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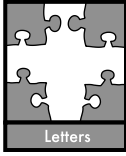


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Lack of melanized keratin and barbs that fall off: how the racketed tail of the turquoise-browed motmot *Eumomota superciliosa* is formed

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The racket-tipped tail of the motmots is uniquely shaped and its formation has attracted much attention. Barbs that grow along the wire of the motmot's two central tail feathers are weakly attached and shed soon after development. The cause of the weak attachment of these barbs is unclear. I induced feather growth by plucking the central tail feathers from seven turquoise-browed motmots *Eumomota superciliosa* and then collected the regrown feathers before the barbs along the wire had fully shed. I compared the barb-rachis junction (petiole of the ramus) along the distal flag (the racket-tip of the tail) where barbs are not shed, to the barb-rachis junction along the wire where barbs would later be shed. In these two regions, I examined the size and structure of the attachment of the barb to the rachis with a scanning electron microscope (SEM). I also used a light microscope to score the grayness of the proximal rami of these two regions to estimate the amount of melanized keratin. SEM imaging showed that the barbs are attached to the rachis with a larger supporting flange along the distal flag compared to along the wire. Images from a light microscope showed that the rami along the distal flag were black, whereas rami along the wire were translucent or gray. The lower gray-scale color score of the rami along the wire is likely due to reduced melanized keratin. These data suggest that the barbs along the wire are weakly attached due to a combination of a reduced structural attachment and a lack of structurally enhancing melanin.

The distinctive racket-tipped tail of motmots has captured considerable attention (Darwin 1874, Skutch 1947, Murphy 2006). Most species of motmot have long central tail feathers that terminate in blue-and-black rackets that appear to hang, unattached below the body of the bird. The apparent detachment occurs because the feather shafts proximal to each racket-tip (wires) are devoid of barbs. Although barbs originally grow along the wires, the barbs are later lost to give the tail feathers their racketed shape (Forshaw and Cooper 1987). In contrast, racketed feathers of other avian species (e.g., paradise kingfishers, parrots, hummingbirds, birds of paradise, drongos) attain a racketed appearance because the wires are lined with short, scarcely visible barbules (Bleiweiss 1987). Thus the growth and subsequent shedding of barbs is unique to the racketed tail of the motmots.

The formation of the motmot's racketed tail has been subject of wild speculation, and there is a long-standing

belief that motmots intentionally pluck off the barbs along the wire of their tail (Salvin 1873, Darwin 1874). Although behavioral modification of plumage has been reported in other avian groups (great hornbills *Buceros bicornis*, Hingston 1933; bearded vultures *Gypaetus barbatus*, Negro et al. 1999; red knots *Calidris canutus*, Piersma et al. 1999; rock ptarmigan *Lagopus mutus*, Montgomerie et al. 2001), there is no support for the hypothesis that motmots behaviorally modify their tail feathers. Indeed, almost one hundred years ago, Beebe (1910) noted that the barbs along the wire are weakly attached due to a narrowing of the rami at the point of attachment to the rachis. Wagner (1950) later provided evidence that the barbs are shed without the aid of behavioral modification by showing that the barbs along the wire break off due to abrasion with natural substrates. Despite these lines of evidence, the belief that motmots intentionally modify the barbs along the wire continues to be pervasive today (e.g., a placard in the aviary of the

Baltimore Aquarium states: “Motmots pluck their tail feathers to make paddle-shaped tips . . .”).

In order to further describe the mechanisms that underlie the weak attachment of the barbs to the wire, I studied tail racket formation among wild turquoise-browed motmots *Eumomota superciliosa*. To induce feather growth, I plucked the two central tail feathers and then later recaptured the same individuals and collected the newly grown tail feathers before the barbs along the wires had fully shed. Using SEM and color microscopy, I compared the barb-rachis junction (petiole of the ramus) in two places: (1) along the distal flag (the racket-tip of the tail) where the barbs are not shed, and (2) along the wire where the barbs would be later shed.

Methods

Both sexes of the turquoise-browed motmot have long tails that comprise approximately sixty percent of the total body length and terminate in large rackets (Murphy 2008; Fig. 1). The tail of the turquoise-browed motmot is the most elaborate among the ten species within the family due to the long wires, which comprise approximately one-third the length of the central tail feathers (Snow 2001).

The turquoise-browed motmot breeds colonially in the Yucatan Peninsula of Mexico in sinkholes, freshwater wells, and other man-made structures (Orejuela 1977, Scott and Martin 1983, Murphy 2008). I studied tail racket formation at a small colony located in a freshwater well near the Ria Lagartos Biosphere Reserve in Northern Yucatan, Mexico (21°33'N, 88°05'W). Individuals were captured with mist nets and banded with individually recognizable color bands.

In 2002, I plucked the two central tail feathers from seven turquoise-browed motmots (2 male, 3 female, 2 undetermined sex). Only adults (\geq second year of life) were included in the experiment, and age class was determined based on the degree of feather wear (Murphy 2005). After the central tail-feathers had partially regrown, and before the barbs along the wire were fully shed, birds were recaptured and their central tail feathers were again collected.

Scanning electron microscopy (SEM)

I inspected the ventral side of one tail feather with a Hitachi S4500 field emission scanning electron microscope (Hitachi Instruments, San Jose, California). I removed a 1cm piece of rachis and its attached barbs from the middle of the distal flag and a 1 cm piece from the middle of the wire. Each segment was attached to an SEM aluminum stub and sputter coated with approximately 90 nanometers of gold/

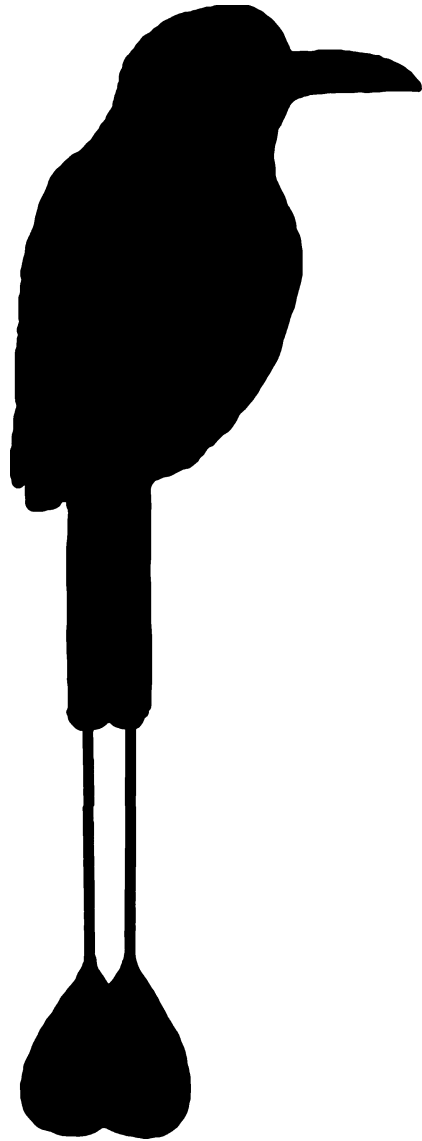


Fig. 1. Racketed tail of the turquoise-browed motmot. Barbs are shed from the wire to give the tail its racketed shape.

palladium in a Bal-Tec SCD 050 sputter coater (Bal-Tec, Liechtenstein). Feathers were viewed at 3 kV, and images were collected digitally on a Sun workstation using Imix software (Princeton Gamma Tech., Princeton, NJ 08542-0863).

Light microscopy

I inspected the dorsal side of one tail feather from each bird (total of 7 feathers) with a Leica MZFLIII light microscope, and images were collected digitally on a Leica DC 300F. Feathers were laid flat on a white

platform, and were viewed at 10x power under standardized lighting. I examined the proximal 1–2 mm of the ramus (shaft of the barb) at the point where it attached to the rachis. Five barb-rachis junctions were examined in the middle of the distal flag as well as five barb-rachis junctions in the middle of the wire. I scored the color of the rami in these regions by eye. Color scores were based on a simple 1–3 scale: score 1 represented translucent keratin with little to no pigmentation, score 2 was gray, and score 3 was black. I took all measures, and repeatability (the intraclass correlation coefficient) was calculated by measuring the same feathers on different days. Repeatability was high ($F_{13,14} = 18.0$, $P < 0.001$, $r = .89$) (Lessells and Boag 1987) and all disagreements were between translucent and gray.

Results

SEM showed that the structural attachment of the barbs to the rachis was more pronounced along the distal flag compared to the along the wire. Along the distal flag, the barbs were attached to the rachis with a large structural support. Each barb was anchored to the rachis with a prominent supporting flange that extended laterally away from the junction with the rachis (Fig. 2a). The outward projecting flange effectively increased the surface area that each barb was attached to the rachis. In contrast, the structural support along the wire was comprised of a thinner connection, and there was not a prominent lateral flange (Fig. 2b).

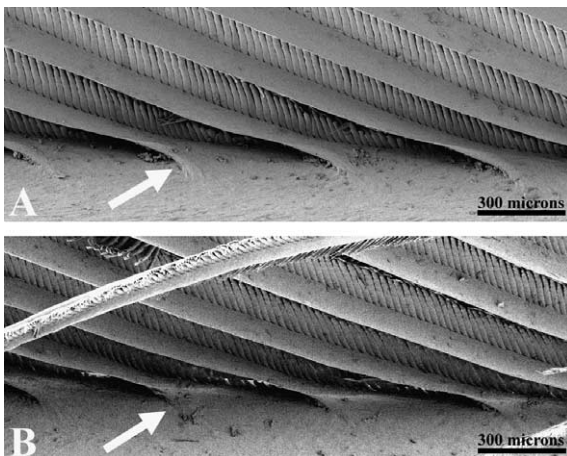


Fig. 2. SEM imaging of the structural support at the barb-rachis junction: (A) along the distal flag where barbs are not lost, and (B) along the wire where barbs will be later lost. The arrow in the top image identifies a large structural attachment with a lateral flange connecting the barb to the rachis, and the arrow in the lower image shows a reduced structural attachment.

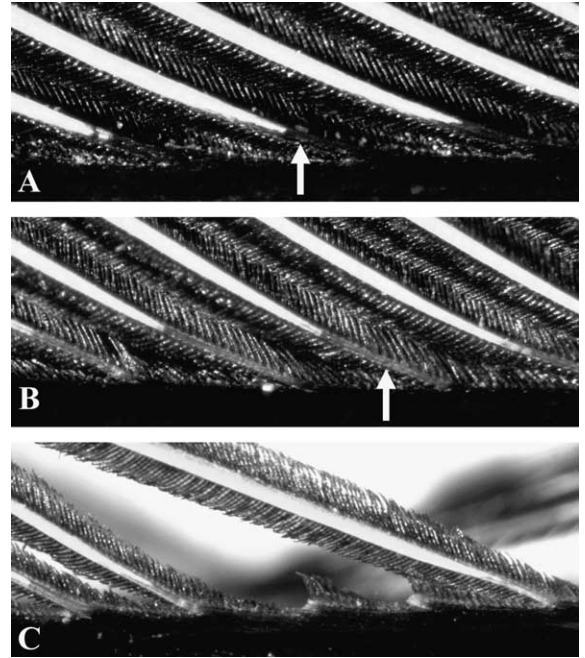


Fig. 3. Images show typical color differences of rami at the barb-rachis junction: (A) along the distal flag where barbs are not lost, and (B) along the wire where barbs will be later lost. Arrows indicate where the color of each ramus was measured (between the black horizontal rachis and the highly reflective blue of the ramus). The rami at the barb-rachis junction along the distal flag are black, indicating highly melanized keratin. Along the wire, the rami are translucent or gray, indicating reduced melanized keratin. Barbs break off along the wire where the rami are translucent or gray (C).

Light microscopy showed that there was no variation in color score of the rami at the barb-rachis junctions along the distal flag: all birds had black rami with a score of 3 (Fig. 3a). In contrast, the rami at the barb-rachis junctions along the wire were translucent or gray: all birds had a score of 1 or 2 (Fig. 3b). There was a significant difference in the color scores of rami between the two regions of the feather (color score mean \pm SE, distal flag: 3.0 ± 0.14 ; wire: 1.4 ± 0.14 ; Kruskal–Wallis: $\chi^2 = 11.58$, $P < .001$, $n = 14$; Table 1). Among feathers that had already shed some barbs along the wire, the barbs had broken where the rami were translucent or gray (Fig. 3c).

Discussion

Naturalists have speculated that motmots purposely shape their racketed tails by plucking barbs from their tail (Salvin 1873, Darwin 1874). In the early and mid twentieth century Beebe (1910) and Wagner (1950) presented evidence against the tail-plucking hypothesis

Table 1. Color score of barbs at the barb-rachis junction along the distal flag (left) and along the wire (right) for seven birds. Color was scored on a 1–3 scale (1 =translucent, 2 =gray, 3 = black). All birds had black barbs along the distal flag, whereas barbs were translucent or gray along the wire.

Bird ID	Color score of barbs along the distal flag	Color score of barbs along the wire
A	3	2
B	3	2
C	3	1
D	3	2
E	3	1
F	3	1
G	3	1

by demonstrating that the barbs along the wire of the motmot's central tail feathers are weakly attached. Furthermore, Wagner (1950) presented behavioral evidence that the barbs were shed without the aid of behavioral modification. Indeed, barbs along the wire readily fall off when slight pressure is applied (personal observation). To address the mechanism underlying the shedding of these barbs, I investigated the causes of the weak attachment of the barbs along the wire of the turquoise-browed motmot's tail.

SEM shows a clear difference in the size and shape of the structural attachment of the barb to the rachis along the two regions of the central tail-feathers. Along the distal flag (where barbs are not lost), the structural attachment at the barb-rachis junction is more pronounced and each barb is attached to the rachis with a large structural support characterized by a lateral flange that extends outward away from the ramus. The structural support of barbs along the wire (where barbs will later be lost) is reduced and thinner, and there is not a pronounced lateral flange.

Light microscopy shows that the rami at the barb-rachis junction along the distal flag are black, indicating that the keratin in this region is highly melanized. In contrast, the rami at the barb-rachis junction along the wire are clear or gray, indicating a reduced deposition of melanin. Indeed, in many individuals, the keratin at the barb-rachis junction along the wire contains such reduced melanin that the rami and barbules are translucent. Melanin has an important role in strengthening keratin. When imbedded within a keratin matrix, melanin granules create a composite that is harder than noncomposite keratin (Bonser and Witter 1993). Melanin strengthens feathers, making them harder and also less prone to breakage (Burt 1986, Bonser 1995, but see Butler and Johnson, 2004). In addition, highly melanized feathers are more resistance to abrasion than are non-melanized feathers (Burt 1979, 1986, Barrowclough and Sibley 1980, Bonser 1996), and melanized keratin reduces feather damage in wild populations (Kose and Møller 1999).

The raked shape of the motmot's tail is attained when weakly attached barbs fall off, and the barbs along the wire appear to be weakly attached due to a combination of a reduced structural attachment and a lack of structurally enhancing melanin in the proximal rami of the barbs. Data provided in this paper provide evidence that certain barbs are designed to fall off, and that the shape of the motmot's tail is pre-determined at the time of development. This finding is relevant in light of recent research that has shown the length of the wire of the male turquoise-browed motmot is likely to function as a sexually selected signal. Males with longer wires have greater pairing success, pair with females that lay larger clutches, and have greater reproductive success (Murphy 2007). Thus, because motmots do not mold the shape of the tail to fit their preferences, it is reasonable to predict that the length of the male wire may reflect an individual's intrinsic quality in a similar way that elaborate plumage reflects quality in other species. Future research into the function of the motmot's raked tail will help determine what information the length of the wire conveys, and whether wire length is an honest signal of quality.

Other avian species have been shown to change appearance of their plumage by a similar process of wearing of feathers. For example, house sparrows lose white feather tips to increase black badge size (Møller and Erritzoe 1992), and snow buntings lose white feather tips to attain black breeding plumage (Lyon and Montgomerie 1995). Changing appearance in these species is thought to facilitate signaling or camouflage during different seasons or social contexts (for review see Montgomerie 2006). In contrast, there is little opportunity for motmots to signal with fully barbed tail feathers because barbs are shed soon after the growing feather emerges from the follicle. Thus, it seems unlikely that there is a signaling function to the two stages of motmot tail-development.

Although the research presented here does not directly test the tail-plucking hypothesis, I have described two mechanisms that are likely to account for the weak attachment of the barbs along the wire. Shedding of these weakly attached barbs does not require behavioral modification, as these barbs are likely to fall off due to wearing against environmental substrates and during routine preening. Indeed, because there are no reliable accounts of motmots plucking their tails, the more parsimonious process of shedding barbs without their purposeful removal seems more likely to account for the formation of the unique raked tail of the motmot.

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