

Sticking ability in Spix's disk-winged bat, *Thyroptera tricolor* (Microchiroptera: Thyropteridae)

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Abstract: Roosting Spix's disk-winged bats, *Thyroptera tricolor*, use disks on their wrists and ankles to cling to smooth leaves. In 584 trials we tested the ability of 31 *T. tricolor* and 121 other bats lacking disks (461 trials with 18 species from three families) to adhere to (i) medium-grade sandpaper, (ii) Lexan polycarbonate, (iii) solid sheet aluminum, and (iv) porous sheet aluminum. While *T. tricolor* readily adhered to smooth surfaces, the other species did not. *Thyroptera tricolor* did not show the same ability to adhere to rough surfaces as the other species that were tested. As was demonstrated by their performance on porous aluminum and sandpaper, the disks of *T. tricolor* worked by suction and sometimes by wet adhesion. In the course of adapting to adhere to smooth surfaces, *T. tricolor* appear to have lost some ability to roost on rough ones, although one adult *T. tricolor* climbed on a screen covering the inside walls of the polycarbonate cage by interlocking its thumb claws with the surface.

Résumé : Pour se percher, les chauves-souris *Thyroptera tricolor* s'aident des ventouses qu'elles portent aux poignets et aux chevilles pour s'agripper à des feuilles lisses. Au cours de 584 essais, nous avons mesuré la capacité de 31 *T. tricolor* et de 121 autres chauves-souris sans ventouses (461 tests : 18 espèces à trois familles) de s'agripper à (i) du papier de verre de grain moyen, (ii) du polycarbonate Lexan, (iii) de l'aluminium en feuilles pleines et (iv) de l'aluminium en feuilles poreuses. *Thyroptera tricolor* s'accroche facilement à des surfaces lisses, alors que les autres espèces ne le peuvent pas. En revanche, *T. tricolor* semble moins habile que les autres espèces à s'agripper aux surfaces rugueuses. Comme le démontre leur performance sur de l'aluminium poreux et sur du papier de verre, les ventouses de *T. tricolor* collent par succion et parfois par adhésion humide. En s'adaptant à se coller aux surfaces lisses, *T. tricolor* semble avoir perdu de sa capacité de se percher sur des surfaces rugueuses, bien qu'un adulte ait été observé grim pant sur du grillage en entrecroisant les griffes de ses pouces avec la surface.

[Traduit par la Rédaction]

Introduction

Researchers have investigated the ability of animals in four phyla to adhere to and walk on smooth vertical or overhanging surfaces. Limpets and cephalopods (Mollusca), starfish (Echinodermata), frogs, and geckos (Chordata) cling to smooth surfaces using mechanisms ranging from suction in the Mollusca (Smith 1991a, 1991b) to intermolecular adhesion in geckos (Autumn et al. 2000). The ability to adhere to smooth surfaces also appears in the Arthropoda (e.g., Stork 1980; Walker et al. 1985; Lees and Hardie 1988; Roscoe and Walker 1991). Other taxa exhibit similar abilities but are less well studied. Although some mammals climb easily on smooth surfaces, our knowledge of how attachment is maintained has been inferred from anatomical investigations. Observations of living animals, which have been essential to our understanding of this behaviour in other taxa (Emerson

and Diehl 1980; Hanna and Barnes 1991; Smith 1991b), have been lacking for mammals.

Disk-like structures on the wrists and ankles of four species of bats, one from Madagascar (Myzopodidae) and three from the Neotropics (Thyropteridae), are presumed to give these animals the ability to grip to smooth surfaces such as the waxy cuticles of furled leaves (Altringham 1996; Fenton 2001, p. 183). The most studied of these species, *Thyroptera tricolor* (Spix's disk-winged bat), which weighs ca. 3.5 g, is from lowland forests from Veracruz, México, to tropical South America (Wilson and Findley 1977). By day, *T. tricolor* have most often been found roosting in the furled leaves of *Heliconia* spp. (Heliconiaceae) and *Calathea* spp. (Marantaceae). At maturity these leaves are elliptical, but during their development they are rolled and tube-like for ca. 24 h, providing roosts for thyropterid bats (Findley and Wilson 1974).

For a bat to remain stationary on a smooth non-horizontal surface, such as the vertical face of a *Heliconia* leaf, it must resist slipping or falling by applying forces that act in static opposition to gravity. In other animals, six mechanisms for achieving this have been reported: gluing, intermolecular adhesion (Nachtigall 1974), wet adhesion, suction, interlocking, and friction (Emerson and Diehl 1980). Gluing involves hardening and combines adhesion (the intermolecular forces between two dissimilar materials) and cohesion (the intermolecular forces among identical molecules), and involves a

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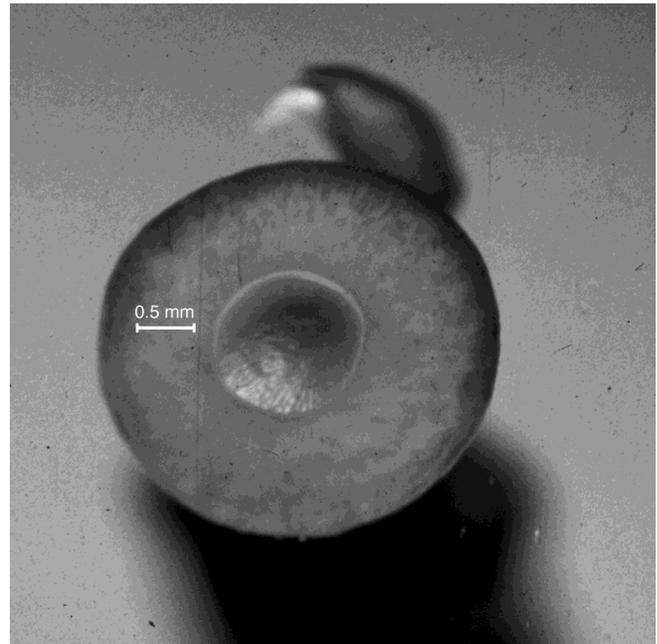
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cement spread between the surfaces (Nachtigall 1974). Intermolecular adhesion describes the attraction between the closely contiguous surfaces of adjacent materials, and requires a very small distance of separation (Nachtigall 1974). Wet adhesion occurs when two solids are held together by an intervening layer of liquid, and there are two types, Stefan adhesion and capillarity. Stefan adhesion occurs when the liquid is present both at the surface interface and around it. The two adhering surfaces are so close that the viscosity of the intervening liquid causes it to resist the flow that must accompany the separation of the surfaces (Smith 1991*b*). Capillarity occurs when the intervening liquid is not present outside the joint. The force in capillarity results from the surface tension of the liquid. Both types of wet adhesion are positively related to the surface area of contact between the two surfaces (Emerson and Diehl 1980). They require no muscular exertion, and function even in holding wet paper to glass (Hanna and Barnes 1991). Suction occurs when an animal creates a partial vacuum over some area of the substrate–body interface (Emerson and Diehl 1980). It is limited by the magnitude of the air-pressure differential produced, and depends on both an uninterrupted seal between the sucking organ and surface (Emerson and Diehl 1980) and a non-porous surface (Smith 1991*a*). Interlocking, the intermeshing of projections from two solid surfaces, is limited by the roughness of the interacting solids. The force supplied results from the resistance of the substrate to compression and its ability to resist breaking (Emerson and Diehl 1980). Interlocking differs from friction, which is the potential energy analogue of interlocking, and only occurs in the presence of a normal force. While the disk may be non-rigid, the surface is rigid, so bending will not put any part of the contact area at an angle other than that of the surface as a whole. Once the surface passes 90°, there is no twisting back to angles <90° as might occur when two non-rigid surfaces meet. The breakdown of Amontons' laws on the molecular scale is due to the interference of other forces, like intermolecular adhesion, which we have addressed. Frictional forces depend on a normal force holding the surfaces together, but after 90° the normal force is negative, so no amount of friction will hold the surfaces together. The greatest functional difference between friction and interlocking is that friction will allow animals to adhere to an inclined surface but not a vertical or overhanging one. Using interlocking, animals can adhere to surfaces at all angles. Both friction and interlocking are independent of the surface area of contact (Emerson and Diehl 1980).

Since the species' description in 1823, many researchers have focused on the disks of *T. tricolor* (Fig. 1), and most have proposed suction as the mechanism of sticking (Wimsatt and Villa R. 1970; Schliemann 1970*a*, 1970*b*, 1974; Thewissen and Etnier 1995). De la Espada (1870) noted that its disks, when adhering to the skin of an observer, produced a sensation similar to that experienced when the air was drawn out of a thimble with the mouth and the tongue was placed over the opening. He stated that the suction ability of the disks depended on exerting musculature intrinsic to the disks. Dobson (1876) later found no musculature in the disks and proposed that evacuation of air from beneath the disk was achieved when the body of the bat pressed the disk into position on a surface. A suction cup could work on the basis of elasticity

Fig. 1. Thumb disk of *Thyroptera tricolor* viewed through the vertical glass surface to which it is attached. Photograph by M.B. Fenton.



when elastic elements are present, but detachment of the cup would be more difficult.

Beneath each disk a cartilaginous plate is attached to a tendon leading to muscles outside the disk, at the metacarpophalangeal joint of the thumb in the foredisks and the metatarsophalangeal joints of ankylosed digits III and IV in the hind disks (Wimsatt and Villa R. 1970). This arrangement permits the disk shape to be manipulated from without, and explains how disk shape could be controlled even without intrinsic musculature. These data led Wimsatt and Villa R. (1970) to conclude that the functional mode of the disks is suction rather than any other sticking mechanism.

The purpose of this study was to investigate the ability of *T. tricolor* to adhere to different surfaces and thus to determine the underlying mechanism, while examining its impact on roost selection and roosting posture. Using behavioural data from live bats we tested two hypotheses, first that suction is the mechanism of sticking (Wimsatt and Villa R. 1970) and second that *T. tricolor* is specialized for roosting on leaves and smooth surfaces to the exclusion of other possible roosts (Findley and Wilson 1974).

Materials and methods

Study areas and animals

From 6 May to 12 June 1999, we conducted fieldwork at the Caño Palma Research Station near Tortuguero, Costa Rica (10°35'N, 83°32'W), where we caught most bats after dusk, using mist nets. We caught some *Rhynchonycteris naso* (Emballonuridae) with hand nets at their day roost in the boat house of the station. Also during daylight hours we searched the forest for plants of any species that exhibited the young, rolled leaves commonly used by *T. tricolor* as day roosts. After experimentation we returned all *T. tricolor* to their roosts of capture and released other bats from the research station.

On the nights of 27 and 28 August 1999 we caught bats with a harp trap (Tuttle 1974) at an abandoned mine near Perth Road Village, Ontario, Canada (44°35'N, 76°19'W). Each night we left the trap at the entrance to a mine before sunset and removed bats from it after midnight. We brought the bats back to nearby Queen's University Biological Station for experimentation and release.

We clipped a patch of hair from every bat before release so that it would be recognised if recaptured. For most species we took the hair from the top of the head, but in *Micronycteris* spp. (Phyllostomidae) we clipped hair from the back to avoid damaging the interaural band. We released recaptured individuals without experimentation.

Rotating platform

To quantify the ability of a bat to stick to a surface we used the protocol of Emerson and Diehl (1980). We placed each bat on the 15.0 by 30.0 cm surface which we rotated with an electronic motor from 0° (horizontal) through 90° (vertical) to 180° at 3°·s⁻¹. A scale divided into 1° increments revealed the angle of the platform at all times.

During rotation the bat could move about on the surface to attain whatever orientation it preferred. We had attached a transparent Lexan polycarbonate cage to the surface and it remained stationary relative to the surface during rotation. This prevented bats from escaping during experimentation. Since *T. tricolor* climbed easily on the surface of the polycarbonate cage, we followed the methodology used in the rotation of tree frogs (Hanna and Barnes 1991), holding open hands about 2 in. from the rotating *T. tricolor* to prevent flight. This was not always entirely effective, so we conducted the rotations inside an enclosed tent. When bats did escape we could quickly recapture them with a hand net.

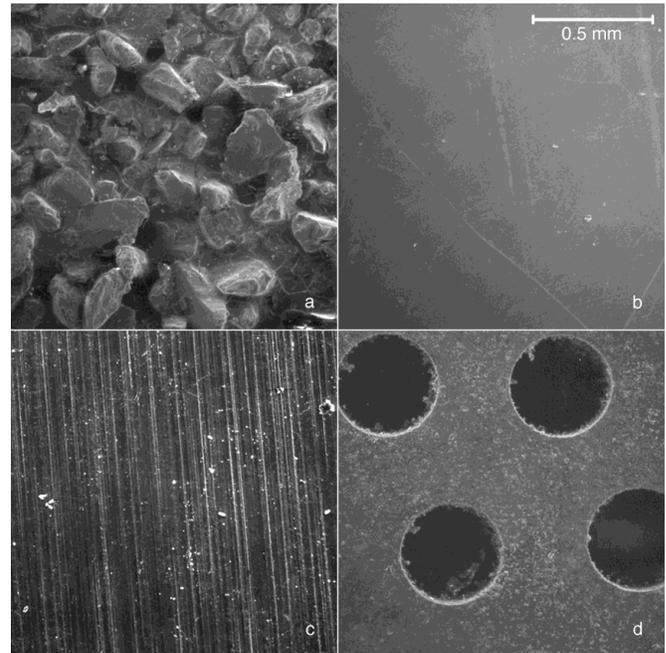
Some bats fell from the surface during rotation. Other bats still held after their rotation was stopped at 180°. In all cases we recorded the last angle at which a bat maintained its hold on the rotating platform. When a bat of any species jumped from the surface prematurely, or used the contours of the cage for gripping, we stopped the trial, placed the bat at the centre of the surface, and repeated the trial. The values obtained for the points at which bats fell are therefore accurate indications of when they lost their grip. Some bats, after several attempts, still would not cling to a surface long enough to allow an accurate measurement of when they lost their grip, so we could not record data for all bats on all surfaces.

We rotated each bat on four surfaces (Fig. 2): medium-grade aluminum oxide sandpaper (emery cloth, ca. 120 diamond grid); smooth transparent Lexan polycarbonate; aluminum utility sheet; aluminum sheet perforated by small holes (ca. 4.5×10^{-4} m in diameter) evenly distributed across the surface with a frequency of 1.72×10^6 holes per square metre (Fig. 2d). These holes permitted air to flow from one face of the aluminum sheet to the other and reduced its surface area by 27% compared with the solid utility sheet. The size and frequency of the holes were such that hind or thumb disks at any position on the surface would completely cover at least three holes. These four surfaces were presented to each bat in a random order. Scanning electron micrographs of each surface demonstrate the texture of the surface at the scale of a *T. tricolor* disk (Fig. 2).

Experimental detection of sticking mechanisms

Gluing can only occur after a liquid cement, spread between two surfaces, has had time to harden, allowing cohesive forces to act (Nachtigall 1974). In invertebrates that use gluing, such as limpets, this process takes several hours (Smith 1991b). Because the entire rotation of a bat through 180° took only 60 s, the secretion and subsequent hardening of a glue beneath the disks were unlikely to have occurred during a trial. The lack of a solid residue remaining

Fig. 2. The four test surfaces used in the rotating-platform experiments: sandpaper (a), Lexan polycarbonate (b), aluminum sheet (c), and perforated aluminum sheet (d).



after the bats had moved on also suggests that *T. tricolor* did not use gluing to adhere to any of the surfaces we tested.

Sudoriparous (sweat) glands open into the outermost zone of each *T. tricolor* disk (Schliemann 1974). They secrete a substance that is non-mucoid and of low viscosity, consisting mostly of water and soluble proteins (Wimsatt and Villa R. 1970). Grooming *T. tricolor* spend considerable time licking the disks of both the thumbs and the feet (Carvalho 1939; Findley and Wilson 1974; Wimsatt and Villa R. 1970), keeping them free of debris. The combination of saliva and exudate from the sudoriparous glands keeps the disk face moist at all times (Wimsatt and Villa R. 1970), producing a fluid-filled joint between the disk and any surface it contacts. The presence of liquid between them prevents intermolecular adhesion, which normally functions only at separation distances of ca. 0.3 nm (Autumn et al. 2000), but may not completely disappear at greater distances (Israelachvili 1992).

The mechanism of friction can only occur when there is a normal force holding two surfaces together, which means that it was experimentally eliminated when animals were rotated past 90°. The mechanisms available to bats after 90° were thus limited to interlocking, wet adhesion, and suction.

To determine whether suction is used by living *T. tricolor*, we compared the sticking ability of *T. tricolor* on sheet aluminum, where suction was possible, with that on porous aluminum and sandpaper, where the seal necessary for suction could not be created. The decrease in surface area from the non-porous to the porous surface is ca. 27%, so if *T. tricolor* used only wet adhesion and not suction, this decreased surface area would result in a lower sticking ability. But *T. tricolor* can hang beneath a smooth surface by only one ankle disk (Wimsatt and Villa R. 1970), indicating that a decrease in disk surface area of ca. 88% (the result of removing two large wrist disks and one smaller ankle from a surface) does not induce falling. Therefore, any decrease in ability to stick to the porous surface can be attributed to the absence of suction.

Interlocking only occurs on a surface that is rough enough to facilitate intermeshing with some part of the organism. Hooke (1665–1667) and Leeuwenhoek (1690) postulated that the adhesive setae

Table 1. Species of bats used in the rotating-platform experiment.

Family	Species	Mass (g) ^a	<i>n</i>	Locality
Emballonuridae	<i>Rhynchonycteris naso</i>	4.5 ± 0.43	8	Caño Palma
Phyllostomidae	<i>Artibeus jamaicensis</i>	50.8	2	Caño Palma
	<i>Artibeus watsoni</i>	10.7 ± 1.40	20	Caño Palma
	<i>Carollia breviceuda</i>	16.0 ± 1.49	5	Caño Palma
	<i>Carollia castanea</i>	14.1 ± 2.40	10	Caño Palma
	<i>Carollia perspicillata</i>	18.1 ± 2.58	8	Caño Palma
	<i>Glossophaga commissarisi</i>	8.1	3	Caño Palma
	<i>Glossophaga soricina</i>	7.8	2	Caño Palma
	<i>Hylonycteris underwoodi</i>	7.3	1	Caño Palma
	<i>Micronycteris brachyotis</i>	13.0	3	Caño Palma
	<i>Micronycteris microtus</i>	5.7 ± 0.47	6	Caño Palma
	<i>Platyrrhinus helleri</i>	17.2	2	Caño Palma
	<i>Uroderma bilobatum</i>	17.6	1	Caño Palma
	<i>Vampyressa nymphaea</i>	11.8	1	Caño Palma
	Thyropteridae	<i>Thyroptera tricolor</i>	3.5 ± 0.79	31
Vespertilionidae	<i>Myotis leibii</i>	4.9	4	Queen's University Biological Station
	<i>Myotis lucifugus</i>	7.0 ± 1.00	26	Queen's University Biological Station
	<i>Myotis nigricans</i>	5.6	3	Caño Palma
	<i>Myotis septentrionalis</i>	6.0 ± 0.82	16	Queen's University Biological Station

^aValues are given ± standard deviation when *n* ≥ 5.

of insects could catch on the minute irregularities of apparently smooth surfaces. But this was dismissed when scanning electron microscopy (SEM) views of glass and Perspex revealed them to have remarkably smooth surfaces, even at the scale of insect setae (Stork 1980). SEM inspection of the polycarbonate and sheet aluminum surfaces we used revealed that they are smooth even well below the scale of a *T. tricolor* disk (Figs. 2*b*, 2*d*). On these two surfaces, bats could adhere only by wet adhesion, suction, and (or) friction.

Results

Rotating platform

In 584 trials, we put 152 bats from 19 species in four families through a rotating-surface experiment (Table 1). On the rotating platform the postures of bats varied among families, but we observed no intrafamilial variation. At angles approximating 90°, vespertilionids, phyllostomids, and emballonurids maintained a head-down orientation, while *T. tricolor* roosted head-up. Vespertilionids and phyllostomids held on only with their hind feet at angles close to 180°, while emballonurids and thyropterids maintained a four-point stance with wrists and hind feet in contact with the surface.

The angles at which bats, grouped by family, stuck to sandpaper, sheet aluminum, perforated aluminum, and polycarbonate (Fig. 3) show that the performance of thyropterids can be readily distinguished from that of other families. Because we stopped trials at 180°, there is an upper limit beyond which bats cannot continue to cling, resulting in data that are not normally distributed. This necessitates the use of non-parametric statistical tests. We performed a Kruskal–Wallis test with tied ranks (Zar 1999) to assess interfamilial differences in sticking ability. We found significant differences in sticking ability among the families on every test surface ($P < 0.0005$; Table 2) and then set out to determine where those differences existed, i.e., which families differed from each other in ability to stick to a given surface. Testing each sur-

Table 2. Kruskal–Wallis tests for differences in sticking ability on each of the four surfaces among bats grouped by family.

	$F_{0.05}$	F	P
Sandpaper	2.67	26.009	<0.0005
Sheet aluminum	2.67	50.415	<0.0005
Perforated aluminum	2.67	80.343	<0.0005
Polycarbonate	2.67	50.051	<0.0005

face separately, we made multiple two-tailed comparisons using rank sums (Table 3), which permitted analysis despite unequal group sizes and tied ranks (Zar 1999).

Sticking mechanisms

A comparison of the performance of *T. tricolor* on sandpaper as well as on solid and perforated aluminum surfaces demonstrates that suction is the sticking mechanism: the bats adhered readily to smooth surfaces but not to perforated ones. On smooth surfaces 93.5% of *T. tricolor* held on through 180° ($n = 31$), while on the perforated surface, *T. tricolor* adhered only to an average of 90.0° ($n = 31$, $SD = 25.02^\circ$); no bats held on past 121°. Nevertheless in the absence of suction, 54.8% of *T. tricolor* ($n = 31$) held on past 90°, indicating the use of interlocking and (or) wet adhesion. Because SEM views of the surface at the scale of a disk revealed very few irregularities that might interlock with the disk face (Figs. 2*c*, 2*d*), and since the disks of living *T. tricolor* are kept moist (Wimsatt and Villa R. 1970), we conclude that wet adhesion was probably the central mechanism of sticking on that surface.

Use of thumb claws

Originally we had intended to use the same cage around rotating *T. tricolor* as we used for the other bats. To stop *T. tricolor* from crawling on the polycarbonate walls of the

Fig. 3. Percentage of individuals in each family of bats tested that had not fallen from a rotating surface (velocity = 3°·s⁻¹), with changing angle of the surface. Surfaces are sandpaper (a), polycarbonate (b), aluminum sheet (c), and perforated aluminum sheet (d); 0° is horizontal with the bat on top, 90° is vertical, and 180° is horizontal with the bat below. Note that 54.8% of *T. tricolor* held onto the perforated aluminum sheet (d) past 90° (vertical line), indicating that these bats used wet adhesion.

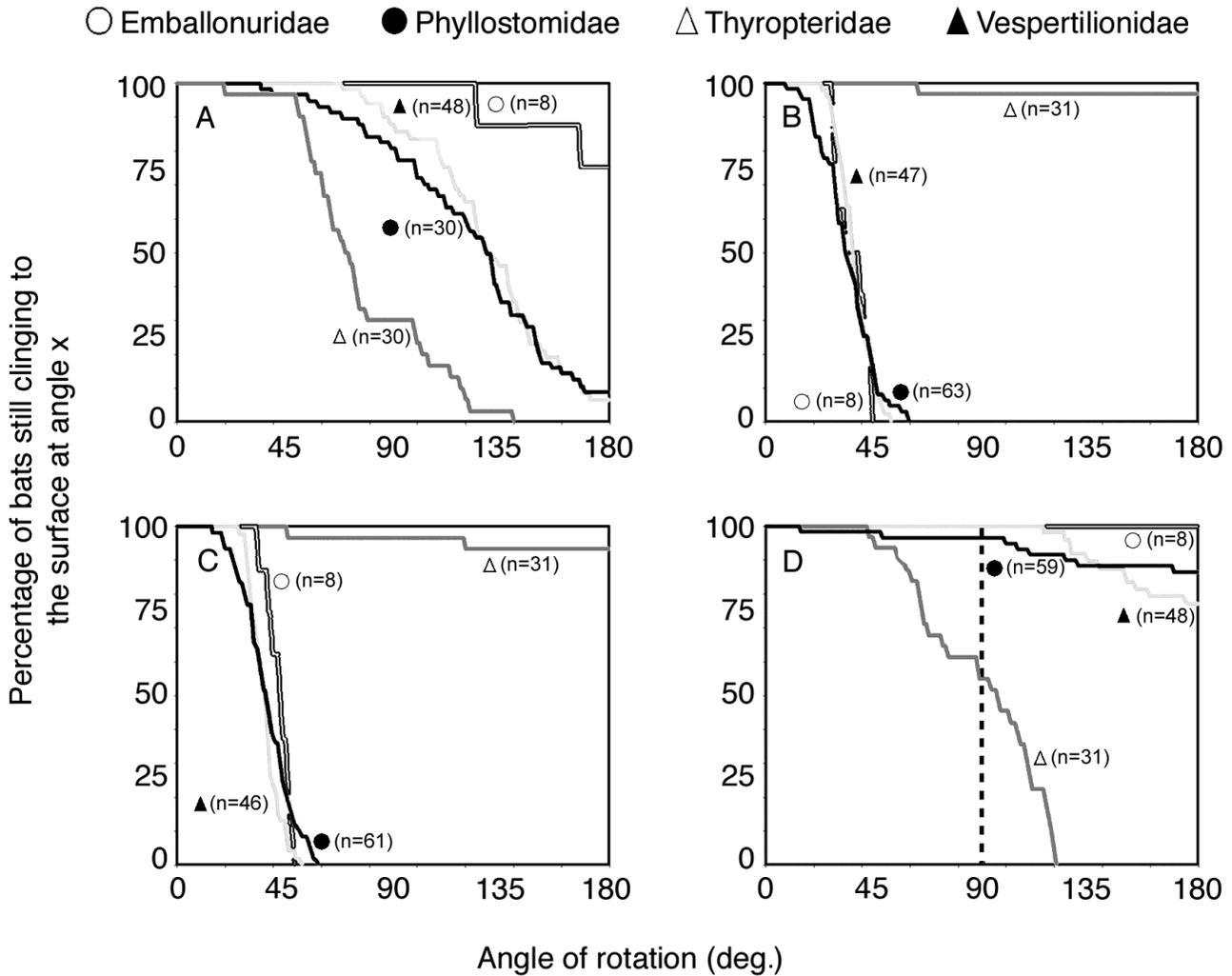


Table 3. *Q* statistics obtained from multiple comparisons (two-tailed) of sticking ability among groups on each of the four surfaces.

	Sandpaper	Sheet aluminum	Perforated aluminum	Polycarbonate
Emballonuridae vs. Phyllostomidae	3.24**	1.56	0.73	0.42
Emballonuridae vs. Thyropteridae	5.97***	2.89*	5.58***	4.23***
Emballonuridae vs. Vespertilionidae	2.77*	1.69	0.93	0.19
Phyllostomidae vs. Thyropteridae	5.10***	7.86***	8.73***	8.37***
Phyllostomidae vs. Vespertilionidae	0.85	0.31	0.41	1.19
Thyropteridae vs. Vespertilionidae	5.66***	7.72***	8.41***	6.94***

**P* < 0.05.
 ***P* < 0.01.
 ****P* < 0.001.

cage we covered its inside walls with screen, a surface upon which *T. tricolor* should not be able to crawl (Findley and Wilson 1974). The first *T. tricolor* placed in the cage, an adult male (forearm 34.0 mm long; mass 3.8 g), immediately

climbed on the walls by interlocking the claws of its thumbs with the holes of the screen. Because the cage was ineffective at preventing bats from leaving the test surface we did not use it in the rotation experiments. No other bats were

placed in the screen cage. We did not observe any *T. tricolor* interlocking the thumb claws with the sandpaper or porous aluminum surfaces.

Discussion

Our data support the predictions from anatomical work that the disks of *T. tricolor* adhere to smooth surfaces by suction (Wimsatt and Villa R. 1970; Schliemann 1970b; Thewissen and Etnier 1995), with a secondary role for wet adhesion. The fluid-filled joint between the disk face and the substrate probably assists in maintaining a seal for suction, but the fluid can also provide the vehicle for wet adhesion. We could not determine which of the two possible components of wet adhesion, Stefan adhesion or capillarity, was used by *T. tricolor*. These components are distinguishable because in Stefan adhesion, the sticking force is exponentially correlated to the surface area of contact, and in capillarity the correlation is arithmetic (Emerson and Diehl 1980). By observing the sticking abilities of several different-sized species of tree frogs, researchers determined that capillarity was the component of wet adhesion in these animals (Emerson and Diehl 1980).

Wet adhesion may serve as an energy-conserving device. A locking mechanism (tendon-locking mechanism; TLM) opposite the proximal phalanges of each toe and pollex allows some bats to hold the digits in flexed positions with no muscular effort. Because *T. tricolor* lack a TLM (Quinn and Baumel 1993), attachment by suction presumably requires constant muscular exertion, so roosting over long periods of time could represent a significant energetic cost if elasticity is not involved. Wet adhesion may conserve energy by allowing complete or partial relaxation of the musculature controlling disk shape. Gluing may also be used when the period of attachment is long, though we did not test for gluing in this experiment.

Although *Thyroptera* species have most often been found in furred leaves (e.g., Findley and Wilson 1974), there are records of them roosting elsewhere. In Trinidad, Goodwin and Greenhall (1961) found *T. tricolor* roosting with *R. naso* in a curled dead *Heliconia* leaf. In French Guiana, 3 of 12 roosting groups of *T. tricolor* found by Simmons and Voss (1998) roosted in dry, curled, dead leaves of *Phenakospermum* sp. (Strelitziaceae). *Thyroptera discifera* have been reported roosting under dead banana leaves (Robinson and Lyon 1901; Torres et al. 1988). Our data demonstrate how the thumb claws can be used by *T. tricolor* to attach to rough surfaces, potentially demonstrating how these bats might use other, unknown types of roosts.

Disks allow the three species of *Thyroptera* and *Myzopoda aurita* (Myzopodidae) to move on smooth surfaces. Schliemann (1970a) described a plausible scenario by which the wrists and ankles of a diskless bat might be modified to form functional suction disks by gradual evolutionary change. Our results indicate that in the course of this evolution, *T. tricolor* lost some ability to use its claws for roosting the way its diskless ancestors did. The thumb of *T. tricolor* is bent dorsally and rotated away from the metacarpophalangeal joint (Wimsatt and Villa R. 1970). This arrangement, not seen in diskless bats, keeps the thumb clear of the disk on smooth surfaces, and appears to have diminished the functionality of

the thumb as a means of gripping rough surfaces. Some vespertilionids without disks (*Tylosystonycteris pachypus*, *Pipistrellus nanus*, and *Myotis bocagei*) may also have some capacity for movement on smooth surfaces (Thewissen and Etnier 1995; Brosset 1966).

Compared with the disk-winged bats, other species of Chiroptera use interlocking, usually between toenails and substrate, to gain purchase and roost on rough surfaces and roost head-down. In *T. tricolor*, the roosting orientation reflects the roosting situation. In furred, tube-shaped leaves, the entrance is at the top, so *T. tricolor* roosting head-up face the entrance, allowing rapid emergence. This provides two selective advantages. First, because emergence time is shortened, the roost is made less conspicuous to predators, and second, for an individual under threat by a predator, rapid emergence decreases the likelihood of being caught (Fenton et al. 1994).

Although adhesive disks have appeared in only one superfamily (Nataloidea) of the Chiroptera (Simmons and Geisler 1998), differences in structural details between the disks of Myzopodidae and Thyropteridae do not support the view that the disks were an ancestral feature of the nataloids (Schliemann 1970b). Although the earliest fossil nataloids occur in Eocene strata, no fossils have been assigned to the Myzopodidae or Thyropteridae (Simmons and Geisler 1998), and some studies indicate that the Myzopodidae and Thyropteridae are not closely related and may not belong in the same superfamily (Van Den Bussche and Hoofer 2001). Pad-like structures on the wrists of some vespertilionids suggest considerable flexibility in structures associated with roosting in bats (Thewissen and Etnier 1995), reflecting the variety of roosting situations exploited by bats (Altringham 1996; Fenton 2001). In a sense, adhesive disks are another way to exploit the roosting opportunities presented by foliage, a variation on the tents used by other bats, mainly phyllostomids (Kunz and McCracken 1996).

Suction occurs in many animal taxa and serves a variety of functions. The suckers of octopus (Cephalopoda), for example, serve in locomotion, anchoring the body, holding prey, collecting and manipulating small objects, chemotactile recognition, and cleaning manoeuvres (Packard 1988). Although mammals rely on suction during feeding, particularly before weaning, its use in locomotion is very rare, probably occurring only in the Hyracoidea and Chiroptera (Dobson 1876). If the data for *T. tricolor* are representative of other thyropterids and the myzopodid, then bats provide yet another example of animals that rely on suction for staying in place and moving about.

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References

- Altringham, J.D. 1996. Bats: biology and behaviour. Oxford University Press, Oxford and New York.
- Autumn, K., Liang, Y.A., Hsleh, S.T., Zesch, W., Chan, W.P., Kenny, T.W., Fearing, R., and Full, R.J. 2000. Adhesive force of a single gecko foot-hair. *Nature (Lond.)*, **405**: 681–685.
- Brosset, A. 1966. La biologie des chiroptères. Masson, Paris.
- Carvalho, A.L. de. 1939. Zur Biologie einer Fledermaus (*Thyroptera tricolor* Spix) des Amazonas. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin. pp. 249–253.
- De la Espada, J. 1870. Alguno datos nuevos o curiosas acerca de la fauna del alto Amazonas (Mamíferos). *Bol. Rev. Univ. Madrid*, 1870: 21–27.
- Dietz, C.L. 1973. Bat walking behavior. *J. Mammal.* **54**: 790–792.
- Dobson, G.E. 1876. On peculiar structures in the feet of certain species of mammals which enable them to walk on smooth perpendicular surfaces. *Proc. Zool. Soc. Lond.* 1876: 526–535.
- Emerson, S.B., and Diehl, D. 1980. Toe pad morphology and mechanisms of sticking in frogs. *Biol. J. Linn. Soc.* **13**: 199–216.
- Fenton, M.B. 2001. Bats. Revised ed. Facts On File, New York.
- Fenton, M.B., Rautenbach, I.L., Smith, S.E., Swanpoel, C.M., Grosell, J., and van Jaarsveld, J. 1994. Raptors and bats: threats and opportunities. *Anim. Behav.* **48**: 9–18.
- Findley, J.S., and Wilson, D.E. 1974. Observations on the Neotropical disk-winged bat, *Thyroptera tricolor* Spix. *J. Mammal.* **55**: 562–571.
- Goodwin, G.G., and Greenhall, A.M. 1961. A review of the bats of Trinidad and Tobago: descriptions, rabies infections, and ecology. *Bull. Am. Mus. Nat. Hist.* **122**: 187–342.
- Hanna, G., and Barnes, W.J.P. 1991. Adhesion and detachment of the toe pads of tree frogs. *J. Exp. Biol.* **155**: 103–125.
- Hooke, R. 1665–1667. *Micrographia*. London.
- Israelachvili, J. 1992. Intermolecular and surface forces. Academic Press, London.
- Kunz, T.H., and McCracken, G.F. 1996. Tents and harems: apparent defense of foliage roosts by tent-making bats. *J. Trop. Ecol.* **12**: 121–137.
- Lees, A.D., and Hardie, J. 1988. The organs of adhesion in the aphid *Megoura viciae*. *J. Exp. Biol.* **136**: 209–228.
- Leeuwenhoek, A. 1690. Collected works (translated by S. Hoole, 1800–1807). Vol. II(3). London.
- Nachtigall, W. 1974. Biological mechanisms of attachment: the comparative morphology and bioengineering of organs for linkage, suction, and adhesion. Springer-Verlag, New York.
- Packard, A. 1988. The skin of cephalopods (coleoids): general and special adaptations. In *The Mollusca: form and function*. Vol. 11. Edited by E.R. Trueman and M.R. Clarke. Academic Press, San Diego. pp. 37–67.
- Quinn, T.H., and Baumel, J.J. 1993. Chiropteran tendon locking mechanism. *J. Morphol.* **216**: 197–208.
- Robinson, W., and Lyon, M.W. 1901. An annotated list of mammals collected in the vicinity of La Guaira, Venezuela. *Proc. U.S. Natl. Mus.* **24**: 135–162.
- Roscoe, D.T., and Walker, G. 1991. The adhesion of spiders to smooth surfaces. *Bull. Br. Arachnol. Soc.* **8**: 224–226.
- Schliemann, H. 1970a. Bau und Funktion der Haftorgane von Thyroptera und Myzopoda (Vespertilionoidea, Microchiroptera, Mammalia). *Z. Wiss. Zool.* **181**: 353–400.
- Schliemann, H. 1970b. Die Haftorgane von Thyroptera und Myzopoda (Microchiroptera, Mammalia)—Gedanken zu ihrer Entstehung als Parallelbildungen. *Z. Zool. Syst. Evolutionsforsch.* **9**: 61–80.
- Schliemann, H. 1974. Haftorgane bei Fledermausen. *Nat. Mus.* **104**: 15–20.
- Simmons, N.B., and Geisler, J.H. 1998. Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. *Bull. Am. Mus. Nat. Hist.* No. 235.
- Simmons, N.B., and Voss, R.S. 1998. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna. Part 1. Bats. *Bull. Am. Mus. Nat. Hist.* No. 237.
- Smith, A.M. 1991a. Negative pressure generated by octopus suckers: a study of the tensile strength of water in nature. *J. Exp. Biol.* **157**: 257–271.
- Smith, A.M. 1991b. The role of suction in the adhesion of limpets. *J. Exp. Biol.* **161**: 151–169.
- Stork, N.E. 1980. Experimental analysis of adhesion of *Chrysolina polita* (Chrysomelidae: Coleoptera) on a variety of surfaces. *J. Exp. Biol.* **88**: 91–107.
- Thewissen, J.G.M., and Etmier, S.A. 1995. Adhesive devices on the thumb of vespertilionoid bats (Chiroptera). *J. Mammal.* **76**: 925–936.
- Torres, M.P., Rosas, T., and Tiranti, S.I. 1988. *Thyroptera discifera* (Chiroptera: Thyropteridae) in Bolivia. *J. Mammal.* **69**: 434–435.
- Tuttle, M.D. 1974. An improved trap for bats. *J. Mammal.* **55**: 475–477.
- Van Den Bussche, R.A., and Hooper, S.R. 2001. Evaluating monophyly of Nataloidea (Chiroptera) with mitochondrial DNA. *J. Mammal.* **82**: 320–327.
- Walker, G., Yue, A.B., and Ratcliffe, J. 1985. The adhesive organ of the blowfly, *Calliphora vomitoria*: a functional approach (Diptera: Calliphoridae). *J. Zool. Ser. A*, **205**: 297–307.
- Wilson, D.E., and Findley, J.S. 1977. *Thyroptera tricolor*. *Mamm. Species No.* 71. pp. 1–3.
- Wimsatt, W.A., and Villa R., B. 1970. Locomotor adaptations in the disc-winged bat *Thyroptera tricolor* I. Functional organization of the adhesive discs. *Am. J. Anat.* **129**: 89–120.
- Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice Hall Inc., Upper Saddle River, N.J.