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BRIEF COMMUNICATION

Anatomy of bristles on the nares and rictus of western barn owls (*Tyto alba*)

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Abstract

Many nocturnal avian species, such as Strigiformes, Caprimulgiformes and Apterygiformes, have sensitive vibrotactile bristles on their upper bill, especially on their rictus. The anatomy of these bristles can vary, especially in terms of sensitivity (Herbst corpuscle number), bristle length and bristle number. This variation is thought to be associated with foraging – such that diurnal, open foragers have smaller and less-sensitive bristles. Here, we describe bristle morphology and follicle anatomy in the western barn owl (*Tyto alba*) for the first time, using both live and roadkill wild owls. We show that *T. alba* have both narial and rictal bristles that are likely to be vibrotactile, since they have Herbst corpuscles around their follicles. We observed more numerous (~8) and longer bristles (~16 mm) on the nares of *T. alba*, than on the rictal region (~4 and ~13 mm respectively). However, the narial bristle follicles contained fewer Herbst corpuscles in their surroundings (~5) than the rictal bristles (~7); indicating that bristle length is not indicative of sensitivity. As well as bristle length and number varying between different facial regions, they also varied between individuals, although the cause of this variation remains unclear. Despite this variation, the gross anatomy of facial bristle follicles appears to be conserved between nocturnal Strigiformes, Caprimulgiformes and Apterygiformes. Understanding more about how *T. alba* use their bristles would, therefore, give us greater insights into the function of avian bristles in general.

KEYWORDS
feather morphology, foraging, narial, rictal, somatosensation, Strigiformes, touch sensing

1 | INTRODUCTION

Nocturnal owls (Strigiformes), such as barn owls (Tyto spp.), can locate prey in complete darkness due to their enhanced auditory localisation ability and binocular vision (Gill, 2007; Martin, 2017; Stevens, 2007). However, they also possess facial bristles, which are simple, hair-like feathers that occur on the upper mandible and surround the bill of many species, including around the nares and rictal regions. Küster (1905) previously described the rictal bristle anatomy of four species of owls (*Bubo bubo*, *Asio flammeus*, *Athene noctua* and *Strix aluco*) and Cunningham et al. (2011) in one species (*Ninox novaeseelandiae*). Küster (1905) found that the bristle follicles were connected by muscle and connective tissue, and associated with nerves and mechanoreceptors (Küster, 1905; Stettenheim, 1973). Küster (1905) and Cunningham et al. (2011) both noticed Herbst corpuscles surrounding the rictal bristle follicles. Herbst corpuscles are mechanoreceptors that are highly sensitive to pressure and rapid mechanical deformations, such as vibration (Cunningham et al., 2013; Gottschaldt, 1985; Necker, 2000; Stettenheim, 2000). Therefore, it is likely that the rictal bristles in these owl species are sensitive to vibrotactile signals. As well as being touch sensitive, Küster (1905) suggested that rictal bristles may also be able to sense sound waves; if so, rictal bristles could play a role in environmental scanning for the sounds of prey (Lederer, 1972). However, overall, the function of these bristles remains relatively unclear.

While previous studies have proposed that the rictal bristles of other bird species, such as Apterygiformes (Corfield et al., 2014) and Caprimulgiformes (Delaunay et al., 2020), may help to guide nocturnal foraging, bristles have yet to be associated with prey capture directly. For example, several tyrant flycatcher species (Passeriformes) have been documented to forage without using their rictal bristles. Specifically, individuals were filmed catching prey with their bill tips, rather than at the base of the bill in the rictal bristle area (Lederer, 1972). Delaunay et al. (2020) found the first association of bristle morphology with foraging, and suggested that Caprimulgiformes that foraged diurnally in open habitats had shorter, thinner rictal bristles that lacked mechanoreceptors at the base, compared to species that foraged after dusk.

Delaunay et al. (2020) also found diversity in bristle morphology between species with similar ecological traits, including variation in bristle shape, length and Herbst corpuscle counts. Herbst corpuscles counts are likely to be associated with the sensitivity of the structures they surround (Schneider et al., 2016). This is thought to be the case in bill tip mechanosensation in Anseriformes, where high densities of mechanoreceptors in the bill tip are paralleled to match the sensitivity and density of homologous corpuscles in primate finger pads (Verendeev et al., 2015). In addition, many bill tip mechanoreceptors are found in species that forage tactually, rather than visually (Barbosa & Moreno, 1999), such as by probing with remote touch sensing (Zweers & Gerritsen, 1997). For example, parrot bills are densely populated with Herbst corpuscles in the distal upper and lower bill region and tongue (Demery et al., 2011), and they use them to tactually discriminate and extract the edible parts of food items. Therefore, we believe that describing Herbst corpuscle counts and distributions are a useful first step in describing bristle anatomy and sensitivity, and that their presence may indicate a possible role in tactile foraging behaviours.

The morphology and anatomy of facial bristles have yet to be described in the majority of bird species. Probably the best described order is now the Caprimulgiformes, due to the recent work of Delaunay et al. (2020), and even then only 12 species have been described. As Strigiformes are phylogenetically close to the Caprimulgiformes order, they represent a useful group to develop further comparative studies, and to increase our knowledge of facial bristle anatomy. Unlike many other nocturnal species, the ecology and behaviour of western barn owls (*T. alba*) are particularly well documented (Frey et al., 2011; Lenton, 1984; Roulin, 2020; Rozman et al., 2021). They are also found all over Europe and sub-Saharan Africa, and are often part of large monitoring studies for population dynamics and evolutionary ecology (Roulin, 2020), which makes it easier to access specimens, as well as other demographic data, compared to other nocturnal species.

Within this study, we will present the first anatomical description of narial and rictal bristles in *T. alba*. Narial bristles occur around the nares, usually covering them somewhat, whereas rictal bristles occur from the rictus to nares, immediately above the line of the upper mandible (diagram in Figure 1a–c). We would expect *T. alba* to have bristles with Herbst corpuscles around the follicles since this has been observed in other species of owls (Küster, 1905). Moreover, we may expect to see some natural variation between individuals in aspects of bristle morphology, such as number and length. There has not yet been a systematic analysis of intra-species bristle morphology for us to base our predictions on, although we may expect bristle length to scale allometrically with other size measurements, since other feathers, such as ornamental feathers (Cuervo & Møller, 2001, 2009), primary feathers (Nudds et al., 2011) and the mass and number of plumage feathers (Møller, 2015) are all associated with body size in some respects.

2 | METHODS

2.1 | Samples

Data collection was carried out in 2018, using wild *T. alba* individuals in the Hula Valley (33°6′N, 35°37′E), Israel as part of a Barn Owl Monitoring Scheme (Peleg et al., 2018). During 2015–2017, the western barn owl monitoring scheme routinely collected cadavers. These included individuals that have mainly died of road traffic collisions. In total, 80 adult cadaveric individuals were included in this study. Cadavers were stored in a chest freezer (−20°C) on site and removed for morphological measurements. These measurements included rictal and narial bristles counts and length measurements. Bristles extending from the rictus to nares on the upper mandible were termed rictal bristles, and bristles around and above the nares were termed narial bristles (Figure 1a–c). Bristles were counted on each side, and a mean was taken for each of them, termed rictal or narial bristle count. The three longest rictal and narial bristles were also measured, from the base of the shaft (flush to the follicle) to the tip of the bristle, on each side using digital callipers, and a mean taken, termed rictal or narial bristle length. Repeating these measurements three times had good agreement (~5%, Table S1); therefore, each specimen was only measured once from hereon in. As well as bristle measurements, other length measurements were also taken to investigate allometric scaling, including tail length (longest right or left tail feather), wing length (mean of the two sides taken from length of the flattened wing from the bird's wrist to the tip of the longest primary; Roulin, 2004), tarsus length (mean of two sides taken by "bending the foot at the intertarsal joint and toes, and measuring the distance between the extreme bending point"; Alatalo et al., 1984) and body mass. Head length (back to front of the head) and width (side to side of the head, behind the eyes) were used to approximate head size (square root of head length x head width, i.e., Geometric Mean; Muchlinski, 2010). Pectinate claw length was also measured

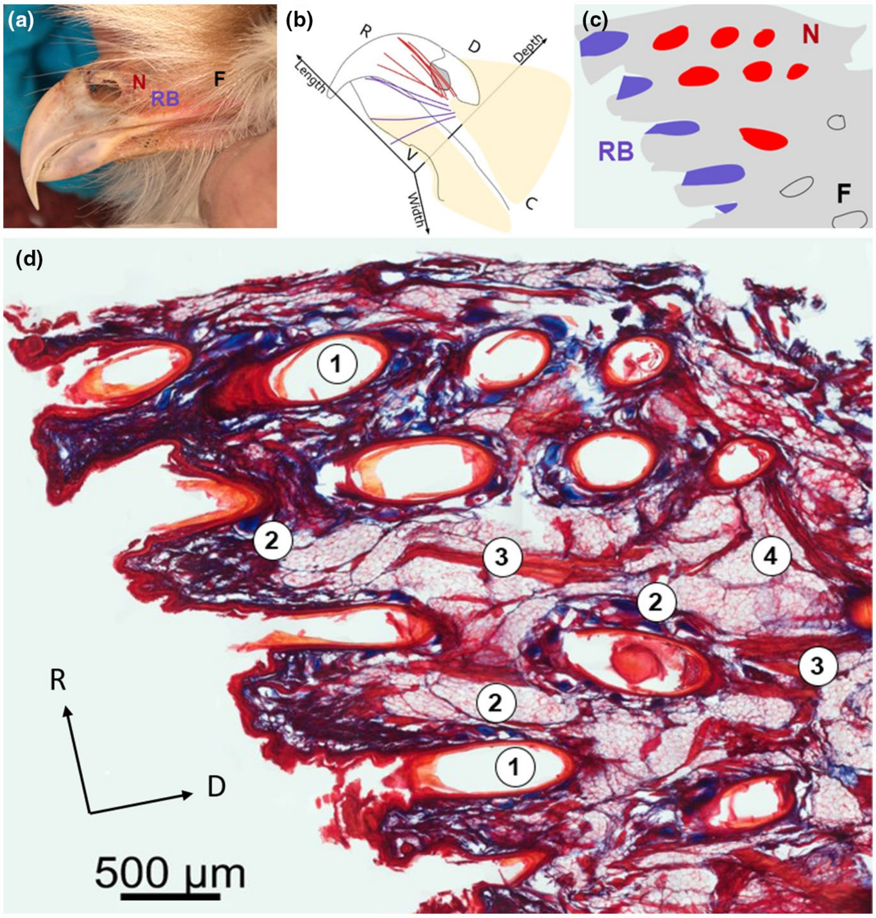

FIGURE 1 Follicle anatomy and morphology of *Tyto alba* bristles. (a) Photograph of *T. alba*'s bill and facial bristles; (b) diagram of the bill, including rictal (RB) and narial (N) bristles; (c) the longitudinal section of the follicles, illustrating the types of bristles, including rictal (RB, in blue) and narial (N in red); (d) example longitudinal slice from nares to rictus in *T. alba*. Including the bristle follicles (1), which reveals the presence of mechanoreceptors, i.e., Herbst corpuscles (2), dermal muscle fibres (3) and adipose tissue (4) surrounding the follicles. Slice stained with Masson's trichrome stain. R and D correspond to the (R) rostral and (D) dorsal directions, with the bill tip positioned ventrally to the rostral extremity

as a mean of the two sides. Bill length (rictus to the rostral part of the bill), width (rictus to rictus) and depth (submandibular to the culmen of the upper mandible) were measured (Figure 1b), and bill length and mouth area (width × depth) were used in further analyses. All works in this study were carried out in accordance with local ethical regulations at Manchester Metropolitan University.

2.2 | Bristle morphology

Following the extraction of measurements from cadavers, rictal bristle measurements were then incorporated into the routine monitoring of live birds that occurred as part of the Barn Owl Monitoring Scheme, which was authorised by the Israel Nature and Parks Authority (permit number 2017/41606). During the 2018 breeding season, 150 nest boxes were monitored (see Charter et al., 2012 for methods) and 38 breeding pairs were found during the period 12 April–5 July, 2018. Since it was not possible to take accurate measurements of the bristle lengths using digital callipers with a live bird in hand, photographs were used instead. During routine monitoring of nest boxes, 34 adult owls were captured, their sex identified and were photographed on one side (Figure 1a) against a scale bar to approximate bristle length. These photographs were then analysed in imageJ. While it was not fully possible to extract bristle number from the photographs as some of the bristles were hard to see, bristle length could be estimated. The three longest and most prominent rictal bristles were measured in imageJ (Figure S1) and a mean taken, termed bristle length. Repeating these measurements three times had good agreement (~10%, Table S1); therefore, each specimen was only measured once from hereon in. This photographic measurement was also in good agreement with the digital calliper method in the same specimen (~13%, Table S1), although it did tend to underestimate bristle length by about 2 mm. The narial bristles were not measured from the photographs, as these tended to emerge out of plane (Figure 1a), and therefore, the measurements would be less accurate. After photographing, standard morphological length measurements were also taken from the live birds, including weight, wing length (mean of the two sides), tarsus length (mean of the two sides) and tail length. Their sex was also noted.

2.3 | Bristle follicle anatomy

Two of the frozen cadavers were selected for further examination of their follicle anatomy. Individuals were selected that had fully intact bristle areas, with no injury or freezer damage to the external skin around the face. The cadavers were defrosted on site and the upper bill region, including the nares and rictal region, was dissected and immediately stored in 4% Paraformaldehyde (diluted with Phosphate Buffer Solution), in which they were transited back to Manchester Metropolitan University and stored in, in a fridge (4°C) for several weeks until processed for the histology work at the university. The latter was conducted by trimming and flattening the skin tissue for 5 h between two sponges in histology cassettes in 70% industrial methylated spirit (IMS). Tissue samples were loaded into a tissue processor (Shandon Citadel 2000) to dehydrate through a graded series of ethanol (70%, 80%, 90% and 100%) and xylene baths and infiltrated with paraffin wax, in a process lasting approximately 20 h. The tissue samples were then embedded in solid blocks of paraffin that were sliced at 10 μm on a rotary microtome (Thermo-scientific microm HM355S) with a water bath (37°C), and mounted on to slides. They were then stained with standard Masson's Trichrome staining and cover-slipped with DPX mountant. Microscope images were taken using Zeiss Zen Pro imaging software on a Zeiss AxioImager M1 Brightfield microscope and AxioCam HMRc. Images were examined to qualitatively describe the follicles and the surrounding tissue, including muscles and adipose tissues. The number of Herbst corpuscles present around each individual follicle were also counted, and the maximum number that was observed in one slice was reported for both narial and rictal bristles.

2.4 | Statistical analysis

Since the majority of measures were not normally distributed, non-parametric tests were employed throughout. Wilcoxon Signed Rank tests were used to compare narial and rictal bristle numbers and lengths within the same individuals. Mann–Whitney *U*-tests were used to compare photographic measurements and cadaveric measurements of rictal bristle lengths. Mann–Whitney *U*-tests were also used to compare rictal bristle lengths of male and female specimens. Median values (Mdn) and inter-quartile range (IQR) will be reported throughout.

3 | RESULTS

3.1 | Bristle follicle anatomy

Since the tissue was sliced on a sagittal plane, a difference in follicle shape can be observed in the histology section (Figure 1b,c). Rictal bristle follicles were elongated in length, i.e., sliced along the follicle while narial bristle follicles were more circular, i.e., in more cross-sectional slices. This can be explained by the orientation and arrangement of the bristle follicles on the face of the specimens (Figure 1a). Rictal bristles emerge from the face in the same orientation (parallel) to the bill (Figure 1a) with each neighbouring follicles positioned in a row (Figure 1c,d), whereas narial bristles emerge out of plane and almost perpendicular to the bill (Figure 1a) with follicles arranged in at least two rows neighbouring the nare dorsally to the row of rictal bristle follicles (Figure 1c,d). In addition, for each of our two dissected specimens, four and five rictal bristles were counted along the edge of the bill in one single line, whereas seven and eight narial bristles were counted around the nares, which was more dorsal to the rictal bristles (Figure 1c,d).

In the integument around the rictal and narial bristles, muscle fibres can be seen, especially towards the bottom of the follicles of the rictal bristles (Figure 1d). These bundles of muscles are likely to be smooth erector or depressor muscle fibres and may connect bristle follicles together, in both the rictal and narial bristles. Surrounding, and sitting caudal and dorsal to the rictal bristle follicles, there was a high concentration of adipose tissue (Figure 1d).

The bristle follicles themselves are simple, single-part capsules (Figures 1d and 2b,c). Herbst corpuscles (Gottschaldt, 1985) could clearly be seen around both the rictal and narial bristles (Figure 1c), indicated by characteristic blue, oval discs, containing an outer capsule, inner bulb and a line through the middle that is likely to contain rows of Schwann cells (* in Figure 2a) (e.g. Cunningham et al., 2013; Necker, 2000). Overall, more Herbst corpuscles were observed around the follicles of rictal bristles than narial bristles (Figure 2b,c), with a maximum of seven Herbst corpuscles observed around rictal bristle follicles and five around the narial bristle follicles.

3.2 | Bristle morphology

In agreement with the two owls studies for the anatomy, cadaveric measurements from 80 owls found around four rictal bristles (Mdn = 4.0, IQR = 3.5–5.0) (Figure 2a–d) and eight narial bristles (Mdn = 8.0, IQR = 7.0–10.0) (Figure 2b,d). In fact, narial bristles occurred in consistently higher numbers than the rictal bristles (Wilcoxon Signed Rank: $Z = -6.854$, $p < 0.001$). Similarly, narial bristles were also consistently longer in the cadaveric specimens (Mdn = 15.5 mm, IQR = 14.1–17.0) compared to the rictal bristles (Mdn = 12.7 mm, IQR = 11.0–14.2) (Wilcoxon Signed Rank: $Z = -6.677$, $p < 0.001$, Figure 2a,c). Rictal bristle length was positively correlated to rictal bristle number ($r = 0.591$, $p < 0.001$, Table S2), indicating that individuals with more numerous rictal bristles tended to also have longer rictal bristles. However, both narial and rictal bristle length and count data were not correlated with any other length measurements, including tail length, body mass, bill length, mouth area, skull size and pectinate claw length (Table S2), suggesting that bristles do not scale with other body measurements.

The photographic measurements of rictal bristle length systematically underestimated length by around 2 mm (Mdn = 10.1, IQR = 7.1–13.2), compared to the cadaveric measurements (Mann–Whitney *U*: $Z = -3.054$, $p = 0.002$, Figure 2a,e). This 2 mm underestimate also agrees with our methods (comparison in Table S1). However, the

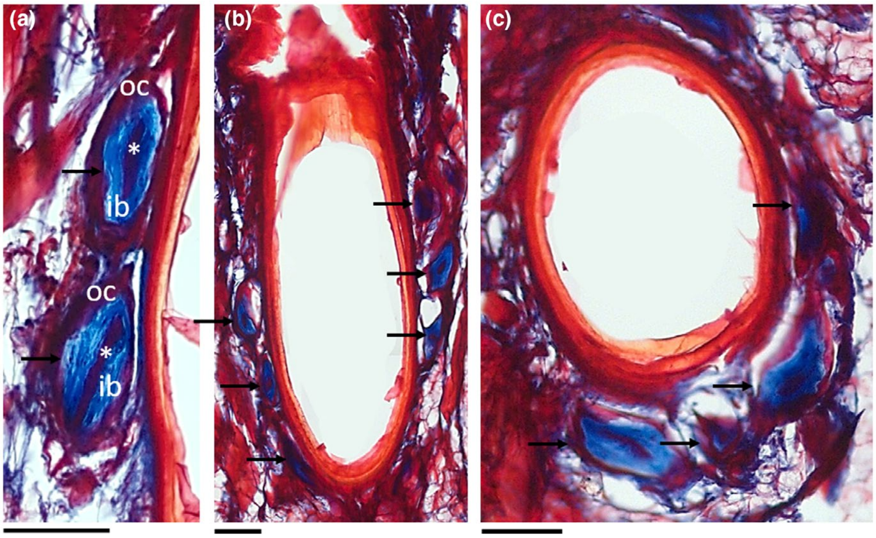

FIGURE 2 Herbst corpuscles surrounding the bristle follicles, indicated by the black arrows in each panel. (a and b) Herbst corpuscles in two example rictal bristle follicles; (c) Herbst corpuscles in an example narial bristle follicle. Labels of the Herbst corpuscles correspond to oc: Outer capsule, ib: Inner bulb and * middle, containing rows of Schwann cells. Arrows indicate the Herbst corpuscles. Slices stained with Masson's trichrome stain. Scale bars are 100 μm

overlapping confidence intervals in Figure 3c,d suggest that these measures are probably roughly equivalent, which gives us confidence to use the photographic measurements in subsequent analyses (see also Table S1 for direct comparisons). Furthermore, in agreement with the cadaveric measurements, photographic measurements of rictal bristle length were not correlated with other length measurements, including body mass, wing length, tarsus length and tail length (Table S3). There was also no significant difference in rictal bristle length between males and females (Whitney U: $Z = -1.436$, $p = 0.159$; Females: Mdn = 11.3, IQR = 7.4–14.1; Males: Mdn = 8.6, IQR = 6.1–11.1).

4 | DISCUSSION

Tyto alba have both narial and rictal bristles. Both bristle types are likely to be sensitive to vibrotactile stimuli, as they both contain Herbst corpuscles around their follicles. Bristle lengths and numbers varied between individuals and facial regions in *T. alba*. Specifically, there were more numerous and longer bristles on the nares of *T. alba*, than on the rictal region. However, the narial follicles contained fewer Herbst corpuscles in their surroundings (~5) than the rictal bristle follicles (~7), suggesting that longer bristles are not necessarily more sensitive.

4.1 | Follicle anatomy

The follicles and surrounding integument of the nares and rictus contained many features that have previously been found in other species of Strigiformes (Cunningham et al., 2011; Küster, 1905), Apterygiformes (Cunningham et al., 2011) and Caprimulgiformes (Delaunay et al., 2020), including muscles and Herbst corpuscles. There were bundles of smooth erector or depressor muscle fibres that connected the rictal bristle follicles and narial bristle follicles together, similar to those documented in other species (Delaunay et al., 2020). The rictal bristles were arranged into a single row, as had also been previously described in other species (Delaunay et al., 2020). The conservation of the gross anatomy of rictal bristle follicles, as well as their arrangement, in Apterygiformes, Caprimulgiformes and Strigiformes suggest that this might be common across other avian orders. It would be interesting to investigate follicle anatomy in more species, especially distantly unrelated groups, such as Passeriformes, Coraciiformes, Trogoniformes and Accipitriformes to establish whether the anatomy is conserved across all birds with facial bristles.

In the *T. alba* specimens studied here, ~5 Herbst corpuscles were counted around the narial bristle follicles and ~7 around the rictal bristle follicles. This is lower than other species of nocturnal birds, including brown kiwi (*Apteryx mantelli*), spotted nightjar (*Eurostopodus argus*), fiery-necked nightjar (*Caprimulgus pectoralis*) and oilbird (*Steatornis caripensis*), which have around 10 Herbst corpuscles surrounding their rictal bristle follicles (Cunningham et al., 2011; Delaunay et al., 2020). However, this amount is similar to the large frogmouth (*Batrachostomus auritus*, 5), Gould's frogmouth (*Batrachostomus stellatus*, 5), European nightjar (*Caprimulgus europaeus*, 6) and the pauraque (*Nyctidromus albicollis*, 5) that, like *T. alba*, are not strictly nocturnal, but forage from dusk (Delaunay et al., 2020). Some species that forage cathemerally lack Herbst corpuscles around their rictal bristle follicles entirely (including common nighthawk, *Chordeiles minor*, and pennant-winged nightjar, *Caprimulgus vexillarius*), and can additionally lack intrinsic muscle fibres (nacunda nighthawk, *Chordeiles nacunda*) (Delaunay et al., 2020). The presence of Herbst corpuscles and muscles around the bristles of our *T. alba* specimens likely suggest that both rictal and narial bristles are functional and can sense vibrotactile signals.

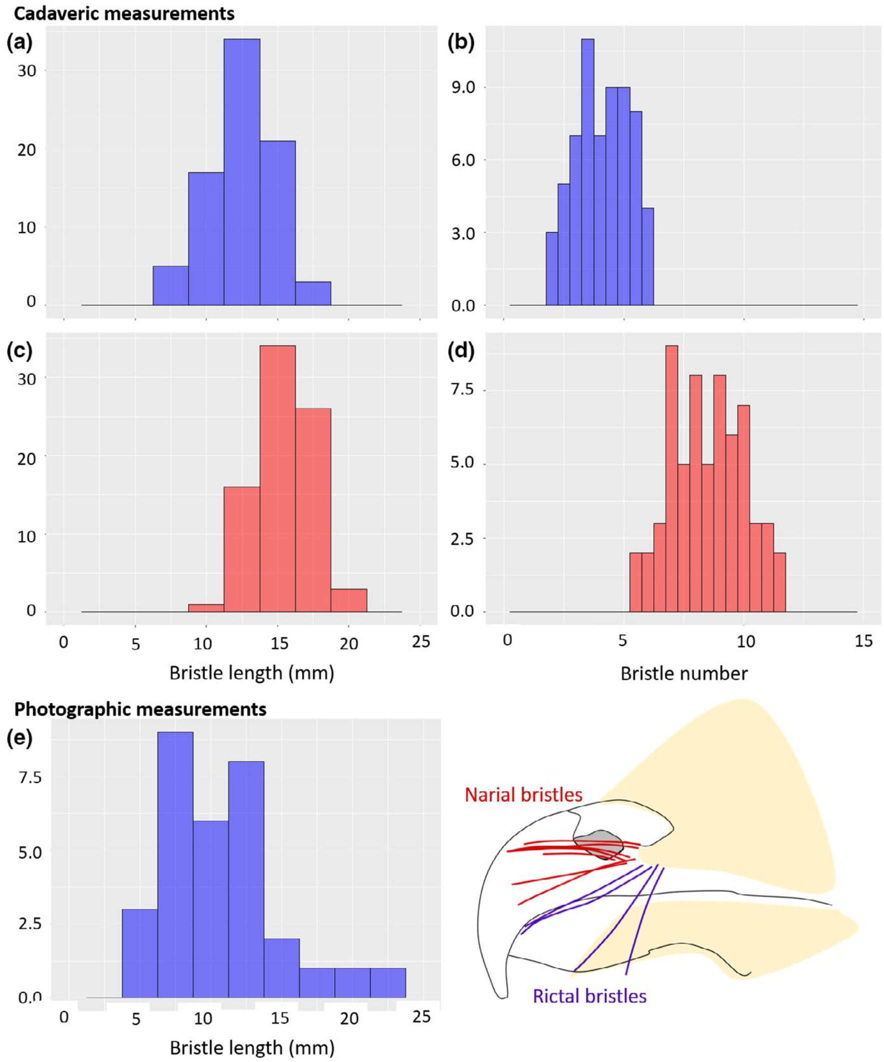

FIGURE 3 Bristle length and number histograms. Bristle lengths are shown in the left hand panels, and bristle numbers (counts) on the right. Red histograms correspond to narial bristles, and blue to rictal bristles, which is also indicated in the bill diagram (bottom right). Two methods were used to measure rictal bristle length – Cadaveric measurements using digital callipers from 80 cadavers and measurements from photographs taken from 34 awake, live birds. Frequency is on the *y*-axes in each panel

4.2 | Bristle morphology

As well as having fewer Herbst corpuscles, the narial bristles were longer (~16 mm) and more numerous (8) than the rictal bristles (~13 mm and 4 respectively). This agrees with the findings of Delaunay et al. (2020) that bristle length cannot imply bristle sensitivity. In mammalian whiskers, longer, thicker and stiffer whiskers tend to have more numerous mechanoreceptors (Ebara et al., 2002). However, this is not the case in avian bristles. In birds, perhaps the longer bristles act like a leaver, transferring larger bending moment and forces to the follicle, so that the same signals can be detected by fewer Herbst corpuscles. Or perhaps the Herbst corpuscles themselves may have different morphologies and sensitivities between the narial and rictal regions (Quindlen-Hotek et al., 2020). Differences between the narial and rictal bristles may indicate regional specialisations in these bristles, where they may play different functional roles. What these roles might be is unclear, but may include active or passive foraging (Cunningham et al., 2011; Keast & Saunders, 1991) and protection of the nostrils and eyes from debris (Conover & Miller, 1980; Corfield et al., 2014; Cunningham et al., 2011). We did not observe differences in rictal bristle length with sex; therefore, they are unlikely to be a sexual trait. Rictal bristle length also did not vary with other morphological lengths; therefore, their variation is not due to simple allometric scaling.

Indeed, it is not possible to infer the functional role of rictal and narial bristles from our study. We have begun to investigate the association of rictal bristle length with measures of fitness (i.e. clutch size and number of fledglings), foraging success (total prey species and percentages of *Meriones tristrami*, *Mus musculus*, *Rattus rattus* and *Crocidura* spp. present in regurgitated pellets; as per Charter et al., 2015) and behavioural attributes (aggressivity scored from 0 = relaxed to 3 = very aggressive, and agitation scored from 0 = docile to 3 = very agitated; see Peleg et al., 2014) (See Supplement 3 for more details). However, we have not seen any correlations with rictal bristle length and these measures so far (Table S4). It is likely that a complex interplay of both genetic and environmental factors cause variation in bristle numbers and lengths. It must be noted that the sample numbers in this study were relatively low and really only form a pilot investigation into the feasibility of incorporating bristle measurements alongside usual monitoring practices. We found that taking photographs of individuals during regular monitoring was relatively straightforward and accurate (Table S1), and we would recommend doing studies of this kind to investigate associations of bristle length with other length measurements and demographic variables, especially in larger sample numbers.

4.3 | Conclusions

Tyto alba have narial and rictal bristles that are likely to be sensitive to vibrotactile information. The gross anatomy of bristle follicles is conserved between nocturnal Strigiformes, including *T. alba*, Caprimulgiformes (including nightjars) and Apterygiformes (including kiwis), including being surrounded by muscle fibres and mechanoreceptors, including Herbst corpuscles. The number of Herbst corpuscles, bristle follicles and the length of the bristles can vary between species. And for the first time, we show here that they can vary between individuals of the same species, as well as between different facial regions of the rictus and nares. The cause of this variation remains unclear, although it is likely to be associated with bristle function, and predicted by individual sources of genetic and environmental variation.

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AUTHOR CONTRIBUTIONS

R.G., M.D. and M.C. designed the study and drafted the manuscript. M.C. collected the cadavers, photographed the live individuals and collected their morphological, ecological and behavioural data. M.D. performed the histology and collected the cadaveric measurements. Analyses and interpretations were performed by R. G. and critically reviewed by M. C. All authors revised the manuscript and provided final approval before submission.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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