely restrict over-ground locomotion by most bats. Many species either cannot crawl or perform a clumsy shuffle when grounded (Vaughan, 1959). Vampire bats demonstrate complex movements and agility during quadrupedal locomotion that is not seen in any other bat species.

Using high-speed still and motion-picture photography combined with electromyography, Altenbach (1979, 1988) determined that quadrupedal locomotion in *D. rotundus* is related to the common vampire's unique feeding habits. Terrestrial gaits, for example, which vary between walking, hopping and spider-like scrambling, are exhibited by *D. rotundus* before, during and after feeding bouts (which usually involve large terrestrial mammals) (Greenhall and Schmidt,

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1988). Additionally, *D. rotundus* employs a repertoire of jumps that vary in direction, magnitude and temporal sequence (Altenbach, 1979). The unique jumping ability of *D. rotundus*, which includes flight-initiating vertical jumps, appears to be related to the terrestrial habits of this bat. *Diaemus youngi*, which feeds primarily upon arboreally roosting birds, does not make flight-initiating jumps (Schutt *et al.* 1993), but Altenbach (1988) reported that *Diphylla ecaudata*, whose diet appears to consist totally of avian blood, does initiate flight by jumping. Jumping in *D. ecaudata* appears to differ from that observed in *D. rotundus*, and this behavior, in a bat reported to feed arboreally, warrants future study.

Under natural conditions, *D. rotundus* consumes between 50 and 100% of its body mass in blood during a single feeding (Wimsatt, 1969). Jumping functions as a primary means of getting the heavily loaded vampire bat airborne from the ground and other surfaces from which it feeds (Altenbach, 1979). Jumping may also serve as an escape strategy to avoid being trampled by large prey such as cattle (Altenbach, 1979; K. F. Koopman, personal communication).

Although Altenbach's (1979) kinematic and electromyographic study presented a great deal of data on the locomotor behavior and functional morphology of *D. rotundus*, he did not characterize the force-generating capabilities of these animals. Altenbach (1979) concluded that the forelimbs were responsible for generating all of the thrust during flight-initiating jumps. However, without direct force records, this could not be verified. Additionally, we were interested in investigating the dynamics and coordination of these unique jumping maneuvers. In the present study, we investigate the mechanics of this flight-initiating behavior in these unique bats using a force platform and high-speed cinematography.

Materials and methods

To determine the forces generated during flight-initiating jumps, we used an electronic force platform. To address the question of the relative contributions of the forelimbs and hindlimbs during jumps, we obtained high-speed motion-picture recordings of the bats on the platform. By synchronizing the force platform data with the high-speed film record, we were able to determine the position of the animal and its limbs relative to the jump force vector to a time resolution of 4 ms (determined by the framing rate of the cine system).

Test system

Design and construction of the force platform

The construction of the force platform used in this study follows the basic design first described by Heglund (1981) and modified as reported by Biewener and Full (1992). The force platform had twelve transducing elements, four oriented in each of the vertical and two orthogonal horizontal directions. The platform was supported by two horizontally oriented aluminum box beams. These beams were supported at each end by short vertical beams attached to the supporting baseplate of

the platform. Specific sites on these aluminum box beams were milled to form a series of double cantilevers supporting the platform and each oriented in one of three orthogonal directions (vertical, horizontal fore-aft and horizontal mediolateral). Load applied to the platform caused deformation in the cantilevers oriented across the direction of the applied load. Cantilever deformation was measured using foil strain gauges (EA-series, Micromeritics Corp., Raleigh, NC, USA).

The horizontal, vertical and mediolateral force beams were glued together using epoxy resin to make a rigid frame for the jumping platform, a stiff aluminum plate glued to a honeycombed plastic panel using epoxy resin. Although epoxy generally does not have sufficient strength to secure a force transducer, the small size of these animals (<30 g) allowed this approach. The plate had a slightly roughened texture to provide a non-skid surface. The plate surface measured 15.5 cm × 15.5 cm. Although this was a rather large area for a platform as sensitive as this, this area was deemed appropriate after observing the animal's posture and movements when preparing for and executing flight-initiating jumps.

The strain gauges were wired into four independent full Wheatstone bridge circuits; two vertical (front and rear) and two horizontal (fore-aft and mediolateral). The front and rear vertical sensor channels gave independent output to enable the calculation of the point of application of the resultant vertical force from the relative output of each (see Heglund, 1981). An excitation voltage of 3.3 V was used. Voltage changes were registered by a strain-conditioning isolation amplifier (National Instruments SCXI-1000 with SCXI-1121 modules). The analog signal was sent to a microcomputer (MacIntosh Quadra 900) using an A/D converter (National Instruments NB-MIO-16H). Data acquisition and analysis were performed using a custom-designed program (written in LabView virtual instrumentation software).

Calibration of the force platform

The force platform was calibrated before use by the methods outlined in Biewener and Full (1992). Briefly, the platform's vertical and horizontal channels were individually calibrated for force up to 10 N (30 times the animal's weight). This allowed us to determine that the instrument was responding linearly over the range of loads applied by the bats. The position of force application was calibrated by placing a uniform weight at known intervals along the length of the platform surface. The position of the resultant force application was calculated by comparing the output of the vertical sensor at one end of the platform with the summed output of vertical force at both ends of the platform. The natural frequency of the individual channels was determined to be slightly greater than 100 Hz. The size of the platform required for these studies and the sensitivity demanded by the small size of the animals limited the characteristics of the platform.

Platform arrangement

The force platform was incorporated into a square wooden

frame supporting a Plexiglas floor section (50 cm×50 cm). The platform was positioned within a 15.7 cm×15.7 cm opening level with the surrounding floor section. The supporting baseplate of the force platform (quarter inch aluminum plate) was seated directly on the cement floor of the study room. The platform and frame were positioned in the center of an experimental chamber (4.2 m×1.5 m×2 m high). This space was adequate to allow the vampire bats to perform jumps including flight initiation.

High-speed cinematography

High-speed motion pictures of bats on the force platform were obtained simultaneously with force platform data. A Hycam K2004E camera, using Kodak 16 mm reversal (double perforation) film, was used to film the bats as they jumped. The objective lens of the camera was focused on the center of the force platform surface orthogonal to one side. To synchronize film and force platform data acquisition, a 50 mm lens on the rear aperture of the cine camera was focused on the screen of an oscilloscope displaying the signal output of one of the vertical force channels from the platform. Thus, we were able to superimpose a force signal trace onto the frame-by-frame record of the bat's activity on the platform. Two 1000 W lights provided sufficient illumination to film at 250 frames s⁻¹.

Experimental procedures

Specimens of *Desmodus rotundus* (Wied-Neuwied, 1826) obtained from the National Animal Disease Center in Trinidad in July 1993 were used in this study. During and after the experiment, these specimens were housed at Cornell under the guidelines of an approved protocol (filed with IACUC-Cornell). A separate manuscript details the maintenance and care of these specimens (W. A. Schutt, F. Muradali, K. Mondol, K. Joseph and K. Brockmann, in review). All bats were fed normally on the night before the experiment and weighed prior to testing.

During the experiment, individual bats were placed on the platform surface and restricted to the platform by a clear plastic cover. When the bat moved into the appropriate position on the platform (i.e. centered on the platform either facing or oriented laterally to the camera), the cover was removed manually. The camera was started and data acquisition from the force platform was triggered (to collect 2.16 s of data at 200 Hz per channel for the four force platform channels). Thirty trials were recorded for *D. rotundus* from four different individuals.

Analysis of force data

The raw binary records were converted to force and time using the calibration constants determined for each channel and the sampling rate (200 Hz). The data were digitally filtered using a custom-assembled program (Butterworth bandstop 58–62 Hz to remove a.c. noise and a 100 Hz low-pass filter).

We used the jump force records to determine the timing of force production, as well as two measures of the magnitude of the jump. These were maximum vertical force (N), from the summed front and rear vertical channels, and impulse (Ns).

Impulse is a measure of the change in momentum of an object when the object accelerates under the influence of a force (Cutnell and Johnson, 1992) and is the product of the mean force and the time interval over which the force acts. A large impulse corresponds to a large response (i.e. one in which the mass of the bat accelerates to a high velocity).

Analysis of position data

To facilitate working with the high-speed film records of the bat jumping, the 16 mm film was transferred to video tape. Because the film had been exposed at 250 frames s⁻¹ and run at 16 frames s⁻¹ during the transfer to video tape, we determined that 15.625 s of video tape was equal to 1 s of film. Since there are 60 video fields per second, there were 3.83 video fields per cine frame.

The video fields were captured and digitized from five representative jumps of *D. rotundus* (two frontal and three lateral views) using a frame-grabber board (Data Translations), a jog-and-shuttle video recorder (Panasonic AG-1960) and image-analysis software (NIH-Image). The oscilloscope signal of the vertical force channel was used to determine the initiation point of the jump on the video. Images were digitized beginning 4 ms before initiation of the jump (the equivalent of one cine frame or four video fields) and continuing every 4 ms for the duration of the jump. A time-base corrector (NOVA 800) was used to stabilize individual video fields prior to capture and digitization. In lateral view, 10 anatomical points were documented from the right profile (tip of the nose, top of the ear, shoulder, elbow, wrist, distal tip of the thumb, hip, knee, ankle and the distal tip of the foot), as well as two stationary reference points. In frontal view, nine points were followed (tip of nose, tips of both ears, both elbows, both wrists and the distal tip of both thumbs).

The force data were then synchronized with the digitized position data and a series of plots was created which displayed a force vector (magnitude, location and direction) superimposed upon the digitized video image of the bat as it jumped from the force platform (Kaleidagraph software). Regression significance was determined using Student's *t*-test.

Results

Our specimens of *D. rotundus* initiated flight by making violent vertical jumps from a horizontal surface in a manner identical to that observed by Altenbach (1979, 1988). An example of the force generated in such a jump is shown in Fig. 1. In the jump depicted, an animal weighing slightly less than 0.3 N was able to generate a vertical force over six times its body weight in 30 ms. The force for this jump is slightly less than the mean for 12 similar jumps (6.51 ± 1.57 N, mean \pm S.D.; Table 1). Our records showed a maximum peak vertical force of nearly 10 times body weight. This resulted in a mean take-off velocity of $2.38 \text{ m s}^{-1} \pm 0.24$ (S.D., $N=12$).

Mediolateral horizontal force was small, but fore–aft horizontal force was approximately 10% of the vertical force generated. The direction and magnitude of horizontal force can

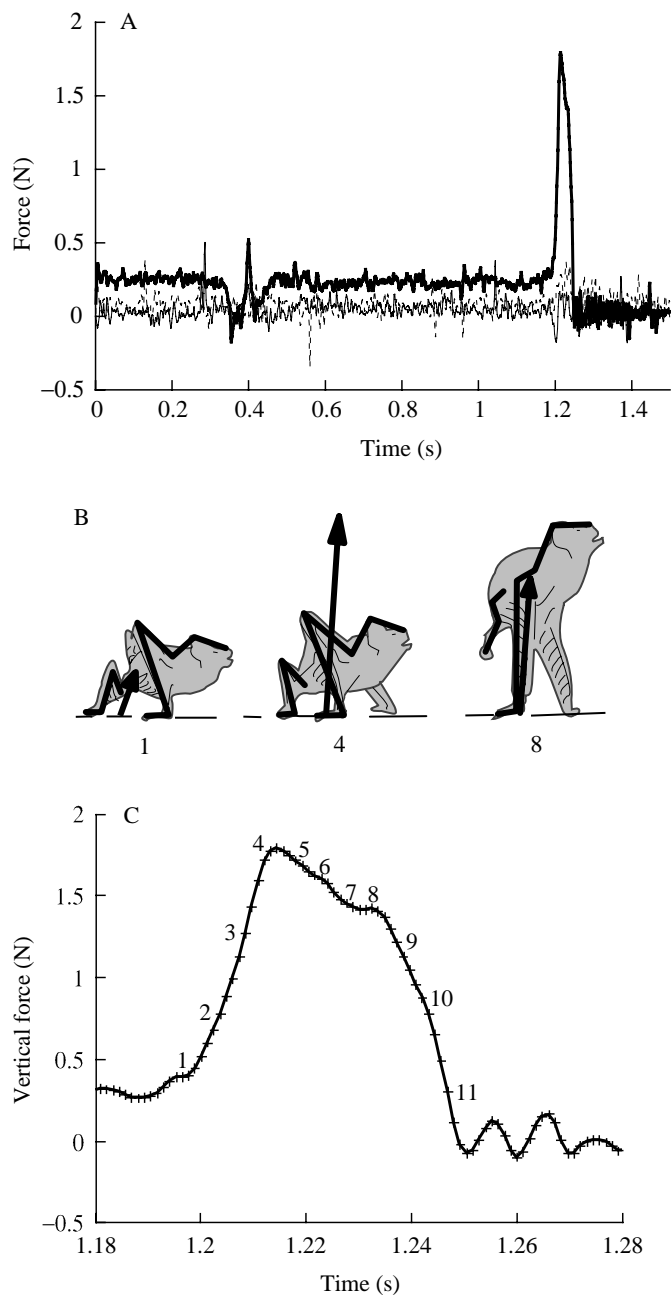


Fig. 1. Illustration of kinetic and motion information derived from this study of jumping bats. (A) A complete force–time record from this jump. The solid line shows summed vertical force output. The lower two traces represent horizontal outputs (craniocaudal and mediolateral). Note that, at the beginning of the record, the animal is on the platform and vertical output indicates the animal's weight. Beginning at approximately 0.30 s, the animal made two small hopping movements, but landed back on the platform surface. At 1.2 s, the flight-initiating jump occurred. (B) Tracings of a lateral view of *Desmodus rotundus* during a jump sequence taken from film images. Superimposed on each image is a digitized 'stick' figure that indicates the position of key anatomical points relative to the ground reaction force vector (arrow). The magnitude of the force vector is indicated by the length of the arrow. The points digitized in this view were as follows: (cranially) tip of nose, tip of ear, shoulder, elbow, wrist and distal tip of thumb; (caudally) hip, knee, ankle and toe. Numbers below the stick figures refer to points on the force–time plot (see C) that correspond with the time when each image was taken. (C) Vertical force output from this jump with the time axis expanded. Numbered points correspond to points shown in Fig. 2.

Following the jump, the mean force levels declined to zero; however, there was some ringing (undamped vibration) seen in all channels of the platform. Although this is not desirable, the large surface area required to allow these animals to maneuver, the sensitivity demanded for such small animals and the multiple directional sensitivity all contributed to this effect. The nature of the signal was not obscured by this variation. The ground reaction force vector, determined from vertical, horizontal and positional data, was synchronized with the images of the animal as it jumped. From this, we were able to track the contribution to force generation by the animal's appendages. Details of the force and impulse characteristics of these jumps are shown in Table 1.

Maximum vertical force was achieved while the animal

Table 1. Jump characteristics from representative jumps by *Desmodus rotundus*

	Body mass (g)	Impulse (Ns)	F_{\max} (N)	$F_{\max}/$ weight	Duration (s)
	25.3	0.0622	1.35	5.34	0.078
	20.5	0.0587	1.40	6.83	0.077
	19.7	0.0585	1.50	7.61	0.066
	23.1	0.0628	1.79	7.75	0.059
	30.1	0.0652	1.35	4.50	0.089
	24.0	0.0625	1.93	8.04	0.059
	29.8	0.0579	1.45	4.87	0.088
	21.2	0.0557	1.25	5.90	0.064
	23.1	0.0419	1.05	4.55	0.064
	19.1	0.0639	1.83	9.58	0.053
	21.2	0.0484	1.38	6.51	0.059
	20.7	0.0559	1.38	6.67	0.071
Mean	23.1	0.0580	1.47	6.51	0.070
± S.D.	±3.6	0.0070	0.26	1.57	0.012

F_{\max} , maximum peak vertical force.

be highly variable for evasive jumps (these animals can leap in any direction). Most flight-initiating jumps have a component oriented in the bat's forward direction. Other jumps may be characterized by a lateral or backwards directional component.

Prior to the jump (Fig. 1A), movements of the animal on the platform can be seen as variations in all outputs, particularly when the animal repositioned itself. The mean output of the vertical force when the animal is stationary is a measure of the animal's weight. During the jump, vertical force rose quickly to a peak, then decreased almost as rapidly (Fig. 1C). There was a characteristic shoulder on the descending vertical force trace that was associated with lifting of the carpus and extension of the pollices (we found this in all jumps).

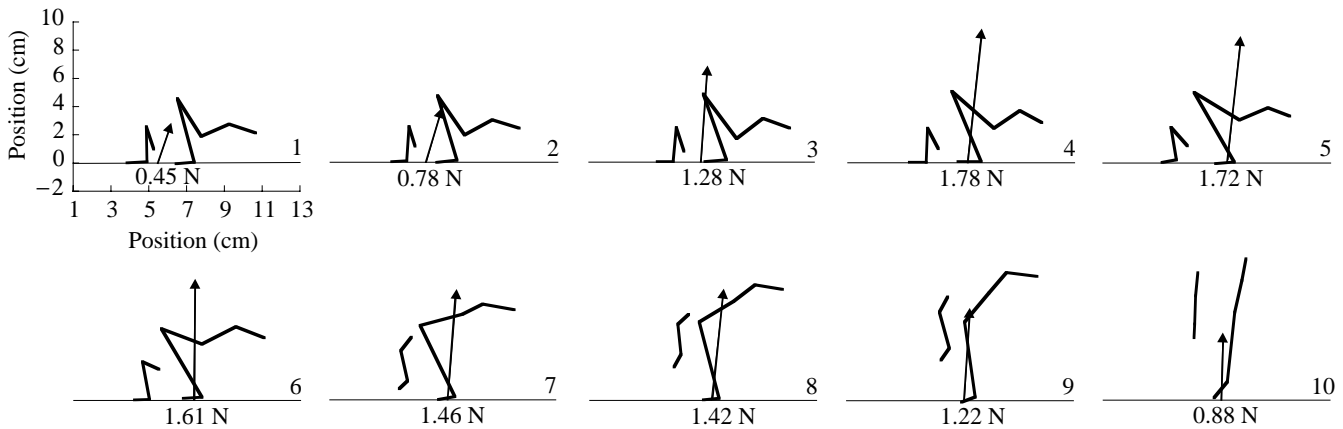


Fig. 2. Lateral view of a representative jump sequence. Digitized points are as described in Fig. 1B, and the numbers correspond to points indicated in Fig. 1C. The force vector orientation, position and magnitude are indicated for each frame (arrow). Note that the initial position of the force vector indicates an even distribution of load between the pectoral and pelvic limbs. Once the jump has started, the position of the resultant force shifts to directly under the pectoral limb.

remained in a crouched posture. However, contact with the platform was maintained as the pectoral limb extended, even though applied force declined. The relationship between vertical jump force and motion of the animal is illustrated in Figs 2 and 3. The joint that undergoes the greatest motion during these jumps is the elbow. There is also adduction at the sternoclavicular, clavoscapular and scapulohumeral joints, but the range of motion at each joint is obscured by skin movement and overlying tissues.

Movement of the pectoral limb indicates that the jump sequence can be broken into three distinct phases, preparatory, jump and flight. In Fig. 4, changes in the angle between the humerus and the forearm (elbow angle) are shown in lateral and frontal views during several jump sequences. The time dimension of these jumps has been adjusted so that the duration of each is equivalent (here the jump is defined as the time from initial force increase until the pollices leave the platform surface). *Desmodus rotundus* begins with a reasonably consistent preparatory phase that involves a slight crouch prior to the initiation of the jump (this can also be seen in the force

trace, Fig. 1A). During the force-generating portion of the jump, the elbow movements are very consistent. During this phase, the elbow extends as the animal pushes itself away from the surface. After the pollices leave the platform, movements that adjust the wing for the first flight downstroke are initiated. Altenbach (1979) has referred to this as the coasting phase, as the animal makes the transition from the jump to the first downstroke of flight.

For flight-initiating jumps by *Desmodus rotundus*, the time required to reach peak force in the vertical direction is inversely related to the magnitude of maximum vertical force (Fig. 5). The difference in time required to reach peak vertical and horizontal force is negatively related to both the magnitude of peak horizontal force (Fig. 6A) and to the rate of vertical force application (Fig. 6B).

Discussion

The data generated in this study are the first direct measurements of the dynamic forces generated by *Desmodus*

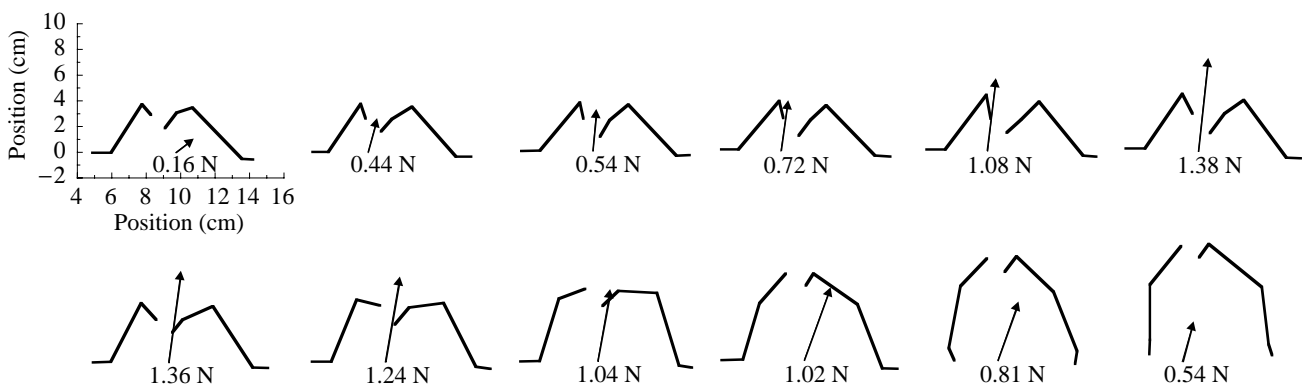


Fig. 3. Frontal view of a jump sequence (a different jump from that shown in Fig. 2). Points digitized were as follows: (left side) tip of nose, tip of ear, elbow, wrist and distal tip of thumb; (right side) tip of ear, elbow, wrist and tip of thumb. The location of the resultant force indicates an even distribution of load between the limbs for this jump.

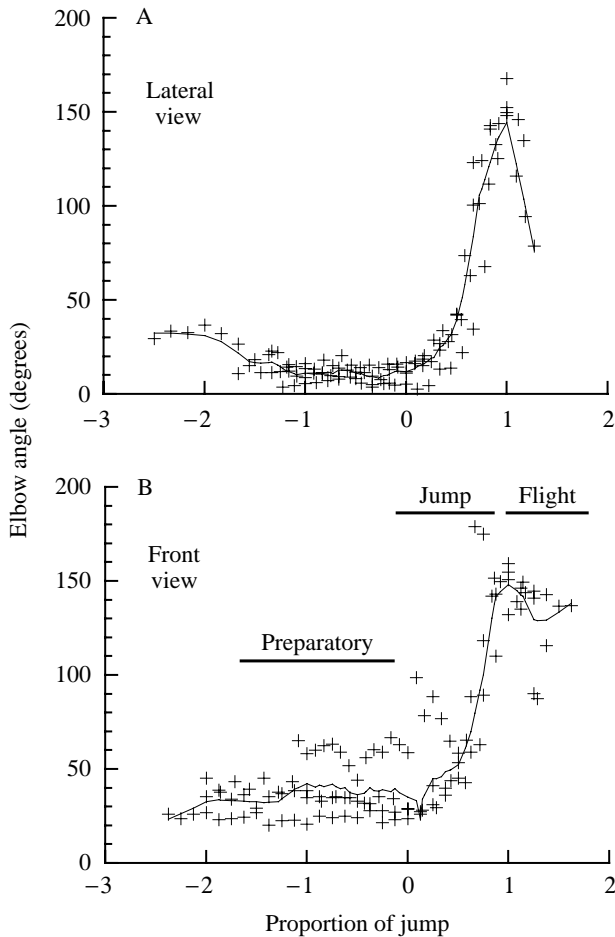


Fig. 4. Elbow angle changes during four jumps from lateral and frontal perspectives. The time frames of jumps have been adjusted so that jump duration (from the initial force increase to take-off) is equal to 1. Although some variability occurs, the jump sequence can easily be divided into preparatory, jump and flight phases on the basis of the pattern of elbow angle change. The lines indicate the results of a weighted mean smoothing function of the combined jumps using a 16% weighting level.

rotundus in its flight-initiating jumping behavior. From these data, previous investigations of electromyographic (EMG) activity (Altenbach 1979, 1988) and muscle fiber-type composition (Hermanson *et al.* 1993), we can arrive at a reasonably complete view of the functional dynamics of this behavior. Of interest are issues of limb function in the jump, muscle composition and design, muscle function within the limb and morphological adaptations responsible for effective jumps in these animals. These issues will be discussed below, and then an interpretation of the function of the pectoral limb in jumping will be provided. Some of the points raised are speculative at this juncture; however, we feel it worthwhile to use this newly available information to generate a more complete view of this behavior. We will make it clear when we move from describing results to interpretation of the data.

Desmodus rotundus is an animal with uniquely adapted pectoral limbs since they are used routinely for flight-initiating

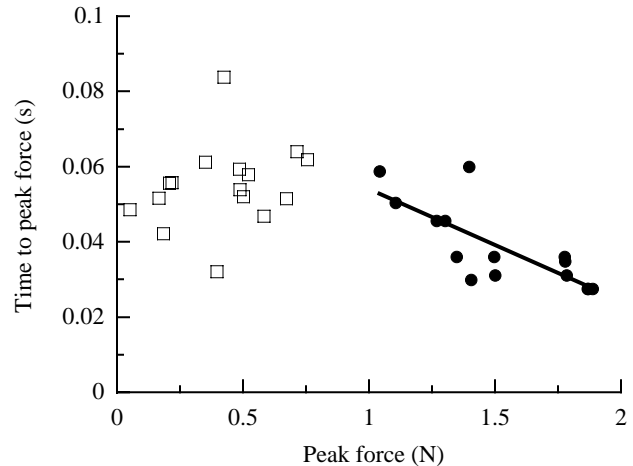


Fig. 5. The magnitude of peak force F_{\max} plotted against the time to reach peak vertical force. Vertical force is plotted as filled circles, horizontal force as open squares. Time to peak vertical force t_{\max} decreases as vertical force increases: $t_{\max}=0.084-0.030F_{\max}$, $r=0.78$, $P<0.001$. Although the time to reach peak horizontal force appears to increase as horizontal force increases, the relationship is not significant.

jumps as well as for powered flight. The capacity to achieve powered flight is very demanding on pectoral limb morphology. Note the substantial deviation of all true flyers from 'typical' vertebrate limb morphology (as seen in terrestrial mammals, for example). Thus, for *Desmodus rotundus*, the capacity for jumping must not compromise the capacity for flight, and jump capability must be provided within the context of limbs designed primarily for powered flight.

Ground reaction force location

Prior to the jump, the resultant ground reaction force is located approximately mid-way between the pectoral and pelvic limb contacts (Fig. 2). As the flight-initiating jump begins, the resultant force vector immediately moves to a position directly beneath the pectoral limb, and it remains at this location until the pollices leave the platform surface at the end of the jump. This indicates that essentially all of the vertical force is generated by the front limb. This is the case even while the rear limb is in contact with the plate surface (frames 1–6 in Fig. 2).

Muscle composition and design

The force-generating capability of the pectoral muscle in the jump must fit within design requirements necessary for efficient powered flight. In an oft-quoted reference to the design of aerial vertebrates, Goldspink (1977) commented that the other contemporary flying vertebrates, the birds, could not 'afford the luxury' of powering their flight with muscles composed of multiple fiber types because of weight constraints. In keeping with this hypothesis, many vespertilionid (Armstrong *et al.* 1977; Brigham *et al.* 1990;

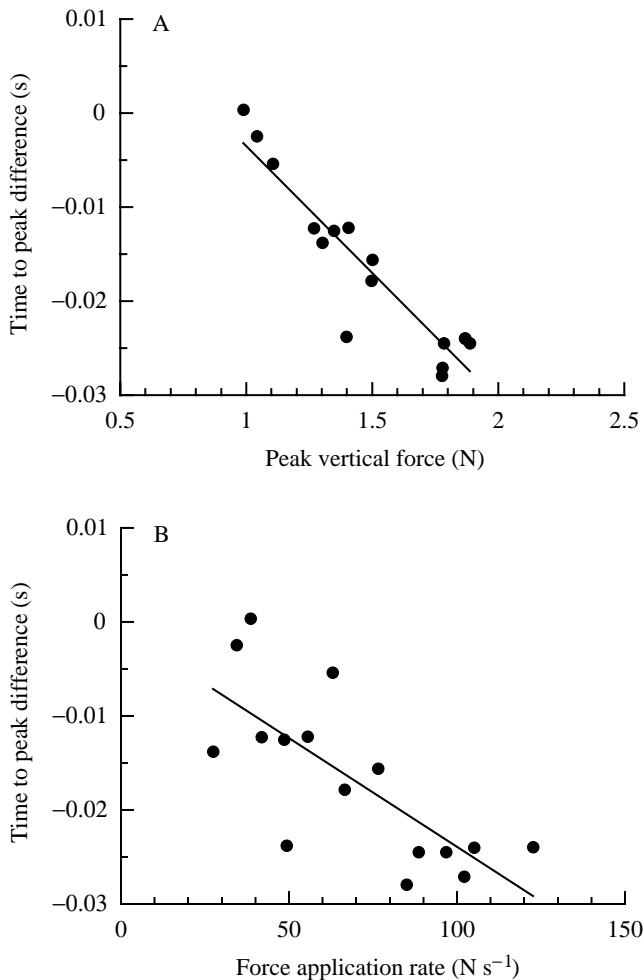


Fig. 6. (A) There is a strong relationship between the difference between the time to reach peak vertical and peak horizontal force D_t and the magnitude of peak vertical force F_{\max} , $D_t = 0.024 - 0.027F_{\max}$ ($r = 0.93$, $P \leq 0.001$). At the lowest peak vertical forces, there is very little difference between the time to reach each peak. As peak vertical force increases, the vertical peak occurs substantially before the horizontal peak. (B) There is a significant relationship between the difference between the time to reach peak vertical and peak horizontal force and the rate of application of vertical force R_v , $D_t = -0.0007 - 0.00023R_v$, $r = 0.74$, $P < 0.01$. There is little difference between the time to reach peak force for horizontal and vertical forces for the slowest force application rates. As force application rate increases, the vertical peak occurs prior to the horizontal peak.

Powers *et al.* 1991; Hermanson *et al.* 1991) and molossid bats (Foehring and Hermanson, 1984) have pectoral muscles composed entirely of type IIa (fast and oxidative) fibers. The phyllostomid bats thus far studied have pectoral muscles composed of two presumed fast-twitch fiber types, both of which are oxidative but that are differentiated on the basis of mATPase and myosin antibody immunocytochemistry (Hermanson and Foehring, 1988; Hermanson, 1997). The pectoralis of *Desmodus rotundus* contains three prominent fast-twitch fiber types that should facilitate precise control over task-dependent recruitment during either jumping or flying

(Hermanson *et al.* 1993). We propose that the force-generation characteristics of the pectoralis during a jump in *Desmodus rotundus* indicates that it is a muscle in which a sequence of different fiber types can be recruited to produce an incremental increase in the muscle force generated.

Sequential recruitment of muscular components within the pectoralis can explain the increase in peak force observed in the most forceful jumps (Table 1). Of particular interest is the negative relationship demonstrated between the time to peak vertical force and the magnitude of the vertical force (Fig. 5). The relationship seen for jumping in *Desmodus rotundus* suggests that, as the pectoralis is recruited to increase jump force, either faster twitch fibers are recruited or the load per fiber is reduced to allow each fiber to increase its effective contraction velocity. Although indirect, this is the first evidence that differential recruitment occurs in the bat pectoralis.

We interpret the change of force generation in terms of the force-velocity relationship of the contraction, rather than as a change in isometric twitch time, because the muscle is probably undergoing substantial shortening even at this stage of the jump. It is known that a shoulder lock is engaged in these animals during the late upstroke and the early downstroke of flight (Altenbach and Hermanson, 1987; J. S. Altenbach and J. W. Hermanson, unpublished observations). Specifically, pins placed in the scapula and greater tubercle (humerus) do not move relative to one another until near the mid-point of the downstroke, when the shoulder lock becomes disengaged. However, the sternoclavicular joint shows significant adductory movement during the early downstroke (Hermanson, 1981). Thus, even though little motion of the animal is observed (Figs 2, 3), it is likely that substantial muscle shortening is occurring at this stage of the jump, assuming that the animal is using a similar pectoral mechanism for the jump and for flapping flight.

Muscular contribution to the jump

The power stroke is a relatively stereotyped behavior in both birds (Dial *et al.* 1991; Dial and Biewener, 1993; Rayner, 1995) and the Chiroptera (Hughes *et al.* 1995; Norberg, 1976; Brandon, 1975). This consistency between the extant flying vertebrates indicates the functional restrictions placed on the pectoral limb in order for it to generate a high-power contraction. It is not surprising, then, that the pectoralis should be used as the main power-generating system for flight-initiating jumps in *Desmodus rotundus*.

Jumping is a rigorous mechanical behavior that provides its own functional demands on the design of the limb system. It is impulse, rather than maximum force, that determines the magnitude of the jump, i.e. impulse determines take-off velocity and take-off velocity determines jump height (Alexander, 1995). Impulse is a measure of the momentum change that results from an applied force and is the product of mean force and the duration over which it is applied. For the same mean force, an increase in the duration of foot contact will result in a proportional increase in jump height:

$$I = Ft = (V_t - V_0)m,$$

where I is impulse, F is force, t is time, m is mass, V_t is velocity at time t , i.e. take-off, and V_0 is the initial velocity, i.e. 0 m s^{-1} . It is a great advantage to a jumping animal to maintain the application of force over a longer period. *Desmodus rotundus* appears to utilize a number of strategies that extend the duration of limb contact during the jump.

As might be expected, much of the power of the jump, particularly in the initial stages, can be attributed to the pectoral muscles. The elbow would probably undergo substantial extension without active contraction of the triceps brachii due to the upward motion of the body resulting from the inertia generated during the early part of the jump. However, appreciable extra impulse is possible with activity of the triceps brachii. Altenbach (1979) suggested that the pectoral muscle is maximally activated during the most forceful jumps (especially when the animal is loaded after a feeding event). During the preparatory phase and very early stages of the jump, the hindlimbs are used to orient the center of mass over the propulsive pectoral limbs.

During flight-initiating jumps, the small forward thrust does not appear to be coupled with the application of upward force. We suspect that the forward thrust detectable by the force platform is independent of the initial vertical thrust and that it indicates activity of elbow extensors, such as the triceps brachii, and retractors of the humerus, such as the latissimus dorsi. Other evidence for the independence of vertical and at least some of the horizontal force comes from comparing the timing of vertical and horizontal force components and their relationship to one another. For the less forceful and slower flight-initiating jumps by *Desmodus rotundus*, there is a negligible difference in the times of peak vertical and peak horizontal force. For more forceful jumps, the difference in timing becomes substantial (Fig. 6A). There is a strong relationship between the difference between the times to peak vertical and horizontal force (D_t) and

both the magnitude of peak vertical force F_{\max} ($D_t = 0.0235 - 0.027F_{\max}$, $r = 0.926$) and the rate of vertical force application R_v ($D_t = -0.0007 - 0.00023R_v$, $r = 0.742$). This evidence supports differential recruitment in the pectoralis muscle and also suggests that vertical and horizontal force are produced by independent muscular systems. *Desmodus rotundus* retains a relatively large muscle mass in the wing and shoulder, presumably to coordinate terrestrial locomotion and to meet the demands of flight-initiating jumps. In the following model of pectoral limb function in the jumps of *Desmodus rotundus*, we provide an explanation of the critical function of these limb muscles.

Interpreting jump force records – a sequential activation model of Desmodus rotundus jumping

The powerful pectoralis muscles are responsible for a large proportion of the jump dynamics, particularly the initial acceleration that overcomes the inertia of the body mass (Fig. 7). However, if only the pectoralis were involved, jump height would be reduced by up to 85% (determined by comparing the velocity of the center of mass at peak vertical force with the velocity and height of the center of mass at the end of contact). If we assume, for convenience, that the contribution of the pectoralis ends at the point of peak vertical force, then the impulse contributed by the pectoralis can be determined as the integral of the force–time curve from the initiation of the jump to the peak vertical force (Fig. 7, the region between A and B). The force generated by the pectoralis will not decrease as abruptly as this, but we can also assume that some of the impulse in the A–B region is contributed by other muscle groups. In the absence of a better estimate, we employ this simple approach for the purpose of illustrating the potential of muscle system interactions within the pectoral limb of *Desmodus rotundus*.

If no other muscle groups were to extend the limb actively beyond this point, then the impulse active to the point of peak

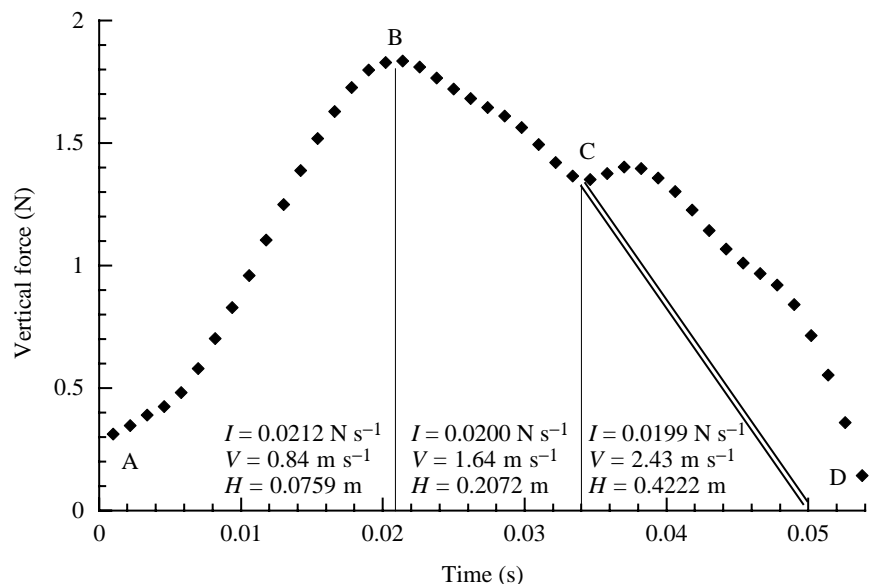


Fig. 7. A model of jump dynamics in *Desmodus rotundus* from which we estimate the contribution of particular muscle groups. To limit redundancy, the complexities of the model, our assumptions and the features labelled on this figure are described in the text (*Interpreting jump force records*). In the calculations, I is impulse, V is vertical velocity and H is jump height.

force (point B) would be responsible for the jump that follows. The terminal velocity at point B under these circumstances can be determined from the impulse and the initial velocity (at A, vertical velocity is zero), and jump height can be calculated from ballistic motion and from the initial height (Fig. 7).

The pectoralis muscles supply the majority of force and contribute much of the vertical acceleration. However, the triceps brachii extends the elbow and performs two functions: (1) it maintains vertical force as the effect of the pectoralis decreases, which increases momentum transfer (impulse); and (2) it provides the forward (horizontal) component that assists in the initiation of the first power stroke following take-off. Altenbach (1979) reported that the triceps brachii, caput longus is active shortly after the initiation of the jump, and this continues until the pollices lose contact with the substratum. Even though absolute vertical ground reaction force declines continuously beyond the peak, we suspect that the decline is mitigated by the active extension of the elbow. The time over which force is maintained (Fig. 7, points B–C) produces an impulse that nearly equals that imparted by the pectoralis. Also, because the force over this region acts to accelerate an object that has already achieved an appreciable velocity, the terminal velocity at the end of this period doubles and total jump height increases threefold (through ballistic motion and a higher absolute take-off point as a result of the extended limb).

The third substantive contributor to the jump dynamics are the pollices. Ventral flexion of this digit is the function of the palmaris longus, abductor pollicis longus and flexor digitorum profundus. The latter is a particularly large muscle in *Desmodus rotundus* (Altenbach, 1979). Although no direct EMG data exist for the activity of these muscles during the jump, their size (particularly the flexor digitorum profundus) and the characteristic ‘shoulder’ observed on the descending force trace corresponding to flexion of the pollices (we observed this on all jump force records) indicate that the thumb makes a substantial contribution to the jump. Even though the change in magnitude of the ground reaction force is small, the animal has already achieved a substantial vertical velocity by the time that the acceleration due to the flexion of the pollices is added (in Fig. 7, note the change in velocity and height between points C and D). The triceps group probably maintains its activity while the thumbs extend, as indicated by EMG records (Altenbach, 1979). It is likely that the thumb is responsible for the shoulder evident in the force record in the latter portion of the jump and the higher overall force level in that region (displacement of the force curve above the slanted double lines in the region C–D, Fig. 7). The action of the thumb alone would be responsible for approximately half the impulse in the region C–D or one-sixth of the total impulse of the jump. The portion of the impulse that we estimate is contributed by the pollices alone is indicated in this diagram by the region under the force–time curve between points C and D, but above the double bars.

Although the wings of *Desmodus rotundus* are short and robust in comparison with those of other bats of similar body size, one of the most distinguishing features of their pectoral morphology is the length of the thumbs (Greenhall and

Schmidt, 1988). We have shown that the pollices can have a substantial effect on the impulse imparted to the substratum during a jump. There are other factors of thumb function during jumping that must also be considered. The pollices add a third segment to the jumping limb in much the same way that the foot adds a third segment to the human leg. Note that the other digits of the bat are involved in the flight apparatus and are folded against the antebrachium during the jump. A three-segment limb can increase jump height, even if overall limb length remains unchanged (Alexander, 1995). A three-segment limb also provides an extra degree of intersegment movement during the jump. It has been shown that this extra degree of freedom substantially increases the potential for optimizing antagonistic muscle force (Kuznetson, 1995). Recent work on human jumping has also shown that power generated in proximal segments can be transferred to distal segments *via* bi-articular musculature (van Ingen Schenau and Bobbert, 1993; Jacobs *et al.* 1996). We have not analyzed power transfer in the present study, but suspect that this may be another strategy employed by *Desmodus rotundus* to maximize jump capability.

Dynamic analysis of flight-initiating jumps in *Desmodus rotundus* provides a unique opportunity to investigate the interaction of the functional constraints necessary for the pectoral limb to provide the animal concurrently with flight capability and impressive jumping ability. The relative timing of vertical and horizontal force peaks suggests that two independent muscular systems are responsible for generating force in these animals, a situation that can be attributed to their pectoral limb specializations.

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