



How do sucker-footed bats hold on, and why do they roost head-up?

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Received 3 July 2009; accepted for publication 9 September 2009

Individuals of most bat species hang head-down by their toenails from rough surfaces, but Madagascar's endemic sucker-footed bat (*Myzopoda aurita*) clings head-up to smooth leaves using specialized pads on its wrists and ankles. We investigated the adhesive performance of 28 individuals and found that attachment performance on brass was not affected by the presence or absence of a seal around the pad–surface interface. Furthermore, on smooth acrylic, the wrist pads were more than nine-fold weaker when lifted perpendicular to the surface than when pulled parallel to it. The unimportance of a seal and the difference in strength in those directions on a smooth surface are characteristic of wet adhesion, but not of suction. Thus, despite its name, the sucker-footed bat appears to adhere using wet adhesion. We observed that when wrist pads were pushed anteriorly, they unpeeled easily from the surface because of deformation of the pads. This most likely permits rapid detachment during crawling, but would also cause passive detachment if bats roosted head-down. This provides an ecomorphological explanation to the head-up roosting behaviour of these unique bats. The results obtained in the present study thus link morphology, behaviour, and roosting ecology for an enigmatic Malagasy endemic. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, 99, 233–240.

ADDITIONAL KEYWORDS: detachment – ecomorphology – head-up posture – *Myzopoda* – roosting posture – suction – *Thyroptera* – wet adhesion.

INTRODUCTION

The ability of some animals to walk on smooth walls and ceilings has long inspired both scientific investigation (Nachtigall, 1974) and popular culture (Lee & Ditko, 1962). It requires an adhesive mechanism that bonds tightly, can detach rapidly and effortlessly with each footstep, and neither diminishes in strength nor accumulates debris over time (Peattie, 2009). This suite of characteristics is still beyond the capabilities of human-engineered adhesives but is widespread in nature (Autumn & Gravish, 2008; Sethi *et al.*, 2008). Indeed, the ability to climb smooth surfaces has evolved multiple times among arachnids, insects, amphibians, and reptiles, but that ability is still rare among mammals (Emerson & Diehl, 1980; Stork,

1983; Autumn *et al.*, 2000; Beutel & Gorb, 2001; Betz, 2002; Clemente & Federle, 2008). Although many mammals possess smooth pads that improve frictional gripping on rocks or tree branches (Nachtigall, 1974; Warman & Ennos, 2009), classical (Coulomb) friction cannot resist forces that pull the body away from a surface. To walk on the underside of a smooth leaf requires some mechanism other than friction, and such adhesive capabilities in mammals are apparently restricted to only a few species (Rosenberg & Rose, 1999), including six species of bats.

Those six bat species occur among two families: four species of disc-winged bats from the Neotropics (Thyropteridae: *Thyroptera* spp.) and two sucker-footed bat species from Madagascar (Myzopodidae: *Myzopoda* spp.). Together, these families represent a striking case of parallel evolution. Bats in each family have evolved adhesive organs on their wrists and

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Figure 1. *Myzopoda aurita*, clinging head-up to a vertical acrylic sheet, by means of pads on its wrists and ankles.

ankles that permit attachment to smooth surfaces; in *Thyroptera* spp., they are termed discs and in *Myzopoda* spp. they are termed pads (Fig. 1). Although the vast majority of bats hang upside down at roosts by their toenails (Riskin *et al.*, 2009), bats in these two families have converged on the habit of roosting inside furled leaves that open at the top. These bats cling to the vertical inner wall of the leaf with their adhesive organs, with an unusual head-up posture that is atypical for bats and is considered to facilitate rapid escape upon disturbance (Wilson & Findley, 1977; Göpfert & Wasserthal, 1995). Whether or not bats of those two families use the same mechanism of attachment is unknown. Thyropterids use suction (Wimsatt & Villa, 1970; Riskin & Fenton, 2001). The identification of the myzopodid attachment mechanism is one focus of the present study. The other focus is on uncovering how the biomechanics of adhesion might have influenced the roosting habits of the species.

Current hypotheses of the myzopodid sticking mechanism have come mostly from histological comparisons of *Thyroptera tricolor* and *Myzopoda aurita* (Schliemann, 1970). The thumb discs of *Thyroptera* spp. are shaped like concave cups, and are supported by an internal cartilaginous plate. The flexor pollicis brevis muscle inserts on that plate, and its contraction was hypothesized by Schliemann (1970) to enable suction by changing the overall disc shape. That hypothesis was later supported by experiments with living animals (Riskin & Fenton, 2001). The faces of the thumb pads of *M. aurita* are flat or slightly convex and, although the pads have no cartilaginous plate, they contain bundles of collagenous fibres into which the tendons of the palmaris longus muscle insert. This arrangement was hypothesized by Schliemann (1970) to also permit suction, although Thewissen &

Etnier (1995) argued that suction was not possible for myzopodids because the pad would not remain sealed at its periphery when the tendons inside the disc were pulled.

If suction is not the mechanism by which *M. aurita* cling to smooth surfaces, wet adhesion, dry adhesion, and gluing are the candidate mechanisms that remain. Wet adhesion is a general term, encompassing several physical phenomena that can occur when a fluid is present between two surfaces. These include capillarity, Stefan adhesion, and some recently uncovered solid-solid interactions (Emerson & Diehl, 1980; Hanna & Barnes, 1991; Federle, Baumgartner & Hölldobler, 2004; Federle *et al.*, 2006; Scholz *et al.*, 2009). Dry adhesion, the mechanism used by geckos (Autumn *et al.*, 2000), cannot occur if the organs are wet, and the pads of *M. aurita* are kept moist by a network of glands within the pad (Schliemann, 1970; Göpfert & Wasserthal, 1995). Gluing was hypothesized as an adhesive mechanism for *M. aurita* by Thewissen & Etnier (1995), but it is likely that the authors were actually referring to wet adhesion because gluing requires adequate time for a glue to be secreted, then harden (Nachtigall, 1974). That process takes seconds to minutes for other animals (Smith, 1991; Santos *et al.*, 2005), and is unlikely for *M. aurita*, especially when the adhesive pads are used during rapid crawling locomotion. Considering the presence of glands on the pad faces of *M. aurita* and their rapid crawling behaviour (Göpfert & Wasserthal, 1995), suction and wet adhesion appear to be the most plausible mechanisms of sticking.

Despite multiple studies on *Thyroptera* spp. (Findley & Wilson, 1974; Riskin & Fenton, 2001), no investigation of adhesion in live *M. aurita* has previously been undertaken, mostly because *M. aurita* are rarely seen in the wild. The recent discovery of a sizeable *M. aurita* population in Eastern Madagascar has led to observations of multiple roosts inside furled leaves of the Traveler's Tree (*Ravenala madagascariensis*), and now facilitates study of those animals (Schliemann & Goodman, 2003). In the present study, we tested for the use of suction in *M. aurita* by quantifying the performance of live animals, as was previously carried out for *T. tricolor* (Riskin & Fenton, 2001). We also investigated the kinematics of detachment to uncover the way in which *M. aurita* separate their adhesive pads from a surface and study the possible influence of detachment behaviour on roosting posture.

MATERIAL AND METHODS

We conducted fieldwork in October 2008 at the village of Kianjavato, Madagascar (21°22'S, 47°52'E). Using

mist nets set across forest trails, we captured 28 *M. aurita* Milne-Edwards & Grandidier, 1878, all of which were adult males (mean \pm SD mass: 9.18 ± 0.82 g). Bats were weighed to 0.01 g, and measurements were taken of forearm length, and of the widths (w) and heights (h) of all four pads to 0.1 mm. The area (A) of each pad was estimated by treating it as an ellipse, and using the equation:

$$A = \frac{\pi wh}{4} \quad (1)$$

All bats, with one exception, were used in experiments then released within 4 h of capture. The other was released after 24 h. We clipped a patch of hair from each bat before it was released to avoid re-sampling.

DIRECTIONALITY OF ATTACHMENT STRENGTH

To determine whether *M. aurita* use wet adhesion or suction, we tested for directionality of adhesive strength. On smooth surfaces, suction is typically stronger when the animal is pulled away from the surface than when the animal is dragged along the surface (Smith, 1992). By contrast, all known biological systems that use wet adhesion share the common characteristic that adhesive force is much greater parallel to the surface than perpendicular to it (Peattie, 2009).

To test for differences in adhesive strength, we restrained a bat in hand, then gently placed its right forelimb pad surface against a horizontal acrylic surface. Acrylic is smooth even at microscopic scales (Riskin & Fenton, 2001), and is commonly sold by the trade names Plexiglas, Perspex, or Lucite. The acrylic surface was clamped to a force platform that measured forces in three dimensions. Forces were recorded at 1000 Hz, then filtered using a 50-Hz Butterworth Lowpass filter. Details of plate construction, calibration, and performance have been described previously (Riskin, Bertram & Hermanson, 2005; Riskin *et al.*, 2006). The acrylic surface was replaced several times each sampling night to ensure that the surface was clean.

For each bat, we measured maximum adhesive strength of the forelimb pad on smooth acrylic in three directions: (1) in 'tension' perpendicular to the plate surface; (2) in 'pulling shear', whereby the bat's body was moved parallel to the surface in a posterior direction with a single pad dragging along the surface anterior to the body; and (3) in 'pushing shear', whereby the bat was moved parallel to the surface in an anterior direction. At the level of the limb, the latter two treatments could alternatively be considered as a proximally directed pulling shear and a distally directed pushing shear, respectively. Preload-

ing can have a significant influence on adhesive strength in biological systems (Autumn *et al.*, 2000), and we were unable to precisely control preloading because bats were conscious and held by hand. To avoid systematic bias in preloading among treatments, the placement of the bat's pad on the surface was performed identically by the same experimenter for each treatment type and the order in which the three directions were tested was randomized.

Next, we tested the adhesive force of the hindlimb in pulling shear by placing the right hindlimb pad against the acrylic and moving the bat's body parallel to the surface, so that the pad was dragged along the surface at the end of an outstretched hindlimb. We performed five consecutive repetitions per individual in each treatment and, for each, the maximum recorded force among the five repetitions was used for analyses. Maximum force per unit area values were calculated by dividing maximum force values by the area of the pad.

We used the maximum, rather than median, aiming to approximate the greatest adhesive strength possible for a bat in a given treatment. We repeated our analysis using medians and obtained the same pattern of significance among our statistical tests as those using maxima; thus, only results using maxima are reported.

ADHESION TO POROUS AND NONPOROUS BRASS

As a second test for the presence of suction, we measured adhesive force in the presence and absence of a seal around the pad-surface interface. If suction is used by *M. aurita*, adhesion should be much greater when a seal is present than when it is not but, if wet adhesion is used, the presence or absence of a seal should have minimal effect on adhesive force (Riskin & Fenton, 2001). We compared the adhesive ability of bat pads on two different brass sheets, constructed of 0.4 mm thick porous brass with 0.13 mm^2 holes at a density of $1.7 \text{ holes mm}^{-2}$, resulting in 22% open area. The difference between them was that one piece was sealed on its underside with cellophane tape, preventing air from passing through the sheet, and the underside of the second sheet was left open. This had the effect that the surface interacting with the pad was identical for the two sheets but only one of them permitted the seal necessary for suction to occur. As on acrylic (see Results), we found that force was extremely weak when the pad was lifted vertically from the brass surface, and so comparisons of the two porous brass surfaces were made based on 'pulling shear' as described above. Fourteen of the 28 bats were used for this part of the experiment, and it was always performed after carrying out the test of directional dependence. Five consecutive

repetitions were performed on each of the two porous brass plates, and the order of the two treatments was randomized.

WHOLE ANIMAL ATTACHMENT AND DETACHMENT

A few individuals were also placed individually on a vertical sheet of acrylic so that the attachment and detachment of the pads could be observed through the surface (Fig. 1). Bats always clung to the surface with a head-up orientation, with the tail propped against the surface in a woodpecker-like fashion (Göpfert & Wasserthal, 1995). Some bats were left to freely ascend the surface so that the pads of walking bats could be observed. We restrained others by their hindlimbs when they tried to ascend the surface so that we could verify that fluid was present at the pad-surface interface, and also to ensure that we could observe the kinematics of pad detachment. In one case, we rotated the acrylic when a bat was attached, to observe whether a bat could cling to the material in a head-down posture at all.

STATISTICAL ANALYSIS

We used paired *t*-tests to compare: (1) the strength of forelimb pad adhesion in perpendicular lifting versus pulling shear; (2) the strength of forelimb pads versus hindlimb pads in pulling shear; (3) forelimb pad attachment to sealed porous brass versus open porous brass; and (4) forelimb pad attachment in pulling shear versus pushing shear. All tests were two-tailed except (3), where we used a one-tailed test expecting adhesion to improve on sealed holes compared to open holes. Pairing was assigned based on the individual from which measurements were taken. The assumption of normality required for a *t*-test was verified based on visual inspection of normal-quantile plots of the data. To account for multiple tests, we used Bonferroni correction; the *P*-value required to reject a null hypothesis was $0.05/4 = 0.0125$ (Rice, 1989).

RESULTS

FORCE MEASUREMENTS

The area of forelimb pads averaged $21.8 \pm 2.3 \text{ mm}^2$ and the hindlimb pads averaged $12.5 \pm 1.3 \text{ mm}^2$. The forelimb pads of *M. aurita* were more than nine-fold weaker when lifted perpendicular to the surface ($3.7 \pm 1.9 \text{ mN mm}^{-2}$ mean \pm SD) than when pulled in shear ($35.6 \pm 9.6 \text{ mN mm}^{-2}$; paired $t = 18.22$; d.f. = 27; $P < 0.0001$; Fig. 2). The force per unit area of the hindlimbs in pulling shear was $44.6 \pm 11.2 \text{ mN mm}^{-2}$, which is slightly stronger than the pads of the forelimbs in shear (paired $t = 3.88$; $P < 0.001$; $N = 28$).

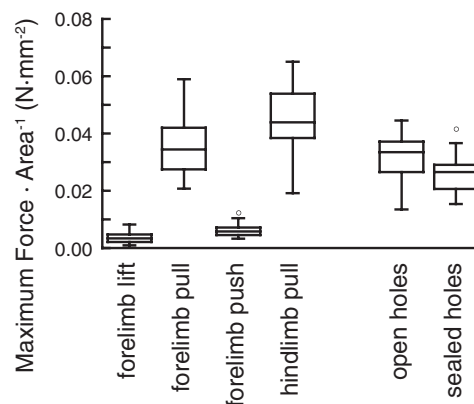


Figure 2. Maximum force per unit area values for a single adhesive organ. The forelimb pad was weaker when lifted perpendicular to the plate (forelimb lift) than when dragged along the surface in a posterior direction (forelimb pull). When moved anteriorly (forelimb push), it detached easily by unpeeling off the surface. The adhesive strength of the hindlimb was slightly greater than that of the forelimb in shear. The absence or presence of cellophane tape on the underside of a porous brass plate (open holes and sealed holes, respectively) did not significantly influence adhesive force. This suggests that suction is not used by *Myzopoda aurita* ($N = 28$ for all treatments, except on porous brass, where $N = 14$).

Force per unit area measurements were not significantly higher on the porous brass surface that was sealed ($25.9 \pm 7.3 \text{ mN mm}^{-2}$) compared to the porous brass surface that was not sealed ($32.1 \pm 9.4 \text{ mN mm}^{-2}$; one-tailed paired $t = 2.60$; d.f. = 13; $P = 0.99$).

DETACHMENT OF THE PADS FROM THE SURFACE

When we pushed a forelimb pad anteriorly, it displayed much lower force per unit area values ($6.2 \pm 2.3 \text{ mN mm}^{-2}$) than when pulled posteriorly (paired $t = 17.02$; d.f. = 27; $P < 0.0001$; Fig. 2). This did not result from a failure of the pad surface to adhere to the glass, but rather from the apparently passive peeling of the whole pad away from the surface (Fig. 3). We also observed peeling of this kind when bats moved their forelimbs anteriorly at the end of stance phase when crawling up the acrylic sheet. When we placed one bat head-down on an acrylic surface, its forelimb pads peeled away in the same manner, and it hung by its hindlimb pads only, with the hindlimbs oriented so that force was applied in pulling shear (along the shaft of the leg), comprising the same orientation that we used in our tests of hindlimb strength.

We also observed a separate, kinematically distinguishable behaviour of forelimb detachment, in which

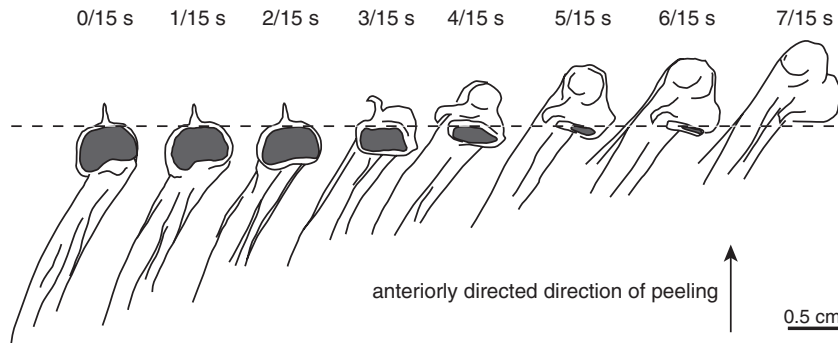


Figure 3. The proximal-to-distal peeling of a right wrist pad of *Myzopoda aurita* from an acrylic surface, as seen through the surface to which it was attached. The area of contact between the pad's ventral surface and the substrate, shown in grey, decreases as the peeling edge migrates anteriorly until detachment is complete. The distal (anterior) edge of the contact area (hashed line) does not shift as the pad peels. Upon detachment, the dorsal aspect of the pad faces the surface. These images were traced from a video taken when the forearm of the folded wing was held by hand, and moved anteriorly, as described in the Material and methods.

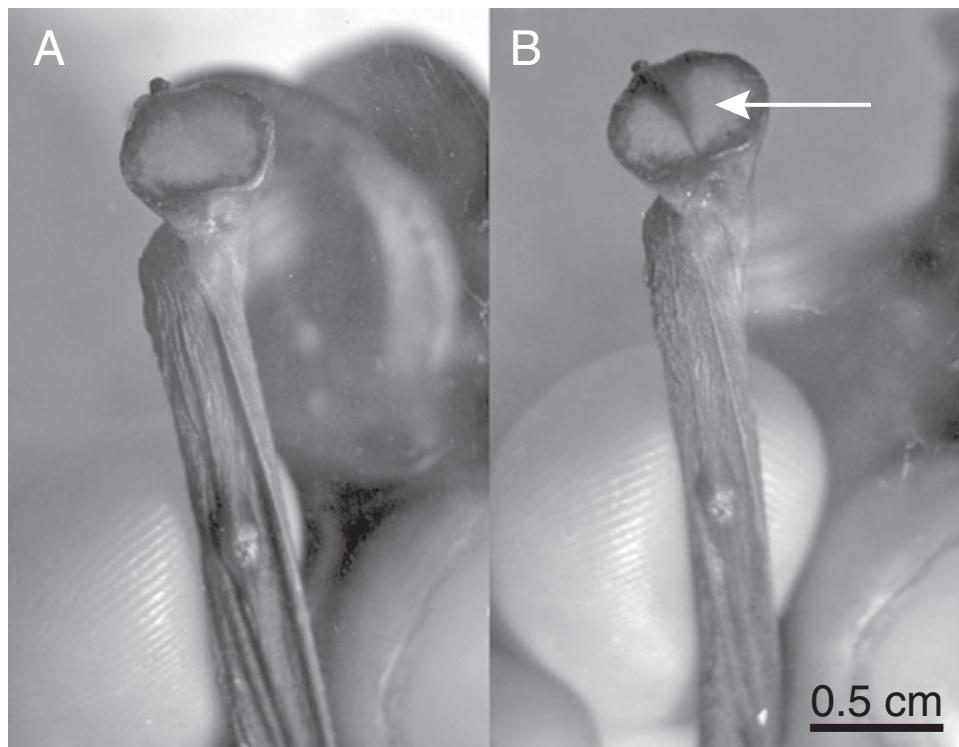


Figure 4. Two sequential images of a pad, viewed through the acrylic surface to which it is attached. A, first the center of the pad is in direct contact with the surface, loaded in pulling shear. B, next, initiation of peeling occurs along a longitudinal fold at the centre of the pad (highlighted by the arrow), thus decreasing the area of attachment and reducing adhesive force. We hypothesize that this peeling results from contraction of the palmaris longus muscle.

separation of the pad from the surface began along its longitudinal midline (Fig. 4). Bats held by their hindlimbs commonly performed this behaviour when attempting to crawl away using the forelimbs on the surface.

OBSERVATIONS OF THE PAD SURFACES

When bats were caught in the nets, their thumb pads glistened from a fluid present on the face of the wrist pad, and that fluid was still present at the onset of

experiments. Over the course of our experiments, the pads sometimes appeared to dry out, and then later appeared moist again. We never observed bats licking the adhesive organs. During attachment, we observed a clear fluid between the pads and acrylic. We did not observe a liquid meniscus around the pad face, but the gentle slope of the convex pad around the area of contact may have obscured our view. We did not observe any cavity between the pad and surface. In some cases, we noted that the thumb claw and thumb pad contacted a surface at the same time.

DISCUSSION

ADHESIVE MECHANISM

The results obtained demonstrate that suction is not used by *M. aurita*, and suggest that wet adhesion is the primary sticking mechanism used by that species. Their pads showed a pattern that is typical of wet adhesive mechanisms, namely greater strength when pulled parallel to a surface than when lifted perpendicular to it (Peattie, 2009), and we found no influence on adhesion as a result of the presence or absence of a seal around the pad–surface interface. We therefore conclude that the sucker-footed bats of Madagascar, despite their common name, do not actually suck at all.

DETACHMENT OF THE PADS AND HEAD-UP ROOSTING BEHAVIOUR

The observations made in the present study suggest that the relatively weak adhesive strength of the pads in pushing shear results from deformation of the pads which, when loaded in pushing shear, cause the surfaces to be peeled vertically from the surface. This pattern has not been described previously for any bats, but has been observed in other organisms that use wet adhesion (Endlein & Federle, 2007; Hanna & Barnes, 1991), and appears to make use of the weak perpendicular strength of the wet adhesion mechanism (Peattie, 2009). The typical walking motions of bats are such that passive detachment is likely to facilitate crawling (Riskin *et al.*, 2006).

We hypothesize that this detachment mechanism underlies the head-up roosting behaviour of this species. Roosting head-up loads the pads in pulling shear where attachment is strongest, and prevents the passive detachment of the pads that would occur from pushing shear in a head-down posture. This hypothesis is supported by our observation that the forelimb pads detached for the individual that we placed head-down on acrylic.

Recently, a second species of myzopodid, *Myzopoda schliemanni*, was described from Western Madagascar, and its roosting ecology differs from that of *M.*

aurita. Some *M. schliemanni* have been found roosting on the stalactites of a cave (Kofoky *et al.*, 2006), and others have been found roosting under dried palm leaves. In both roost types, these bats also roost head-up, presumably for the same reasons as *M. aurita* (Goodman, Rakotondrapary & Kofoky, 2007).

MUSCULAR CONTROL OF THE PADS

Schliemann (1970) suggested that the pads of *M. aurita* function by means of suction because he observed tendons from the palmaris longus muscle that inserted within the tissue of the forelimb pad. Experimental evidence from the present study suggests that suction is not used, which raises the question of what the functional role of that muscle might be. We hypothesize that the action of the palmaris longus muscle causes the longitudinal folding that we frequently observed during pad detachment (Fig. 4). If so, the action of that muscle would facilitate detachment of the pad when the anteriorly directed peeling motion is not used.

Thus, although the muscular insertion to the disc in *T. tricolor* facilitates adhesion to a smooth surface by means of suction, we propose that the muscles of the thumb pads of *M. aurita* function in detachment. When the middle of an adhesive pad is lifted from the substrate, the only difference between attachment via suction or detachment via peeling is the presence or absence of a seal at the organ's periphery.

THE EVOLUTION OF SUCTION ORGANS

One corollary from the present study is the statement that the New World disc-winged bats (*Thyroptera* spp.) are the only mammals, and possibly the only terrestrial vertebrates, that use suction to cling to smooth surfaces. Many bats possess flattened pads that facilitate crawling on smooth surfaces (Thewissen & Etnier, 1995), but how the pads of bats might have evolved to become suction discs in thyropterids is a puzzling question of functional morphology. The origin of thyropterid suction organs has been discussed by Schliemann (1970), but his analysis was based on the assumption that *M. aurita* also possess suction discs.

We hypothesize that the suction discs of *Thyroptera* spp. evolved from pads that superficially resembled those of *M. aurita*, and functioned by means of wet adhesion. Indeed, the discs of *T. tricolor* secrete a fluid, and adhere weakly by means of wet adhesion when they cannot produce a seal (Findley & Wilson, 1974; Riskin & Fenton, 2001). We hypothesize that the flexor pollicis brevis muscle that changes disc shape to permit suction in *Thyroptera* spp. may have

once facilitated detachment of wet adhesive organs, in the way that the palmaris longus muscle presumably does in myzopodids.

Thyroptera tricolor clings easily to smooth surfaces at any angle, including head-down (D. K. Riskin personal observation), but they always roost head-up (Findley & Wilson, 1974). If the wet-adhesive pads of thyropterid ancestors, such as those of *M. aurita*, did not work well in a head-down posture, the modern head-up roosting posture of thyropterids might be retained from a time when wet adhesion was their mechanism of attachment. It is noteworthy that *M. aurita* can make contact with the thumb claw and adhesive organ simultaneously, whereas *T. tricolor* cannot (Riskin & Fenton, 2001) because this may reflect the more specialized morphology required for suction to function.

CONCLUSIONS

The results obtained in the present study suggest that *M. aurita* use wet adhesion, not suction, to adhere to smooth surfaces. For *M. aurita*, detachment of the thumb pads is accomplished by means of anteriorly directed peeling, or by peeling along the midline of the pad, which we hypothesize results from contraction of the palmaris longus muscle. We hypothesize that the anteriorly directed peeling mechanism of detachment prevents *M. aurita* from roosting head-down the way other bats do, and is thus responsible for their unusual head-up roosting posture.

ACKNOWLEDGEMENTS

The authors thank R. Andrianavivelo, M. Ralisata, F. Andriamboavonjy, and Professor O. Ramilijana for assistance in the field. We also thank R. K. B. Jenkins and the staff of Madagasikara Voakajy for logistical support. M. Armour, J. Iriarte-Díaz, Y. Dzal, M. B. Fenton, J. W. Hermanson, K. M. Middleton, A. M. Peattie, M. W. Walters, members of the Swartz laboratory group at Brown University, and several anonymous reviewers made helpful comments on earlier drafts of this manuscript. This work was made possible by a National Geographic Grant to P. A. Racey and D. Rakotoniravony, and by support to D. K. Riskin from a Bushnell Foundation Grant to S. M. Swartz.

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