

Turns in Cluttered Flight Environments:

Responses of *Artibeus jamaicensis* to Constrained Flight Paths

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Abstract

Frugivorous bats must accurately navigate foliage, which can tear wing membranes and adversely affect their flight ability. Previous studies of bat maneuverability have shown changes in height during turns; for this study, bats were made to fly through three square apertures (40 cm square) of constant height, the middle of which was horizontally offset from the other two, to examine changes in performance related to extremity of turns. Six *Artibeus jamaicensis* individuals were selected for their ability to navigate the course, then were recorded flying through offset values ranging from 0 cm to 70 cm by three phase-locked cameras at 1000 Hz. A marker on the body of the bat was digitized in each camera view to determine the three-dimensional location of the bat.

We found that, as the bats were not vertically constrained between each aperture, they passed through the apertures in parabolic paths during which they produced insufficient lift to stay aloft in level flight. To compensate, other periods were spent producing more lift than necessary to stay aloft; in small offsets, these periods did not occur in the volume examined. Bats flying through courses with greater offset values would often go through such periods of positive vertical acceleration between apertures, but their reduction in lift at the middle (horizontally offset) aperture was not dependent on offset value, indicating that this flight maneuver is motivated by constrained space significantly more than by a need to produce lateral thrust. While at low offset bats flew at high speed very close to the edge of the aperture, at higher offsets and lower speeds they flew further from the edge of the aperture.

Introduction

Maneuverability is critical to evolutionary success in bats. Frugivorous bats such as *Artibeus jamaicensis* spend much of their time flying in cluttered habitats, where protruding foliage can tear a wing membrane, adversely affecting flight performance (Norberg, 1994). *A. jamaicensis* individuals eat only ripe fruit and can, with other frugivorous species, clear a fruit-bearing tree in under three days (August, 1981). Although they are canopy foragers, their preferred fruit, figs, are distributed along the inside and outside of tree crowns (Stockwell, 2000). In some environments, they spend most of each 3-to-5 minute feeding flight engaging in circling and hovering flight to select a fruit (Morrison, 1980), creating strong evolutionary pressure to be sufficiently maneuverable to access fruit. Additionally, predators exert pressure for individuals to maintain day-roosting sites and harem locations in densely-cluttered areas (Morrison, 1980).

The importance of maneuverability in access to foliated areas has been demonstrated in insectivorous bats. Additional weight is known to reduce maneuvering ability (Aldridge & Brigham, 1988) and, in insectivores, reduce time spent hunting within or close to foliage in favor of time spent hunting in open air (Kalcounis & Brigham, 1994).

Within a banked turn, lateral acceleration is generated by rolling the body and redirecting a portion of the lift laterally, often resulting in a drop in altitude (Aldridge, 1987, Iriarte-Diaz & Swartz, 2008). In a similar experiment to this one, the extent to which a bat lost height was found to correlate with the horizontal adjustment in course it

was required to make (Au et al, 2010). However, in another analysis of turning flight, bats were observed to compensate through flapping and gain height during the first half of a turn (Iriarte-Diaz & Swartz, 2008).

The average lift (L_a) that a bat produces must, over the course of level flight, counteract the force of gravity (g) on the body's mass (M) (Norberg, 1976).

$$L_a = M * g \quad (\text{equation 1})$$

When a bat produces more or less lift (L) than its weight, its vertical acceleration (the second derivative of its vertical position, or z'') changes, as follows:

$$L = (z'' + g) * M \quad (\text{equation 2})$$

By equation one, a bat in level flight produces an average lift of 9.8 m/s^2 times its mass. When a bat produces less lift than this, its vertical position will accelerate downwards. Inversely, when a bat can accelerate downwards, it need not produce as much lift. Loss of lift to increase lateral acceleration has been described (Aldridge 1985) but not correlated with the extent of the turn performed.

Studies on pigeons have shown that the power required for angled flight can be estimated as the sum of the power required for level flight and the change in potential energy due to gravity (Berg, 2008), and bats have been shown to be able to convert potential energy to kinetic energy with high efficiency (Au, 2010). Rather than increase their energy expenditure during a turn, a bat can decrease their altitude during the turn, then regain that altitude when not turning. This will have a slightly higher overall energy cost, but at a more even rate of energy expenditure.

Bats can also minimize the force necessary to turn by reducing speed (Stockwell, 2000), and have been shown to decrease speed in anticipation of larger turns (Au, 2010). *R. ferrumequinum* in particular has been shown to decrease speed almost to zero before turning extremely tightly, then regaining speed by losing altitude (Aldridge 1987).

In this experiment, bats were made to perform turns through small apertures of constant height. By reducing their ability to decrease height, we hoped to prompt and observe other kinematic adaptations to cluttered flight requiring sharp turns. Data will also be examined to evaluate the viability of apertures as an experimental method to force a specific flight pattern.

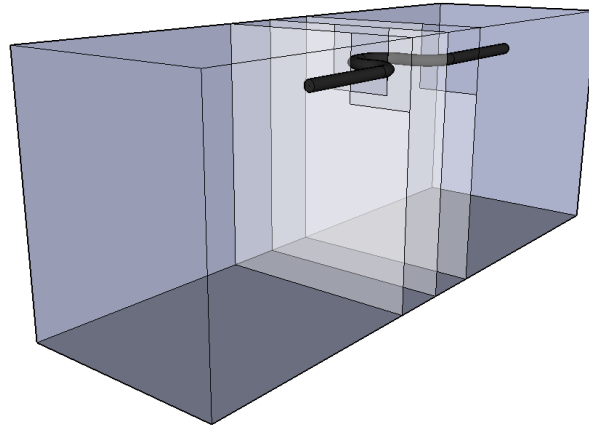
Materials and Methods

Experimental Animals and flight corridor

The sample population for this study was five adult captive-raised male *Artibeus jamaicensis* individuals (body mass 31.91-43.93g), selected from the population housed at Brown University. These individuals were housed in a large cage allowing for short flights and provided with food and water *ad libitum*. They had been trained to fly from one end of a flight corridor to another, with first opaque and then transparent obstacles. They were selected for their willingness and ability to fly through the course.

For this experiment, three parallel walls of transparent acrylic glass were placed in the corridor, each adjacent pair 0.40 meters apart from each other. The walls were made of sheets of acrylic

Figure 1: the flight corridor, with middle window offset 0.42 meters. An idealized flight path is shown in black; the bat would fly away from the viewpoint in this diagram.



glass suspended from the ceiling. In each wall a 0.40-meter section of acrylic glass was suspended 0.40

meters down from the ceiling, creating an aperture in the wall through which the bat could fly. The acrylic glass was cleaned frequently to ensure clear camera views of the bats.

The volume of the obstacle was calibrated at the start and end of each day of experimental flights with the Direct Linear Transformation method (DLT), a technique for calculating 3D coordinates from multiple camera views (Riskin et al., 2008), using a 24-point calibration sheet hung at five locations along the calibrated space, for a total of 120 calibration points. The measurements of the corridor were taken by DLT after the completion of the experiment. Three phase-locked Photron 1024 PCI digital high-speed cameras (Photron USA, Inc., San Diego, CA, USA), located within the flight enclosure, recorded the bats' flights within the calibrated area.

Experimental Treatments

Of the three apertures in the flight enclosure, the first and third were always located in the upper-right-hand corners of the walls of acrylic glass. The middle aperture was horizontally offset 0, 0.20, 0.42, or 0.67 meters to the left; the measurements of these distances were obtained after the experiment by DLT from images taken by the three cameras. Each of the five bats was assigned a random order of four trials, with each trial

having a different offset distance of the middle aperture. Bats were never made to run two consecutive trials.

Each bat was anesthetized with isofluorane gas before its first trial and had three markers painted on it: one on the ventral aspect of each shoulder, and one on the caudal end of the sternum. For subsequent trials faded marks were re-painted without anesthesia of the bat.

In each trial, the bat was weighed, then released alone into the flight corridor and allowed to fly a minimum of five times through the course prior to data collection. We then recorded three flights through the obstacle. The bats' flights through the course were only recorded in one direction. We disregarded any flights in which the bat's course of motion seemed to be upset by a collision with the acrylic glass.

Calculations of flight path

The chest marker of the bat was used to approximate its position at each frame while the bat was inside the course. The coordinate system was global and aligned with the overall direction of flight from the first to third apertures; x was positive forward, y was positive left, and z was positive up. The bat's three-dimensional position was calculated at each frame in which it was visible to at least two cameras, in other frames it was estimated using a third-order over-constrained polynomial fit (Riskin et al., 2008). Each bat's three-dimensional position was tracked between the first and third apertures.

The derivative of position (speed) was obtained as the average of the forward and backward divided differences, with a difference of one frame. The function was then smoothed using the same third-order over-constrained polynomial fit. The heading was

calculated as the arctangent of the x and y components of the speed, and the difference between maximum and minimum heading was calculated as an indication of the extent of the turn performed through the middle aperture.

The derivatives of speed (acceleration) and yaw (angular acceleration) were found to be dominated by the influence of wingbeats. For purpose of taking vertical acceleration, the forward and backward divided differences of speed were taken between the reversal points of the plot of vertical speed, resulting in a resolution of typically two points per wingbeat.

To express the extent to which bats reduced their lift production, we took the ratio of their current lift (L) and their average lift to sustain level flight (L_a). This can be calculated from equations (1) and (2) as:

$$L/L_a = (z''+g)*M/(M*g) = (z''+g)/g \quad (\text{equation 3})$$

The L/L_a value for each bat was calculated over the course of their flight.

The offset of the bat's flight was calculated as the difference between its y-coordinate at the second aperture and the average of its y-coordinates at the first and third apertures. This provided a measurement of how much the bat's flight was perturbed. This will be referred to as the observed offset, as opposed to the offset treatment, which is the offset of the apertures alone, regardless of how bats chose to fly through them.

Each trial's average horizontal speed, L/L_a at the middle aperture, observed offset, offset treatment, distance from the edge of the middle aperture, speed at the middle aperture, maximum difference in heading, and the mass of the bat as weighed before that

trial were evaluated for correlation with standard least squares regression analysis (Matlab 7.5.0) and a cut-off p-value of 0.05. Individual was added as an effect to evaluate variation between bats.

Results

General description of flight

In the first and second offset treatments (with displacements of 0 and .20 cm each), bats flew through the course in one long concave-down parabolic path, accelerating downwards from beginning to end (L/L_a value below one). In the second offset treatments, bats flew to the left of the first and third apertures and the right of the middle aperture, with very little actual perturbation to their flight path.

In the third and fourth offset treatments (displacements of .42 and .67 cm), bats typically made short concave-down parabolic paths through each aperture, and compensated with concave-up parabolic paths between the apertures (L/L_a value above one). In five trials, four of them by the same bat, bats overshot the second aperture, completed a turn between the acrylic glass curtains, and passed through the middle aperture at an angle. These trials were discarded, as they were no longer turning through the middle aperture, but it is notable that they performed concave-down parabolic paths during their extremely constrained 180° turns. Of the retained trials, the average L/L_a at the middle aperture was 0.7 (s.d. 0.2). Some bats accelerated upwards while passing through the middle aperture; this occurred almost exclusively at low offsets.

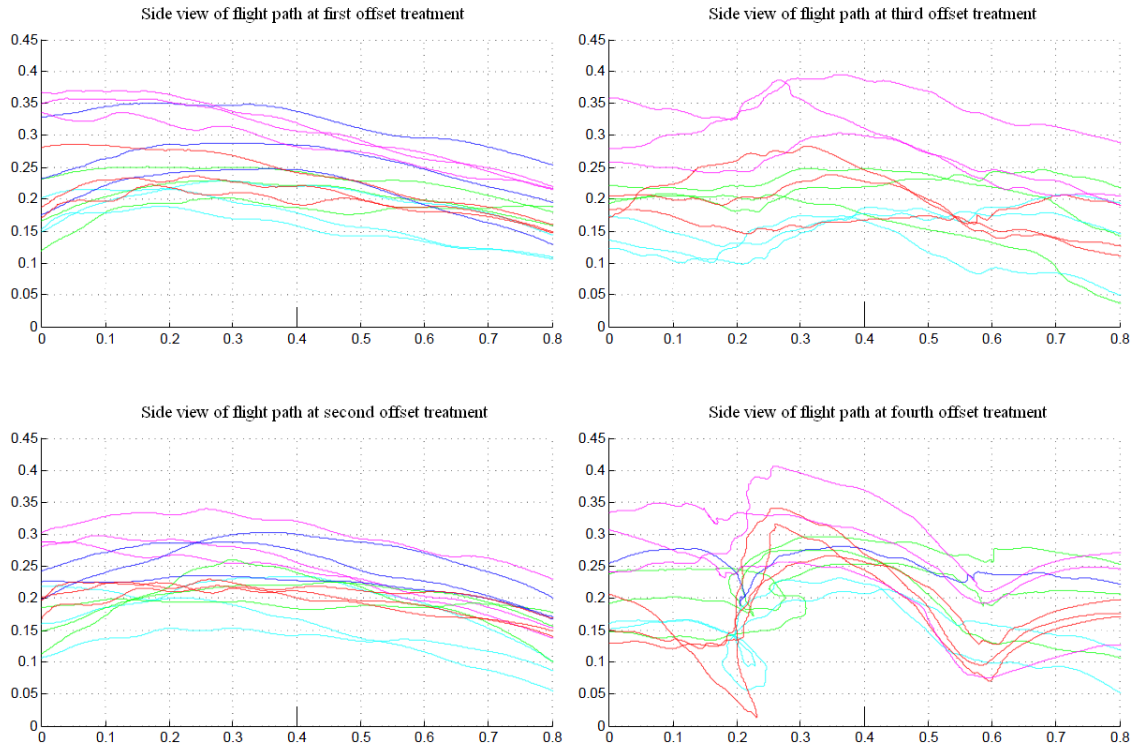
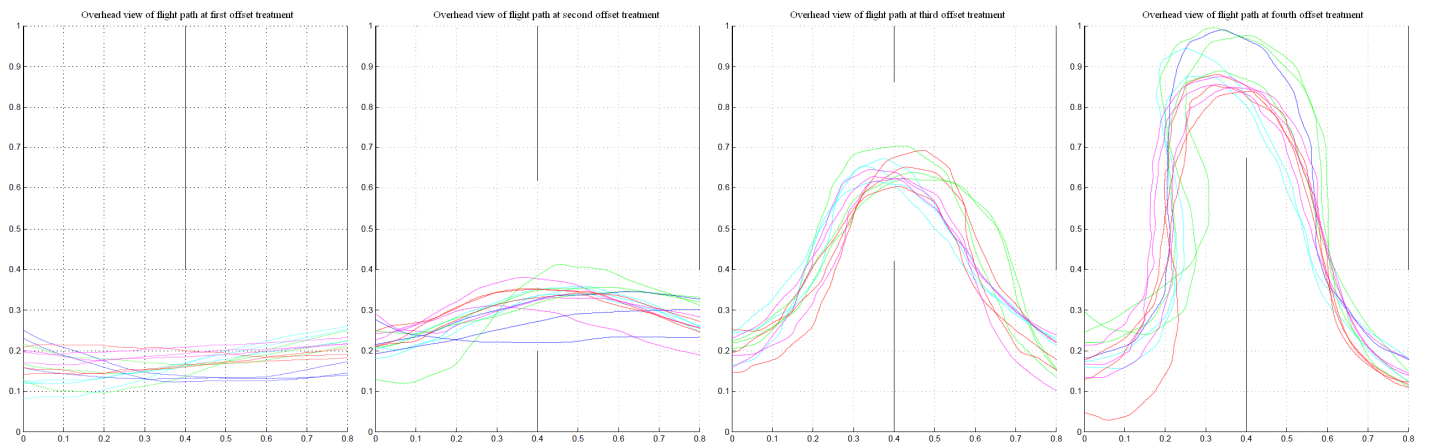


Figure 2: side view of flight paths by offset treatment, paths colored by individual, units in meters. Note that, at the fourth offset, some individuals turned more than ninety degrees and moved backwards. The height of the aperture is marked at 0.4 m. As offset increases, wing beats become more prominent in the bats' paths.

Figure 3: top-down view of flight paths by offset treatment, paths colored by individual, units in meters. Although the offset treatment increases steadily, the observed offset increases sharply between the second and third offset treatments.



The wing beats of the bats proved to be a strong influence on all aspects of their position once first and second derivatives were considered. Problematically, the level of influence of wing beats on the bat's positioning varied both with the degree of roll of the bat and with the level of offset. This limited our ability to obtain results related to yaw in particular, despite aggressive smoothing.

The bats typically passed within an average of 0.16 m (s.d. 0.04 m) of the edge of the second aperture. Although the wingspans of the bats used in this study were not recorded, this is below the typical *Artibeus jamaicensis* wing length of 19.5 cm (s.d. .6 cm) (Stockwell, 2000). The bats typically flew very close to the bottom edge of the first and third apertures.

Effects of Offset

Correlation of the maximum heading difference experienced by each bat with the observed offset confirmed that offset apertures were a reliable way of having bats perform sharp turns ($r = .92$, $p < 0.0001$). However, there was a large gap between observed offsets in the first and second offset treatments, where bats could fly a straight course through the apertures, and in the third and fourth offset treatments.

As observed offset increased, bats' average speed through the trial and their speed at the second aperture decreased ($r = -.74$, $p < 0.0001$). There was no statistically significant correlation observed between the offset treatment, observed offset, or maximum yaw and L/L_a at the second aperture; the bats reached the same levels of L/L_a regardless of the treatment.

As offset increased ($r = .52$, $p < .0001$) and speed decreased ($r = -0.41$, $p = 0.0019$), bats' distance from the edge of the middle aperture increased; they flew through the middle aperture closer to the center.

Effects of Individual

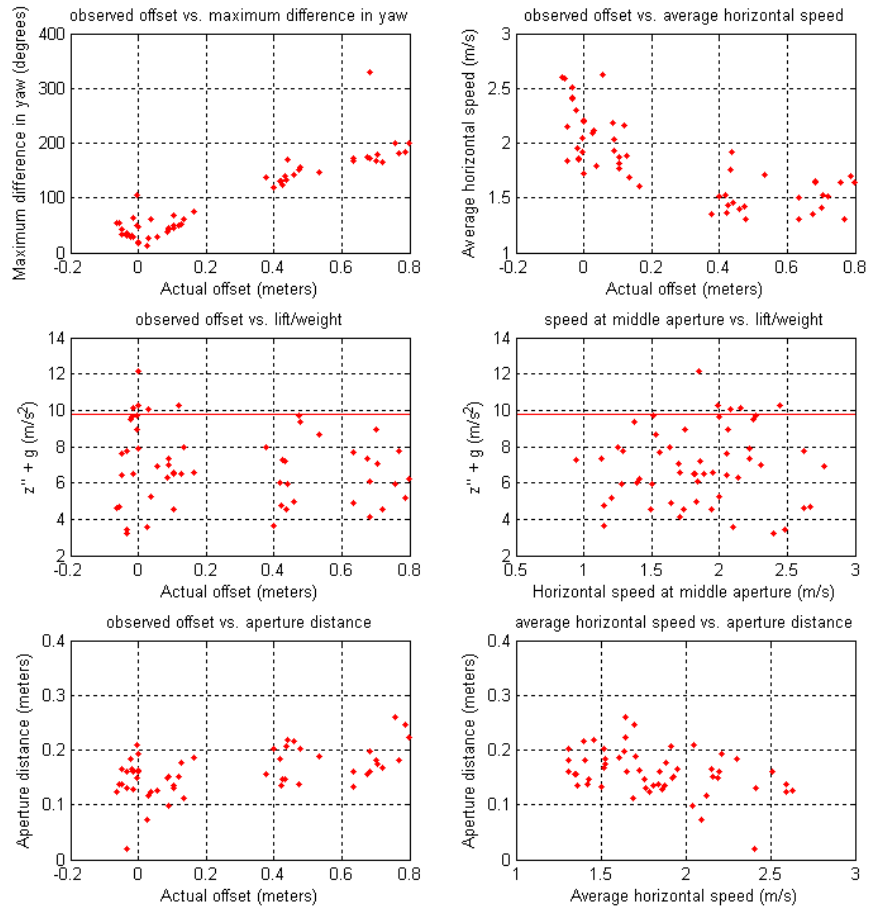
Statistically significant variation between individuals was found for both L/L_a and average horizontal speed. However, no correlation was found for velocity at the middle aperture. Additionally, the weight of the bat was not found to correlate with any measured quantity.

Fig 4-8: values plotted over all trials.

Fig 4-5: as the observed offset increases, so does the difference between bats' maximum and minimum yaw, and average horizontal speed decreases.

Fig 6-7: L/L_a is presented here in relation to gravity. Values below the red line indicate L/L_a values below one; the red line is the force of gravity. No correlation was found in either case.

Fig 8-9: bats were observed to pass closer to the aperture (lower aperture distance) with lower offsets and higher speeds.



Discussion

All bats flew through the course with a net negative z'' , or an L/L_a of less than one. Increase in offset prevented the bats from sustaining a continuous concave-down parabolic flight path typical of negative z'' within their constrained range of altitude; the bats instead performed two to three concave-down parabolic flight paths punctuated with one to two concave-up parabolic paths, or periods of positive z'' . However, there was no correlation between the L/L_a during the turn and the difficulty of the turn, indicating that the parabolic flight path was a response to the aperture, and not to the need to generate lateral acceleration. The negative correlation between observed offset and average speed indicates that reduced speed was the main method of generating increased lateral thrust, and that the reduced lift was a response to the cluttered environment.

Reduced Lift Production

Bats significantly reduced their lift while passing through the aperture, by an average of 30%. However, we believe this reduction in lift was neither to produce lateral thrust nor to reduce turning radius, as has been previously described (Aldridge, 1985, 1987), or there would have been a correlation between it and the observed offset, as the turns of increasing difficulty were performed within periods of reduced lift.

Because the effect remained even with zero offset, i.e., the bats flying in a straight line through the apertures, but by mathematical principles could not be sustained in normal flight, one reasonable explanation is that reduced lift is a result of the aperture set-up, and that *A. jamaicensis* individuals typically reduce lift while passing through areas of clutter. However, it is also possible, because the apertures were adjacent to the ceiling,

that the bats were trying to maintain distance from the ceiling, and this was the most energy-efficient method of doing so.

Further experimentation to clarify these effects would involve varying aperture size and location. Apertures and corridors are a convenient way of prompting consistent flight patterns (Aldridge, 1985, 1987), but these results contain troubling indications for the extent to which data from such experiments can be generalized to open-air flight paths.

Reduction of Velocity and Wing Beat Timing

Speed has been documented as decreasing turning radius (Stockwell, 2000; Aldridge, 1987). Our data support this conclusion; reduction of speed was one of only two observed correlations to increased offset. The other correlated value was the distance from the edge of the aperture.

Studies on maneuverability typically use vertical objects as obstacles (Stockwell 2000; Sleep, 2003; Orbach 2010; Au 2010), often characterizing maneuverability as an ability to pass between two close vertical objects, or navigate a field of vertical objects. However, species such as the helicopter damselfly, a species with low maneuverability under parameters of predator-avoidance or control of heading in flight, demonstrate great maneuverability in surface gleaning of spiders from their webs. Because of their low wingbeat frequency, they are able to glean spiders from their webs without becoming entangled themselves, by being able to swoop in between wingbeats (Dudley 2002).

We theorize that the increased distance from the aperture was the result of maneuverability related to the timing of wingbeats: as wingbeat density

(wingbeats/meter) increased with reduced speed, it was no longer possible for the bats to pass by the edge of the aperture during a period of their wing beat in which wing profile was minimized.

Influence on Evolutionary Pressure

A. jamaicensis has been considered to be under conflicting evolutionary pressures. For flights beneath the canopy and foraging within crowns of canopy trees, a high aspect ratio and shorter wings are favored (Stockwell, 2000). However, for long flights spent commuting or searching, lower aspect ratio and longer wings are favored (Norberg, 1987). An indication of their varied lifestyle is their echolocation frequency, which spans a wide range (Stockwell, 2000): high-frequency for resolution of nearby objects, and low-frequency for long-distance sensing (Sleep, 2003). Evaluation of these environmental pressures may be reconsidered in light of potential relevance of wingbeat density, as higher speeds during flight may allow them to pass closer to targets such as figs, which they evaluate for ripeness before eating (Morrison, 1978).

Future research

Within the data obtained in this study more insight may be gained from doing further digitization of points on the bat. These would allow for consideration of body kinematics such as roll, pitch, and yaw and, if points on the wing were included, a center-of-mass study, using a model developed for *Cynopterus* individuals (Iriarte-Diaz et al., 2008). Such investigation would hopefully yield definitive conclusions on the cause of loss of lift and the mechanics behind timing wingbeats around apertures.

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