REVIEW

Redefining the study of sexual dimorphism in bats: following the odour trail

Mariana MUÑOZ-ROMO* (iD) *Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panamá and Laboratorio de Zoología Aplicada, Departamento de Biología, Facultad de Ciencias, Universidad de Los Andes, Mérida, 5101, Venezuela. Email: munozml@si.edu*
Rachel A. PAGE (iD) *Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panamá. Email: pager@si.edu*
Thomas H. KUNZ *Center for Ecology and Conservation Biology, Department of Biology, Boston University, Boston, 02215, USA.*

ABSTRACT

1. Sexual dimorphism is the condition in which males and females of the same species are easily distinguished by specific traits (secondary sex characteristics), often related to body size, colour patterns, weapons, and ornaments. Males of many mammal species tend to be larger or more ornamented than females, and these characteristics tend to be more pronounced in polygynous, diurnal, and open-habitat species.
2. Bats have long been considered a largely non-sexually dimorphic group due to lack of conspicuous differences in body size and other cranial and skeletal characters. However, bats, like many mammals, exhibit a diverse array of soft-tissue integumentary glands and non-glandular odour-producing structures with intense odorous substances that have not been thoroughly investigated, although postulated functions include facilitating mate selection in their generally polygynous associations.
3. To date, there has been no systematic assessment of the occurrence or expression of sexually dimorphic traits in bats, many of which show intriguing sexual dimorphism in soft tissue, and most of which involve intense odours. In this study, we review evidence of integumentary glands and non-glandular odour-producing structures known in bats, as a first step towards identifying future research pathways to study sexual dimorphism in bats.
4. Highly variable glands and non-glandular odour-producing structures have been noticed in ten different regions of the body, but are most frequently found on the head and the ventral region of the neck. They have been described in nearly 9% of bat species and in 70% of 21 extant bat families.
5. Our review, based on extremely scattered and unevenly detailed literature, unveils the extraordinary sexual dimorphism that has been observed in Chiroptera to date, identifying not only target body parts where sexually dimorphic traits are likely to be found, but also critical avenues for future investigation and discoveries, and stressing the importance of the timing of secondary sexual trait observations, behavioural studies, and chemical analyses.

RESUMEN EN ESPAÑOL

1. El dimorfismo sexual es la condición en la que machos y hembras de la misma especie se distinguen fácilmente por rasgos específicos (características sexuales secundarias), a menudo relacionados con el tamaño corporal, patrones de color, elementos de defensa/competencia y ornamentos. Los machos de

muchas especies de mamíferos tienden a ser más grandes o más ornamentados que las hembras, y estas características tienden a ser más pronunciadas en especies poligínicas, diurnas y de hábitat abiertos.

2. Durante mucho tiempo se ha considerado a los murciélagos como un grupo en su mayoría sexualmente no dimórfico debido a la ausencia de diferencias notables en el tamaño corporal y otros caracteres craneales y esqueléticos. Sin embargo, los murciélagos, como muchos mamíferos, exhiben una gama diversa de glándulas tegumentarias (tejidos blandos) y estructuras no glandulares odoríferas con sustancias de olor intenso que no se han investigado a fondo, aunque las funciones postuladas incluyen facilitar la selección de pareja, en sus asociaciones generalmente poligínicas.

3. Hasta la fecha no se ha realizado una evaluación sistemática de la aparición o expresión de rasgos sexualmente dimórficos en murciélagos, muchos de los cuales muestran un dimorfismo sexual intrigante en tejidos blandos, y la mayoría de los cuales involucran olores intensos. En este estudio, revisamos evidencia de glándulas tegumentarias y estructuras no glandulares odoríferas conocidas en murciélagos, como un primer paso hacia la identificación de futuras vías de investigación para estudiar el dimorfismo sexual en murciélagos.

4. Se ha observado glándulas y estructuras no glandulares odoríferas muy variables en diez regiones corporales diferentes, pero se encuentran con mayor frecuencia en la cabeza y la región ventral del cuello. Estas han sido descritas en 9% de las especies y en 70% de las 21 familias de murciélagos existentes.

5. Nuestra revisión, basada en literatura extremadamente dispersa y desigualmente detallada, revela el extraordinario dimorfismo sexual que se ha observado en Chiroptera hasta la fecha, identificando no sólo las partes del cuerpo clave donde es probable que se encuentren rasgos sexualmente dimórficos, sino también rumbos críticos para investigación y descubrimientos futuros, y enfatizando la importancia del instante de las observaciones de rasgos sexuales secundarios, de los estudios de comportamiento y de los análisis químicos.

INTRODUCTION

Sexual dimorphism is the condition in which males and females of the same species are easily distinguished by specific traits, irrespective of differences in genitalia (Andersson 1994). These secondary sexual characteristics are often related to body size, colour patterns, weapons, ornaments, and chemical cues and are commonly associated with or exhibited during specific behavioural repertoires. Secondary sexual characteristics may be prominent (exaggerated) or cryptic (requiring specialised sensory tuning for detection), depending on the type and degree of sexual selection (Andersson 1994).

Intraspecific competition for access to the other sex can result in sexual dimorphism, where one sex, usually the male, tends to be larger or more ornamented than the other, generally the female (Andersson 1994, McPherson & Chenoweth 2012). Sexually dimorphic traits are driven by sexual selection and are often not advantageous for individual survival. The traits tend to be more pronounced in polygynous, diurnal, and open-habitat species (Emlen & Oring 1977, McPherson & Chenoweth 2012).

Most mammals are polygynous (Emlen & Oring 1977, Clutton-Brock 1989) and display unequivocal sexual differences in diverse characteristics, from highly pronounced in some groups (e.g. primates, pinnipeds, proboscideans, some artiodactyls) to less conspicuous in others (rodents, insectivores, sirenians; Ralls 1977, Lu et al. 2014). Ralls (1977) determined that in 16 of the 20 mammalian orders, the degree of sexual dimorphism shown by most species is small to moderate. When dimorphism occurs, males are usually larger than females except in the mysticetes, lagomorphs, and some chiropterans, in which females are larger than males (reverse sexual dimorphism *sensu* Racey 2009). In some species, female bats are larger than males, allowing them to carry and provision young (Ralls 1976, Racey 2009). As an order, in terms of body size, Chiroptera is not recognised as sexually dimorphic (Ralls 1977, Lu et al. 2014). However, distinguishing between sexual dimorphism in size and sexual dimorphism in other traits

is key, because in many cases, bats included, the degree of sexual dimorphism in structures used in behavioural displays may be more important for mate choice, copulation, and hence reproductive success than differences in body size (Ralls 1977, Andersson 1994).

Most mammals display significant sexual differences in chemical cues (Quay 1970, Eisenberg & Kleiman 1972, Mykytowycz & Goodrich 1974, Blaustein 1981, Brennan & Kendrick 2006), and most of the odours come from glands (Quay 1970) and other odour-producing structures, such as soft tissue or bodily substances (Voigt & von Helversen 1999, Muñoz-Romo et al. 2011a, b, Flores & Page 2017). Although striking sexual differences in odours in bats have been noted by researchers over the course of nearly a century (Dunn 1934, Herreid 1960), few species have been studied in depth. This lack of study could be the result of difficulties in studying flying, nocturnal organisms (Dechmann & Safi 2005), and because many soft-tissue traits have gone unnoticed for decades, even in some well-studied species. Soft tissues and odours can be cryptic to human perception (Voigt 2014), and this may partially explain why investigators have largely ignored sexually selected odorous traits in bats. Overall, olfaction has long been under appreciated in the study of bat behaviour (Bloss 1999, Dechmann & Safi 2005, Voigt 2014).

Darwin also failed to recognise sexual dimorphism in bats at first glance: "Hardly a single species amongst the Chiroptera (…) presents well-developed secondary sexual differences" (Darwin 1871). However, a few years later,

Dobson (1873) recognised secondary sexual traits in several species of bats, publishing the first contribution on this topic: *On Secondary Sexual Characters in the Chiroptera*. Dobson's publications (1873, 1878) included written and visual descriptions of bats' odorous, sexually dimorphic traits, illustrating and recognising their existence and importance (Fig. 1). Dobson's contribution was crucial, sparking a re-evaluation of the apparent lack of sexual dimorphism in bats. A year after Dobson's 1873 publication, Darwin (1874) wrote: "The males, and rarely the females, of many kinds of bats have glands and protrudable sacks situated in various parts; and it is believed that these are odoriferous". Darwin (1874) suggested that the exaggerated displays of males, including "glands for emitting odours", evolved through sexual selection, and posited that defence and reproduction were the two most important functions of scent glands and odours in bats. With respect to reproduction, and especially integumentary glands, Darwin (1874; p. 542) wrote: "The development of these organs is intelligible through sexual selection, if the most odoriferous males are the most successful in winning the females, and in leaving offspring to inherit their gradually perfected glands and odours".

Although the recognition of these sexually dimorphic odorous traits occurred nearly a century and a half ago, our understanding of these traits has not increased proportional to the time passed. With the exception of a few cases, the structure, development, and function of most odorous traits in bats remain unknown.
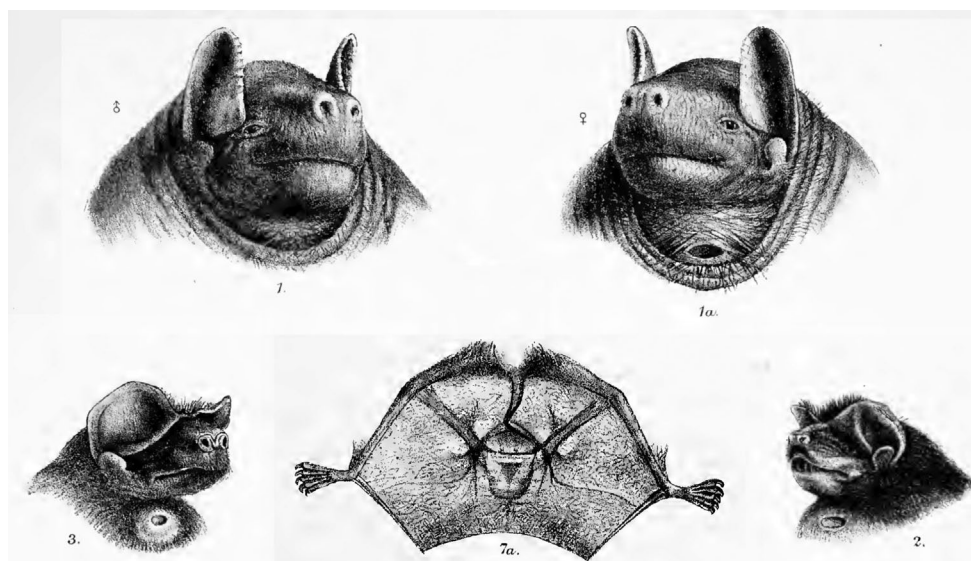

Fig. 1. Drawings of sexually dimorphic gular glands in *Cheiromeles torquatus* (1 female without gland, 1a male with gland; note that the sex symbols were accidentally reversed in the original publication), two species of *Molossus* (2 and 3), and uropatagial gland of a male *Diclidurus albus* (7a) from 1878, all included in the *Catalogue of the Chiroptera in the Collection of the British Museum* by George Edward Dobson. Modified from Dobson (1878).

The most remarkable case of extreme sexual dimorphism in bats belongs to the hammer-headed fruit bat *Hypsignathus monstrosus* (Fig. 2a) from Africa (Rosevear 1965, Bradbury 1977b, Langevin & Barclay 1990). Males possess an enlarged rostrum, larynx, and lips that they use to produce loud honking calls, which are extremely resonant and attractive to females (Bradbury 1977b). Although sounds and wing displays are crucial for female attraction and mate selection in this polygynous species (Bradbury 1977b), new evidence suggests that odour could be an underestimated trait also involved in mate selection. Researchers studying *Hypsignathus monstrosus* (Olson et al. 2019) describe a musty smell from adult, heavy males (Sarah H. Olson, personal communication) also perceived as musky and sharp (Stephanie N. Seifert, personal communication). Even when using N95 filtering respirators, researchers can detect a strong musty smell in large males that is absent in females. S. N. Seifert described how sometimes (presumably during the reproductive season) while processing *Hypsignathus monstrosus* on a sampling table, researchers would unequivocally identify by odour a bat waiting in holding line (still in a capture bag) as a large male from over 9 m away; females or younger bats have a smell that it is not nearly as conspicuous.

Apart from the hammer-headed bat, only one other bat species, the Neotropical greater sac-winged bat *Saccopteryx bilineata* (Fig. 2b), has been extensively investigated in the context of sexual dimorphism and will be discussed below in the section on Emballonuridae. Male *Saccopteryx bilineata* perform wing displays towards females involving enlarged odoriferous wing sacs (Fig. 2b) filled with different fluids that become active signals after bacterial decomposition (Voigt et al. 2005).

To date, there has been no systematic assessment of the occurrence or expression of the extent of sexually dimorphic traits in bat species, some of which show intriguing types of sexual dimorphism in soft tissue. By soft tissue, we refer to small sections of the body that are not hardened by ossification processes: glands, skin folds, substance-covered skin or fur, or specialised hair, most of which involve intense odours. Females direct their attention to male odours, which convey information on sex, age, sexual receptiveness, social status, group membership, and identity (Blaustein 1981, Johansson & Jones 2007). The secretion of glands is sometimes perceived by humans as having a penetrating smell and is considered to be responsible for the specific odour of many bat species (Schmidt 1985). Male chemical signals might also advertise health status or genetic quality to prospective mates (Penn & Potts 1998, Johansson & Jones 2007).

The universality of soft-tissue, odorous sexually dimorphic traits within Chiroptera is unknown, as are most chiropteran mating systems (Bradbury 1977a, McCracken & Wilkinson 2000). However, since many bats exhibit some form of polygynous association (Bradbury 1977a, McCracken & Wilkinson 2000, Adams et al. 2020), it would be reasonable to expect remarkable sexual dimorphism in soft-tissue, odorous traits. The first step in fully understanding the expression of these sexually dimorphic characteristics in bats is to identify these traits and then to investigate trait variation in males in focused, oriented studies. Thus, the main goal of our study is to compile, examine, and identify sexually dimorphic odorous traits in bats through an extensive review of the available literature. We have restricted our survey to species for which published information is available, and therefore, our review is likely to be incomplete with respect to bat species, as more than 1400 species have been described to date (Simmons & Cirranello 2020). We provide guidelines for future efforts and priorities for investigating and understanding patterns of sexual dimorphism in bats.
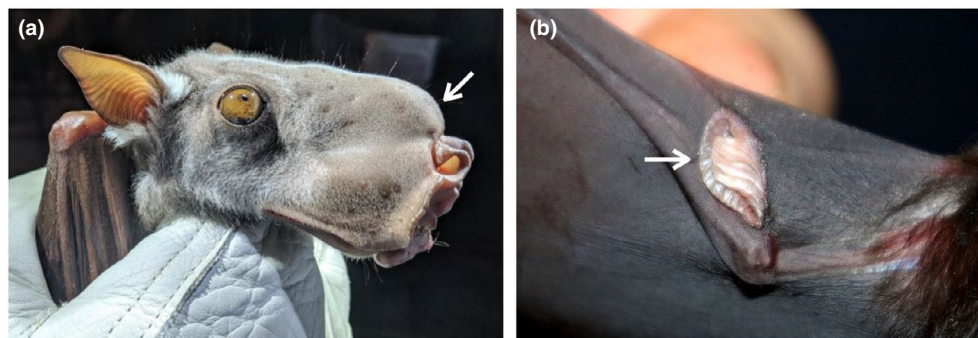

Fig. 2. Two well-known sexually dimorphic bat species: (a) adult male hammer-headed fruit bat *Hypsignathus monstrosus*, showing an enormous head and enlarged rostrum for producing loud honking calls (photo: Sarah H. Olson, Wildlife Conservation Society); (b) detail of the wing of an adult male greater sac-winged bat *Saccopteryx bilineata* (photo: Karin Schneeberger).

METHODS

Several sources of information were used to search for articles that included information on sexually dimorphic odorous traits in bats: 1) all three authors' private libraries with books and journals on bats obtained over several decades, 2) multiple specific targeted searches on Google Scholar and Web of Science, 3) the list of references from each article, and 4) photographs taken by numerous researchers, all over the world. Terms used for online searches included bat, Chiroptera, gland, sexual dimorphism, attraction, mating, odours, and the name of each family of bats.

SEXUALLY DIMORPHIC ODOROUS TRAITS IN BATS

More than 94 references with specific information about sexually dimorphic traits in bats were found and included in this review. We present information by family, following the standard phylogenetic order for Yangochiroptera and Yinpterochiroptera (Simmons & Cirranello 2020). The available information is extremely scattered and unevenly detailed in the literature: for the vast majority of the over 1400 bat species worldwide, there is no detailed characterisation of traits; for a few species, traits are clearly described.

Depending on the species, integumentary glands and non-glandular odour-producing structures are present in different regions of the body (head, mouth, throat, shoulders, axillae, forearms, back, wings, and urogenital regions) and are highly variable in morphology (Appendix S1, Fig. 3).

Skin glands and non-glandular odour-producing structures are common sexually dimorphic characteristics in bats, although most remain poorly studied, and many have been unnoticed until recently. To our knowledge, ours is the first thorough compilation of scent glands in bats. We found information on the existence of sexually dimorphic traits in a small number of species (121 of the 1421 bat species described to date; 9%) in 15 families of bats: Emballonuridae, Cistugidae, Molossidae, Miniopteridae, Natalidae, Vespertilionidae, Mystacinidae, Noctilionidae, Phyllostomidae, Pteropodidae, Craseonycteridae, Megadermatidae, Rhinonycteridae, Hipposideridae, and Rhinolophidae (Fig. 3). Much variation among species was observed in the sexual dimorphisms described, without clear phylogenetic patterns driving these patterns of sexually dimorphic trait diversity (Fig. 3). We found no records in the literature on sexually dimorphic structures for the remaining six families of bats.

Most odorous sexually dimorphic traits are found in the anterior region of the body, followed by the posterior and middle body regions. In the anterior region, these
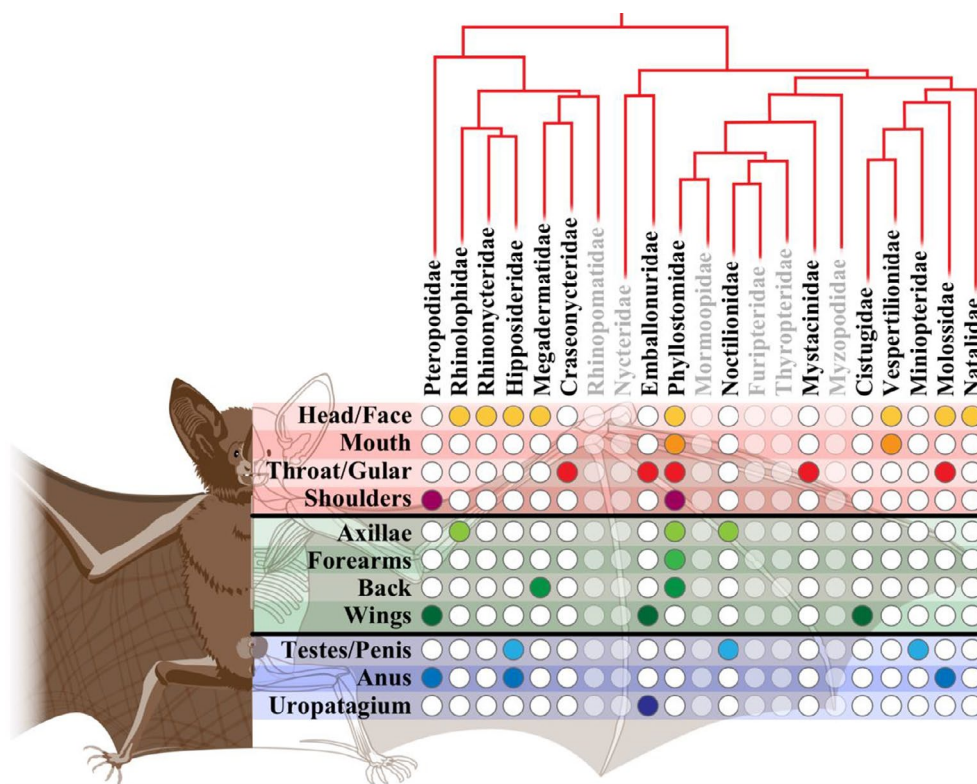

Fig. 3. Phylogeny depicting the 21 families of extant bats. The 15 families in bold text have been reported in the literature to have species with an odour-producing gland or structure, the location of which is indicated by coloured dots. Illustration by Damond Kyllo.

traits are most frequently found on the head and on the ventral region of the neck (Fig. 3). The family Phyllostomidae shows the highest diversity of sexually dimorphic odorous traits, as expected based on its high species diversity (Simmons & Cirranello 2020).

Emballonuridae

In the family Emballonuridae (55 species; Simmons & Cirranello 2020), one of the best-documented cases of sexual dimorphism is found in the Neotropical greater sac-winged bat *Saccopteryx bilineata*. This species uses a rich and complex repertoire of vocalisations in its social and sexual interactions (Behr & von Helversen 2004, Knörnschild 2014, Voigt 2014). In addition, males attract females by performing wing displays involving enlarged odoriferous wing sacs (Fig. 2b). These sacs were long assumed to have glandular properties (Dobson 1878, Goodwin & Greenhall 1961), but Voigt and von Helversen (1999) demonstrated that the sacs were actually wing folds used for storage and display of a mixture of compounds from different fluids (saliva, urine, gular gland secretion from sexually dimorphic glands; Caspers et al. 2009) and for bacterial fermentation (Voigt et al. 2005), ruling out a glandular function. Several other Neotropical emballonurid bats show similar wing sacs (Jones & Hood 1993).

An unusual gland has been observed in the uropatagium of several species of Neotropical ghost bats, genus *Diclidurus* (Fig. 4). The 'uropatagial sac' (Voigt & von Helversen 1999) was first described by Dobson in 1878 (7a in Fig. 2), but this structure remains unknown and intriguing.

According to Jones and Hood (1993), there is a large and distinct glandular area on the uropatagium, especially prominent in males during the breeding season. It remains unknown whether this gland is used by males in a similar way to wing sacs.

Two different gular structures have been observed in the ventral surface of the throat of species of *Taphozous*: pouches and glands (Dobson 1878). Gular glands cannot be easily observed because the fur covers them, although the glands can be detected when the resulting secretion 'stains' the hairs surrounding the gland, as in the black-bearded tomb bat *Taphozous melanopogon* (Fig. 5a) and in Hildegarde's tomb bat *Taphozous hildegardeae* (Fig. 5b). Gular pouches or sacs, also located on the ventral surface of the throat, are easily observed as folds of skin (Fig. 5c). Male naked-rumped tomb bats *Taphozous nudiventris* have large gular pouches and also exhibit deep circular glands in the upper part of the chest, whereas in females, the gular sac is less visible, and the gland is absent. The chin and throat are essentially naked (hairless) in both sexes (Desai et al. 2012). Gular sacs are also reported for the long-winged tomb bat *Taphozous longimanus*, from India and surrounding areas, and in the naked-rumped pouched bat *Saccolaimus saccolaimus* (Nanayakkara et al. 2012) from Asia.

A detailed examination of the pouch of male yellow-bellied pouched bats *Saccolaimus flaviventris* (previously *Taphozous flaviventris*) revealed that it has no connections to any gland (Hall & Gordon 1982). Although the pouch itself has been confirmed as non-glandular in this species, posterior to the pouch there is a large sebaceous gland that opens on the throat surface; both the pouch and the

Fig. 4. Uropatagial gland of an adult male northern ghost bat *Diclidurus albus* (photo: Manuel Sánchez-Mendoza).

Fig. 5. Gular glands in adult males of (a) the black-bearded tomb bat *Taphozous melanopogon* (photo: Ram Mohan) and (b) Hildegarde's tomb bat *Taphozous hildegardeae* (photo: Paul Webala); (c) gular pouches in naked-rumped tomb bats *Taphozous nudiventris* (photo: Ram Mohan).

gland are absent in females. According to Hall and Gordon (1982), the proximity of the sebaceous gland to the pouch indicates that the secretions from this gland could enter the pouch and spread over its inner folded surface. There is a lack of uniformity in the distribution of pouches in species of the genus *Taphozous* (Hall & Gordon 1982).

Cistugidae

The only two species of the family Cistugidae, formerly considered vespertilionid bats, are called wing-gland bats. According to Voigt and von Helversen (1999), male Angolan wing-gland bats *Cistugo seabrae* and male Lesueur's wing-gland bats *Cistugo lesueuri*, from Africa, have 'glands' on their wings that resemble those in the greater sac-winged bat *Saccopteryx bilineata*.

Molossidae

In the family Molossidae (130 species; Simmons & Cirranello 2020), adult males show the most conspicuous skin glands in the Chiroptera: the chest (gular) glands (Fig. 6a–c), first described by Dobson (1873, 1878; Fig. 1). Histological

description was provided in *Tadarida* and *Molossus* (Werner et al. 1950, Werner & Lay 1963), without information about potential function. The gular gland is a specialised sebaceous gland located in the skin of the suprasternal region of adult males (Werner et al. 1950, Werner & Lay 1963, Horst 1966, Quay 1970, Gutiérrez & Aoki 1973, Wilkins 1989, Krutzsch 2000, Fenton et al. 2002, Hunt et al. 2003). This gland in Brazilian free-tailed bats *Tadarida brasiliensis* consists of an aggregation of simple branched tubulo-acinar glandular units, and each acinus is composed of densely packed sebaceous cells, more abundant during the mating season (Gutiérrez & Aoki 1973).

Breeding males of the family Molossidae have been observed smearing the exudate from the gular gland directly on the backs of females (Häussler 1989, Heideman et al. 1990, Rasweiler 1992), and females have been observed being attracted to the gular gland of the male. Despite these observations, the potential for other functions (e.g. mate selection) may be underestimated. Some, but not all, males of the large-eared giant mastiff bat *Otomops martiensseni* have well-developed chest (gular) glands (Fenton et al. 2002). Whether or not the gland is opened or closed could be an important indicator for assessing gland
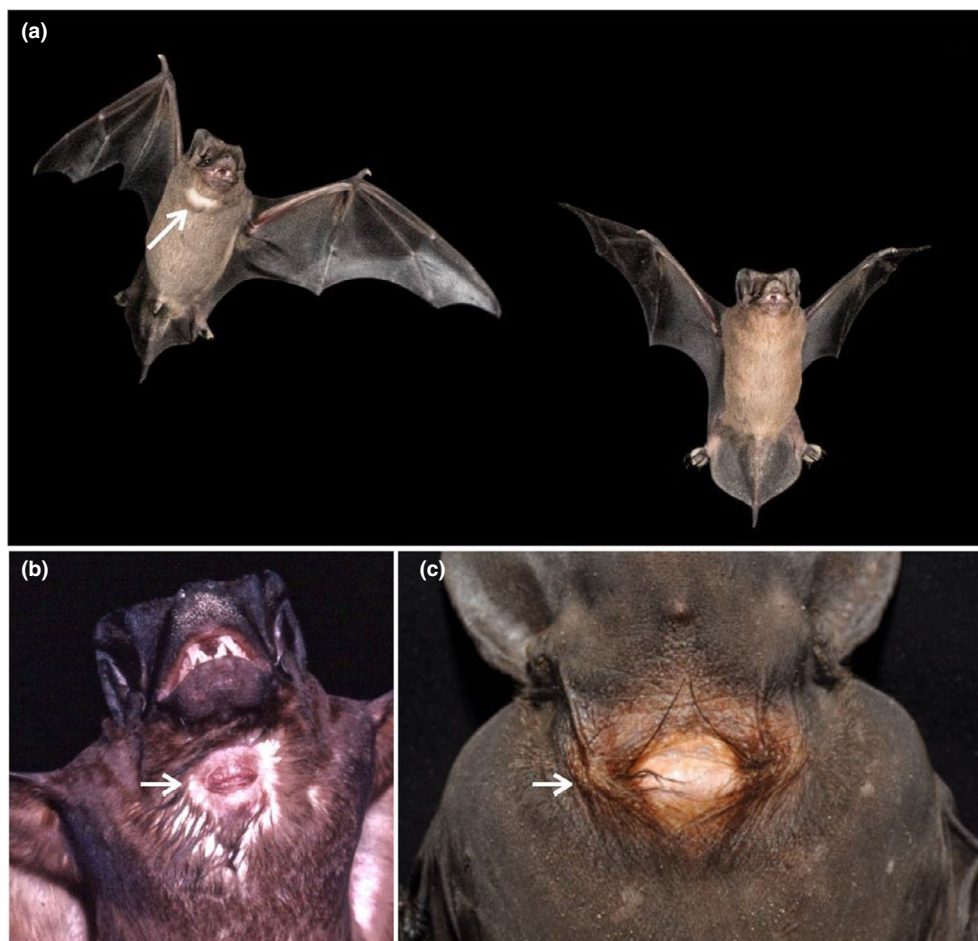
Fig. 6. (a) Adult male (left) and female (right) of the Palla's mastiff bat *Molossus molossus*, showing remarkable differences in gular regions (photo: Sherri and Brock Fenton); gular gland of an adult male of: (b) *Molossus molossus* (photo: Thomas H. Kunz) and (c) the greater naked bat *Cheiromeles torquatus* (photo: Tzi Ming Leong).

development (Ober et al. 2016). Most groups of the Florida bonneted bat *Eumops floridanus* only had one adult male with an open gular gland, and body mass and testes length of males with open gular glands were significantly greater than those of males with closed gular glands, despite similar forearm lengths (Ober et al. 2016).

Adult male greater naked bats *Cheiromeles torquatus*, from Southeast Asia, display a conspicuous gular gland (Fig. 6c). According to Leong et al. (2009), this gland exudates viscous, oily secretions from the gular sac that males may use in sexual behaviour. The odour from this secretion is described as a 'repulsive stench', and after handling the bats, the oily exudate inevitably impregnates fingers and nails, where the smell lingers for days, despite numerous washings (Leong et al. 2009).

Glandular areas in bats and other specialised odour-producing organs are frequently observed in conjunction with specialised hairs growing within or around them (Quay 1970, Hickey & Fenton 1987). These structures, called osmetrichia, are sexually dimorphic specialised hairs for the retention and dispersion of odours, easily recognised by their greater length and distinctive colour (Hickey & Fenton 1987, Scully et al. 2000). The most remarkable example of osmetrichia associated with interaural glands is found in pale free-tailed bats *Tadarida* (*Chaerephon*) *chapini* (Fig. 7a), in which males, unlike females, show conspicuous hair crests (12-15 mm; Fenton & Eger 2002) that are erectile under sexual stimulus (Rosevear 1965). Interaural crests of male little free-tailed bats *Tadarida* (*Chaerephon*) *pumilus* are prominently displayed, and production of scent – involving the erection of the pungent interaural crest, presumably to dispense the pheromones – is likely to play an important role in individual mating success (McWilliam 1988). Bouchard (2001) observed that males had more glandular tissue in the interaural area (containing osmetrichia) than females, and also tested the use of chemical signals, possibly pheromones, in Angolan free-tailed bats *Mops*
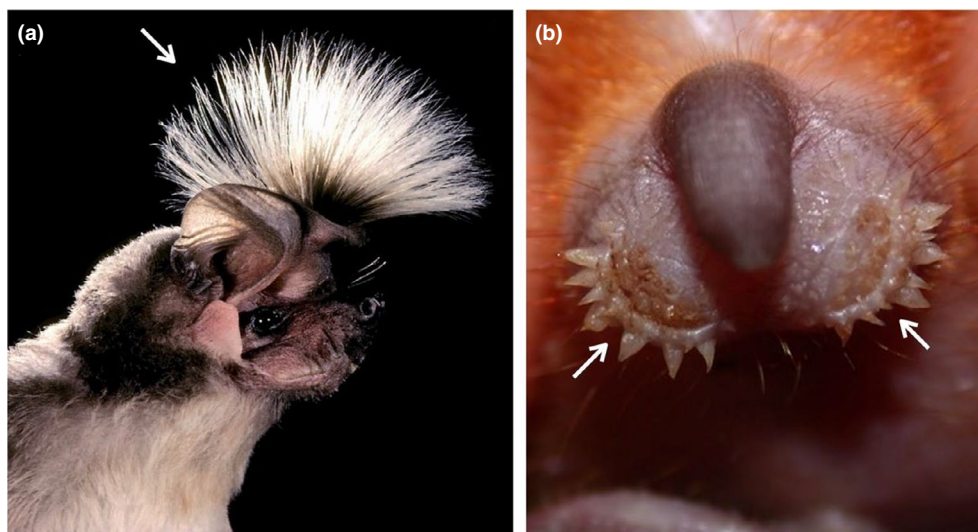
Fig. 7. (a) Adult male pale free-tailed bat *Tadarida* (*Chaerephon*) *chapini* displaying an interaural crest (photo: Merlin Tuttle); (b) parascrotal folds in an adult male lesser bulldog bat *Noctilio albiventris* (photo: Dina Dechmann).

condylurus and *Tadarida* (*Chaerephon*) *pumilus* that could be used to discriminate between sexes based on odours collected from the interaural and muzzle glandular areas. Finally, southern free-tailed bats *Mormopterus planiceps* differ from most molossids in that it has para-anal glands with unclear function (Krutzsch & Crichton 1987).

Miniopteridae

In the family Miniopteridae (34 species; Simmons & Cirranello 2020), male least long-fingered bats *Miniopterus minor*, from Africa, are reported to form an 'olfactory lek' through the production of an 'odour plume' that resembles the odour of strongly odouriferous urine (McWilliam 1990). However, no specific gland has been described for males. Toth and Parsons (2013) criticised the premature conclusion about forming leks without strong evidence to support it (i.e. no copulations were ever observed at the display site). It remains unclear whether this intense odour is wholly or partially the result of glandular activity, or comes from other source.

Natalidae

The natalid organ is a male trait present only in adults in species of the Neotropical family Natalidae (11 species; Simmons & Cirranello 2020). This organ is composed of a mass of tubules separated by layers of connective tissue thought to have glandular properties, but externally inconspicuous and of unknown function (Dalquest 1950, Goodwin & Greenhall 1961). All adult males of the genus *Natalus* possess this unique organ on the head composed of cells closely resembling sensory cells. Evidence of

glandular function was observed by Dalquest (1950) and later confirmed by Goodwin and Greenhall (1961). In Mexican greater funnel-eared bats *Natalus mexicanus*, the natalid organ is a bell-shaped, flattened mass that covers the frontal region of the skull.

Vespertilionidae

In the family Vespertilionidae (504 species; Simmons & Cirranello 2020), facial glandular structures have been extensively studied to clarify taxonomic relationships (Harrison & Davies 1949, Werner & Dalquest 1952, Walton & Siegel 1966). Most facial glands of vespertilionids are located in the pararhinal region, and a light pressure on the mystacial skin leads to sebum expulsion (Haffner 2000). Although several vespertilionids have facial glands that secrete sebum that may be used in grooming, the glands also have the potential for being involved in chemical communication (Haffner 2000). Considering the size, abundance, and position of the sebaceous and apocrine glands of bats, some regions of the face could function as scent organs (Haffner 2000).

Adult male common noctules *Nyctalus noctula*, distributed throughout Europe, Asia, and North Africa, have well-developed oral glands in both sides of the cheeks (Appendix S2a), as have many other vespertilionid bat species, such as male black-winged little yellow bats *Rhogeessa tumida* from Central America (Appendix S2b).

Aufdermaur et al. (1995) microscopically examined glands of male and female common pipistrelle bats *Pipistrellus pipistrellus*. Ano-rectal glands are more voluminous in males than in females, reach their maximum

size during the mating season, and presumably play an important role during this period (Aufdermaur et al. 1995).

Mystacinidae

In the family Mystacinidae (two species; Simmons & Cirranello 2020), males of the endemic New Zealand lesser short-tailed bat *Mystacina tuberculata* secrete a brown oily substance from a gland located in the throat region. The secretion has a distinctive musky smell which serves to attract females (Lloyd 2001). The bark around the bat's roost entrance is polished with a brown oily secretion from the males' throat glands (Lloyd 2001).

Noctilionidae

In the family Noctilionidae (two species; Simmons & Cirranello 2020), males of both species of the Neotropical bulldog bats genus *Noctilio* (*Noctilio albiventris* and *Noctilio leporinus*) show inguinal or parascrotal folds of skin, sometimes described as pouches (Fig. 7b), that become visible only when the testes are descended into the scrotum or in the inguinal region, and are most prominent during the breeding season (Dunn 1934, Studier & Lavoie 1984, Brooke & Decker 1996). These pouches produce a strong, musky odour that is probably involved in secondary sexual functions. Dunn (1934) described these structures in male lesser bulldog bats *Noctilio albiventris* in some detail, emphasising their uniqueness, but Studier and Lavoie (1984) determined that these structures are not glandular and that the odour was the product of bacterial metabolism. No direct sexual function has yet been ascribed to these pouches that are markedly more developed in males than females in both species (Dunn 1934, Studier & Lavoie 1984).

Phyllostomidae

Phyllostomidae, the most diverse family of Neotropical bats with at least 218 species in 65 genera (Simmons & Cirranello 2020), shows the highest diversity of sexually dimorphic odorous traits among bats (Fig. 3). Species within the Phyllostomidae show sexually dimorphic traits in the head, mouth, chest, shoulders, axillae, forearms, and back (Fig. 3), reflecting not only diversity, but also some of the most unusual sexually dimorphic features in Chiroptera.

In four genera of bats in the subtribe Stenodermatina (Stenodermatinae), unusual structures are found on adult male bats. Adult male visored bats *Sphaeronycteris toxophyllum* develop a visor-like structure on the forehead (Fig. 8a) that is conspicuously larger than any facial protuberances exhibited by females (Angulo et al. 2008).

Unusual sexual dimorphism is also found in the wrinkle-faced bat *Centurio senex*. Males have tube-like structures on

their faces that resemble wrinkles (Fig. 8b) and are more conspicuously developed than those in females (Snow et al. 1980). Observations indicate that males of this species also have loose skin on their chins that can cover the face. This loose skin has received little attention, but it could be associated with a gland or may have glandular properties itself, as this loose skin has been reported as having a distinct, musky, skunk-like odour (Goodwin & Greenhall 1961), and it was observed to be so swollen that some thought that the individual could be a different species (Rehn 1901). Odorous properties associated with swollen tissue (Goodwin & Greenhall 1961) are likely present in the other species within this subtribe. The original observation of these sexually dimorphic loose skin bands was by Dobson (1878), who described them in great detail, pointing out the odorous sections. This trait remained unstudied for decades (Goodwin & Greenhall 1961), but recent work suggests a role in courtship (Rodríguez-Herrera et al. 2020). Males congregate to engage in what appears to be lekking behaviour, producing distinctive vocalizations and wing beat displays that culminate in the male covering its face completely with its skin folds (Rodríguez-Herrera et al. 2020). The role of the male's distinctive odour remains unknown, but observations of males rubbing their bodies on their perch suggest scent-marking (Rodríguez-Herrera et al. 2020).

Adult males of the little white-shouldered bat *Ametrida centurio* have protruding chest glands, swollen pads below each eye (Dobson 1878, Peterson 1965, Vilar et al. 2015), and armpit glands (Fig. 8c), recently discovered by Vilar et al. (2015), all absent in females. The function of these characteristics remains intriguing. Swollen periorbital, submandibular, and forelimb tissues have also been observed in the Ipanema broad-nosed bat *Pygoderma bilabiatum* (Fig. 8d; Myers 1981, Tavares & Tejedor 2009). These forelimb swellings, varying in development and form, could be correlated with sex as they are not found on females and appear to be synchronised with periorbital and submandibular swellings (Tavares & Tejedor 2009).

The dorsal patch of male Curaçaoan long-nosed bats *Leptonycteris curasoae* (Fig. 9a) is a striking example of an odour-producing structure developed during the mating season after stereotypical behaviour of smearing different body fluids onto the interscapular region (Muñoz-Romo & Kunz 2009, Muñoz-Romo et al. 2011a, b). The characteristic smearing behaviour of males (Muñoz-Romo et al. 2011b) seems to be related to the development of the so-called sebaceous patch (*sensu* Nassar et al. 2008). Muñoz-Romo and Kunz (2009) suggest that dorsal patches are unlikely to be the result of sebum secretion (*sensu* Nassar et al. 2008), but rather the outcome of a mixture of body fluids being transferred to the interscapular region by adult males during the short mating season (Muñoz-Romo et al. 2011b). Moreover, as in the case of the greater

Fig. 8. Adult males of four species of Phyllostomidae. (a) The visored bat *Sphaeronycteris toxophyllum*, displaying a visor-like structure in the forehead; observations indicate that the loose skin on the males' chins can cover their faces (photo: Marco Tschapka). (b) The wrinkle-faced bat *Centurio senex*, with marked wrinkles covering the face; skin folds under the chin are partially visible, starting at the base of the ear (photo: José Gabriel Martínez Fonseca). (c) The little white-shouldered bat *Ametrida centurio* displaying chest and armpit glands (photo: Emmanuel Messias Vilar). (d) The Ipanema broad-nosed bat *Pygoderma bilabiatum*, displaying periorbital swellings (photo: Roberto L. M. Novaes).

sac-winged bat, bacterial fermentation is likely to affect the resulting odours (Gaona et al. 2019).

Forearm crusts of adult male fringe-lipped bats *Trachops cirrhosus* are odorous sexually dimorphic traits that extend over the surface of the forearm (Fig 9b; Flores & Page 2017, Flores et al. 2019, Muñoz-Romo et al. 2020). These crusts are located on the dorsal region of the middle section of the forearms and have an intense odour, based on human perception. Observations of this recently discovered trait suggest that the crust may be involved in a kind of wing display, although no evidence of this has been observed so far. Muñoz-Romo et al. (2020) found a positive relationship between forearm crust size and testosterone during the mating season. Males with higher

concentrations of testosterone exhibit larger forearm crusts, supporting the supposed relationship between crust display and mating season (Muñoz-Romo et al. 2020).

Trachops cirrhosus is also sexually dimorphic in the development of the chest gland which has been observed enlarged and active (producing a white secretion) in males during the mating season (Fig 10a), although activity of the gland is not clearly related to the crust (Flores & Page 2017). Although the function of this gland is still unknown, other bat species also develop a similar gland in their throats.

Male pale spear-nosed bats *Phyllostomus discolor*, for example, also have conspicuous chest glands that produce a white, thick secretion with an intense odour that is characteristic of the species. A single opening
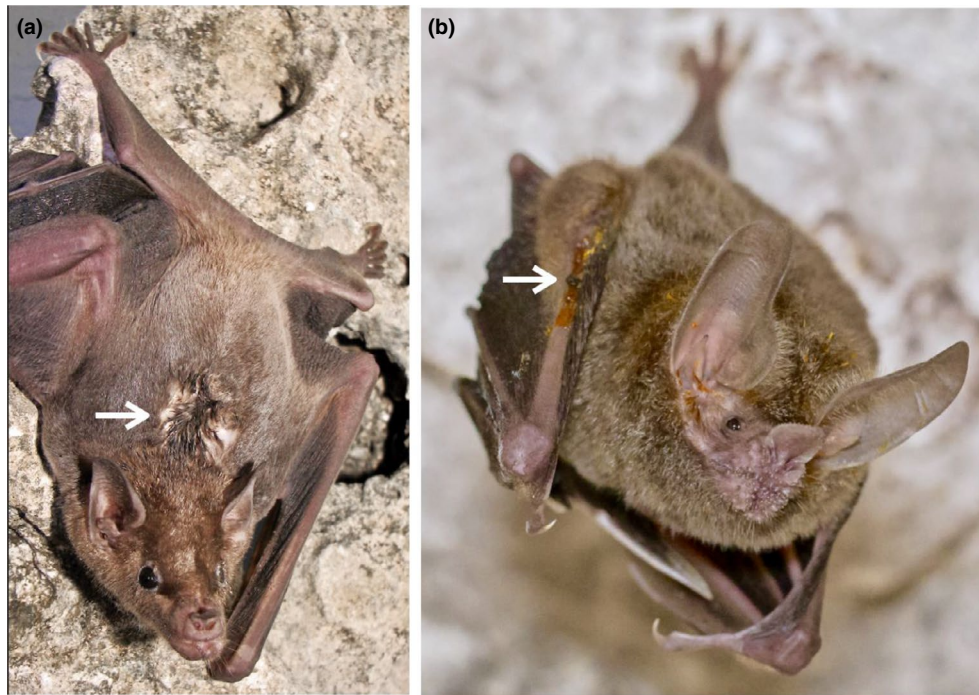
Fig. 9. Two of the most recent discoveries of male bats with odorous structures created by smearing bodily fluids. Adult males of: (a) the Curaçaoan long-nosed bat *Leptonycteris curasoae*, displaying a well-developed dorsal patch (photo: Mariana Muñoz-Romo); and (b) the fringe-lipped bat *Trachops cirrhosus*, displaying a crust on the forearm (photo: Paul B. Jones).

is present in the mid-ventral line of the chest of both males and females, but glandular tissue is present only in males, and the odour may have a function in sexual recognition (Valdivieso & Tamsitt 1964). Female *Phyllostomus discolor* sniff the gular gland of males, which open their glands while flapping in front of females (Müller-Schwarze 1983). Males are able to distinguish between their own odour and that of another male (Höller & Schmidt 1993).

A recent study demonstrated the function of the chest gland in male greater spear-nosed bats *Phyllostomus hastatus* (Adams et al. 2018). Males possess a sexually dimorphic gland on the chest that produces an odouriferous white secretion, which seems to play an important role in social interactions. Males that roost with and defend groups of females (harem holders) have significantly different chemical profiles from males roosting in all-male groups (bachelors). Chemical profiles also differ significantly among individuals. These results suggest that chest secretions may serve as chemical signals conveying information about both mating status and individual identity (Adams et al. 2018). A similar function is expected in other species of phyllostomid bats displaying throat glands (e.g. the pale-faced bat *Phylloderma stenops*; Fig. 10b). Reproductive males of *Phylloderma stenops* show well-developed gular glands with odour similar to musk (Turcios-Casco et al. 2020).

Male buffy flower bats *Erophylla sezekorni* presumably include olfactory displays as part of their mate attraction strategy (Murray & Fleming 2008). Mature males exhibit a garlic-scented, supraorbital secretion (Appendix S3a), visible as a fluid secretion that wets the fur above the eye (Appendix S3b). When the secretion dries, it leaves a yellow, powdery residue. Murray and Fleming (2008) were able to recognise males of this species easily by the strong smell of the secretion itself. The secretion was clearly sexually dimorphic, as the authors never observed supraorbital secretions on immature males or females. They did find this secretion on males throughout the year (Murray & Fleming 2008). As in *Trachops cirrhosus*, the authors did not know whether the *Erophylla sezekorni* secretion was produced where it was found (above the eyes) or whether it had been sequestered there from glandular secretions (or other bodily products) from elsewhere on the body.

The white-winged vampire bat *Diaemus youngi* has glands in the oral cavity (Fig. 11a) that expel an odoriferous substance when the bat is disturbed (Goodwin & Greenhall 1961). Three males had well-developed glands that discharged a sprayed substance with pungent odour, while a female appeared not to have such glands, although it could not be examined in detail (H. A. Delpietro, personal communication). The chemical profile and potential
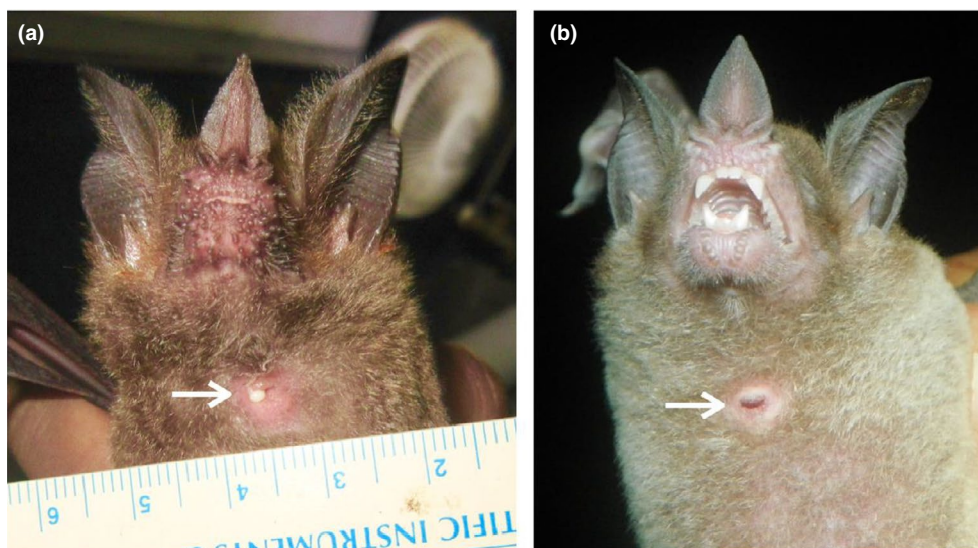
Fig. 10. Adult males of: (a) the fringe-lipped bat *Trachops cirrhosus*, displaying a well-developed chest gland (photo: Mariana Muñoz-Romo), and (b) the pale-faced bat *Phylloderma stenops*, also with a well-developed chest gland (photo: Manfredo Turcios-Casco).

function of these glands or their chemical secretions have not been investigated.

Males of some species of yellow-shouldered bats, genus *Sturnira*, have conspicuous, intense yellow, shoulder patches or epaulettes (Fig. 11b) with underlying shoulder glands (Gannon et al. 1989, Giannini & Barquez 2003). The little yellow-shouldered bat *Sturnira lilium* has been recognised as a sexually dimorphic species based on the darker and larger shoulder glands found in adult males (Gannon et al. 1989). González-Quiñonez et al. (2014) found diverse bacteria in these male odorous yellow patches, many in common with bacteria found associated with other sexually selected bat male traits (e.g. inguinal pockets of *Noctilio*

leporinus, wing sacs of *Saccopteryx bilineata*, and dorsal patches of *Leptonycteris curasoae*).

Pteropodidae

In the family Pteropodidae (201 species; Simmons & Cirranello 2020), adult males of some species of epauletted fruit bats *Epomophorus*, from Africa, display structures frequently called skin pockets, usually associated with white hairs on their shoulders (Fig. 12a,b). Epaulettes are also present in species of *Epomops*, *Micropteropus*, and *Nanonycteris* which are usually concealed within a pouch or turned outwards and visibly displayed at will (Rosevear 1965). The
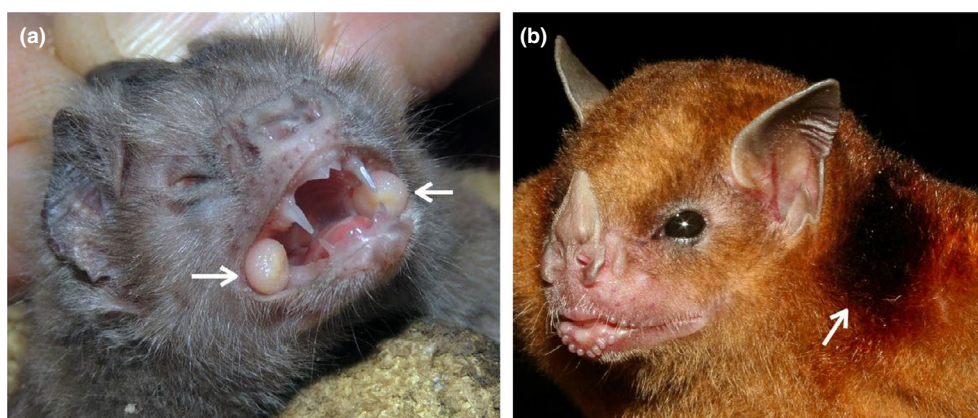

Fig. 11. Adult males of: (a) white-winged vampire bat *Diaemus youngi*, displaying paired oral glands (photo: H. A. Delpietro and the American Society of Mammalogists' Mammal Images Library), and (b) the little yellow-shouldered bat *Sturnira lilium*, with well-developed epaulettes (photo: Roberto L. M. Novaes).

hairs resemble those associated with integumentary glands, but no secretory structures have been found in skin pockets (Schmidt 1985). White hairs in everted epaulettes resemble a blossom in a tree to attract, but it is unknown whether these tufts are scented or attractive (Wickler & Seibt 1976). According to Wickler and Seibt (1976), the erected tuft has a vibratory movement, likely to be related to general wing quivering. The skin pouch is considered a reversible glandular pocket because the edges of shoulder pouches were moist, but fewer glands are present within the pouches than in normal skin, suggesting that the pouches are complex structures involving a combination of both chemical and optical signals (Wickler & Seibt 1976).

A crescent-shaped welt occupying the lower neck and upper chest forms the sexually dimorphic gland of males of the dagger-toothed long-nosed fruit bat *Macroglossus lagochilus* (Hood & Smith 1984), a pteropodid from Indonesia. The welt is comprised of hypertrophied tubular apocrine-type glands.

In the spectacled flying fox *Pteropus conspicillatus*, a pteropodid from Australia, males have been observed to anoint their neck ruffs with a cranberry-red secretion produced from the urogenital tract that contains a high concentration of long-chain fatty acids (Spencer & Flick 1995).

Adult males of the Sierra Leone collared fruit bat *Myonycteris leptodon*, from Africa, display conspicuous yellow collars (Fig. 12c), but their glandular nature (Rosevear 1965) still needs to be confirmed. Adult males of Angolan soft-furred fruit bats *Lissonycteris angolensis* (Fig. 12d) and Woermann's long-tongued fruit bats *Megaloglossus woermanni* display similar collars of stout hairs (Rosevear 1965).

Finally, males of the greater short-nosed fruit bat *Cynopterus sphinx* develop sebaceous glands in the ventral side of the plagiopatagium (Baskaran et al. 2015) and frequently deposit saliva on this region before wing fanning towards females (Vanitharani et al. 2007).

Craseonycteridae

Among bats, hog-nosed bats *Craseonycteris thonglongyai*, from Thailand, of the family Craseonycteridae (one species; Simmons & Cirranello 2020), has a unique glandular structure: a rounded glandular swelling at the base of the throat, which is well-developed and prominent in males but much less so or absent in females (Hill 1974, Hill & Smith 1984). No additional details on this sexually dimorphic structure are available.
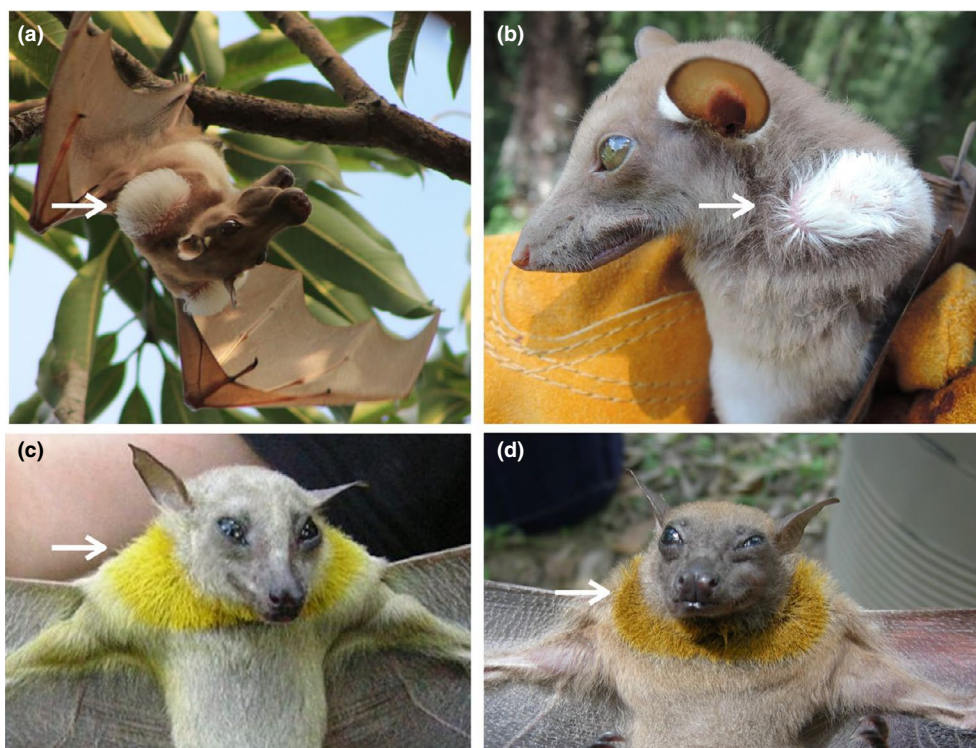

Fig. 12. Adult males of: (a) the Gambian epauletted fruit bat *Epomophorus gambianus* with well-developed epaulettes (photo: Kofi Amponsah-Mensah), (b) the little epauletted fruit bat *Epomophorus labiatus* (photo: Paul Webala), (c) the Sierra Leone collared fruit bat *Myonycteris leptodon,* and (d) the Angolan soft-furred fruit bat *Lissonycteris angolensis* (photos: Nicolas Nesi).

Megadermatidae

In the family Megadermatidae (six species; Simmons & Cirranello 2020), males of the African yellow-winged bat *Lavia frons* display glands on the lower back, which exude a yellowish secretion (Rosevear 1965). This secretion of unknown function appears to discolour the fur of that area and probably causes the typical odour of males (Rosevear 1965, Bergmans 1977, Vonhof & Kalcounis 1999). Observations on greater false vampire bats *Megaderma lyra* indicate hypertrophied sebaceous skin glands on tarsal, facial, cervical, oral, and preputial regions in both sexes, and, although no significant sexual dimorphism was observed (Begum & Alexander 1993), more detailed studies are needed on the seasonality and glandular exudates of these varied skin glands.

Rhinonycteridae

In the family Rhinonycteridae (ten species; Simmons & Cirranello 2020), the Persian trident bat *Triaenops persicus* has a complex frontal gland consisting of a superficial haired layer with sebaceous glands and saccular apocrine glands, and a deeper-lying enormously convoluted peculiar type of apocrine gland (Mainoya 1979). Noticeable sexual dimorphism expressed in both the development and activity of the frontal gland in males suggests a clear role in reproduction (Mainoya & Howell 1977).

Hipposideridae

In the family Hipposideridae (90 species; Simmons & Cirranello 2020), individuals of several species of *Hipposideros* have been observed displaying a median frontal sac, more developed in males than in females (Mainoya & Howell 1977). Commerson's leaf-nosed bat *Macronycteris commersoni* (formerly *Hipposideros commersoni*; Appendix S4) displays tri-lobed sebaceous glands associated with hair follicles and modestly enlarged simple saccular apocrine glands. Males of Noack's leaf-nosed bat *Hipposideros ruber* display a coiled-lobule type of apocrine gland; females only have a rudimentary gland without any sac.

Males of the striped leaf-nosed bat *Macronycteris vittatus* display a similar frontal gland that presumably can be everted, as can be achieved by using a small amount of pressure from the fingers (Bruce Patterson, personal communication; Fig. 13a–c). The tufted nasal glands of male *Macronycteris commersoni* were observed everted over the nasal region of females during courtship (McWilliam 1988). The forehead gland of adult males of the Philippine forest leaf-nosed bat *Hipposideros obscurus* has been observed secreting a dark substance from the frontal tube (Jodi Sedlock, personal communication; Fig. 13d–f).

Rhinolophidae

In the family Rhinolophidae (106 species; Simmons & Cirranello 2020), adult male horseshoe bats *Rhinolophus landeri*
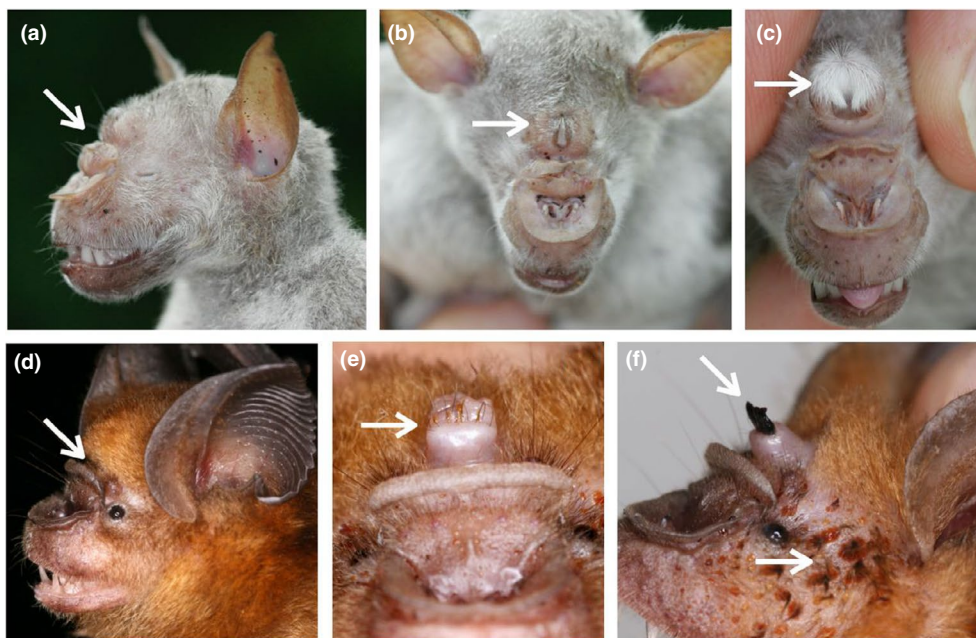

Fig. 13. (a) Frontal gland in an adult male of the striped leaf-nosed bat *Macronycteris vittatus,* from Africa, in natural state (b) and everted by researcher (c; photos: Bruce Patterson). (d) Frontal gland behind the noseleaf in an adult male of the Philippine forest leaf-nosed bat *Hipposideros obscurus*. Note the tube details (e) and the dark substance protruding from the tube and covering the cheeks (f; photos: Jodi Sedlock).

and *Rhinolophus alcyone*, from Africa, exhibit tufts of long hairs in the armpits, defined as axillary tuft glands of orange-red colour (Rosevear 1965, Hall 1989), that are presumably involved in seasonal sexual interactions (Fig. 14). These structures are associated with a gummy secretion. Males also exhibit an unusually pronounced development of the nipples at the base of the tufts. Colour variation has been observed in individuals from different locations, with reports of white tufts as well as orange-red ones (Rosevear 1965).

FUTURE RESEARCH DIRECTIONS

Timing

Timing is a critical component in studying bat sexual dimorphism. The importance of the timing of an investigation is illustrated by those species historically considered to be lacking sexual dimorphism (Willig & Hollander 1995, Lu et al. 2014). The study of sexual dimorphism of soft tissues and odours is time-dependent: the transient expression of some sexual traits is the reason that their existence has largely gone unnoticed until recent years: the dorsal patch (*Leptonycteris curasoae*) and the forearm crust (*Trachops cirrhosus*) are examples of sexually dimorphic traits that are not permanently or conspicuously present, but are presumably paramount for successful reproduction (Muñoz-Romo & Kunz 2009, Muñoz-Romo et al. 2011a, b, Flores & Page 2017, Muñoz-Romo et al. 2020). We are convinced that numerous similar cases in the order Chiroptera have yet to be noticed, because odorous structures are not easily visible or recognised in bats, especially when they only develop in adult males during short mating seasons (Krutzsch 2000).

Behavioural observations

Behavioural observations are a priority in the assessment of bat sexual dimorphism: observing an animal's actual behaviour is critical for understanding the function and nature of otherwise largely inconspicuous body parts. The wing sac (Voigt & von Helversen 1999), dorsal patch (Muñoz-Romo et al. 2011b), and forearm crust (Flores & Page 2017),

for example, can only be understood after witnessing males performing stereotyped, repeated behaviours.

The wing sacs found on male greater sac-winged bats *Saccopteryx bilineata* were considered glandular (Dobson 1878, Goodwin & Greenhall 1961), until detailed behavioural studies revealed that they are not glands (Voigt & von Helversen 1999). Rather, the sacs are skin folds functioning as pockets, in which males mix different bodily fluids that became active as useful signals after bacterial decomposition (Voigt et al. 2005).

Behavioural observations also helped clarify the nature of the sexually dimorphic dorsal patches of male *Leptonycteris curasoae*, originally described as 'sebaceous' (Nassar et al. 2008). In fact, males create these patches by smearing saliva, faeces, and presumably urine or semen, to create an odorous patch on their upper backs. This is called a dorsal patch (Muñoz-Romo & Kunz 2009, Muñoz-Romo et al. 2011a, b), a more appropriate term that does not imply a chemical-defined nature, and, more importantly, does not define the area as glandular. Histological preparations (Nassar et al. 2008) show an unclear distinction between the common interscapular fat tissue and the 'sebaceous' portion of the patch.

The third example is the forearm crust in the fringe-lipped bat *Trachops cirrhosus*: a sexually dimorphic yellowish secretion is applied to the forearms through a series of stereotypic behaviours (Flores & Page 2017). This ephemeral substance smeared on forearms is the sole basis for redefining *Trachops cirrhosus* as sexually dimorphic, opening the possibility of studying this species in the context of sexual selection. We are convinced that, through the intense study of behaviour, many more examples like these will be discovered in the order Chiroptera in the years to come.

Chemical analyses

Chemical analysis of substances produced by glands and by non-glandular odour-producing structures in bats should be performed, in order to understand variation in and function of these odorous traits. Chemical composition analyses of male odorous structures are scarce (Dapson et
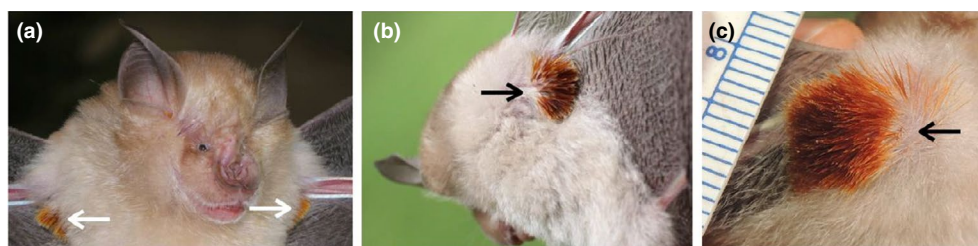

Fig. 14. (a and b) Axillary tuft glands in an adult male Lander's horseshoe bat *Rhinolophus landeri* (photos: Paul Webala), and (c) detail of a tuft (photo: Bruce Patterson).

al. 1977, Brooke & Decker 1996, Lily & Vanitharani 2005, Wood et al. 2005, Vanitharani et al. 2007, Wood & Szewczak 2007, Caspers et al. 2009, Muñoz-Romo et al. 2012, Adams et al. 2018, Faulkes et al. 2019, Flores et al. 2019), but identifying compounds potentially involved in bat chemical communication is critical. The chemical compound 2-aminoacetophenone has been reported in odorous wing sacs of male *Saccopteryx bilineata* and *Saccopteryx leptura* (Caspers et al. 2009), in odorous dorsal patches of male *Leptonycteris curasoae* (Muñoz-Romo et al. 2012), in odorous forearm crusts of male *Trachops cirrhosus* (Flores et al. 2019), and in body parts of female *Eptesicus fuscus* (Bloss et al. 2002). In addition, 4-methylquinazoline was found in odorous dorsal patches of male *Leptonycteris curasoae* (Muñoz-Romo et al. 2012) and in odorous forearm crusts of male *Trachops cirrhosus* (Flores et al. 2019). Experiments testing how individuals respond to these and other specific chemical substances are indispensable.

Some compounds released by odorous structures in bats derive from microbiological activity (Mykytowycz & Goodrich 1974, Dapson et al. 1977, Studier & Lavoie 1984, Scully et al. 2000, Voigt et al. 2005, González-Quiñonez et al. 2014, Gaona et al. 2019). Volatiles are ideal chemicals for social interactions because they constitute honest signals that are labile to changes in health status and almost impossible to fake (Penn & Potts 1998, Voigt 2014).

Future experiments will reveal whether the compounds associated with sexually dimorphic structures in male bats constitute biologically active substances to which females respond. As suggested by Voigt and von Helversen (1999), odours produced by bats may play an important, although often-underestimated, role in the mating strategies of males and females.

CONCLUSIONS

Literature on odour-producing structures – glands, skin pouches, smeared body surfaces, and other soft tissues used to store and display odorous substances – in Chiroptera is available, but is extremely scattered and sparse, to the point that research is completely lacking in six of the 21 bat families (29%). An excellent case in point is found in the family Mormoopidae. Six decades ago, a tuft of long stiff hairs on the shoulders and a glandular condition that seemed to change the colour of the back of the head in an adult male *Mormoops megalophylla* captured the attention of Goodwin and Greenhall (1961), but it remained as an isolated observation made on a specimen they had examined. Sixty years later, there has been no follow-up or systematic study of this intriguing observation. This is one of several examples suggesting that absence of information does not indicate that glands and non-glandular odour-producing structures are not exhibited

by bats, but rather that likely these sexually dimorphic structures are yet to be discovered. Moreover, the absence of conspicuous glands does not exclude the possibility that individuals can select mates by olfaction, owing to the ubiquitous small facial glands found in most bat species (Schmidt 1985, Rehorek et al. 2010), and to other odorous structures still undiscovered.

Difficulties related to studying nocturnal and elusive organisms have constrained the discovery of a wide variety of sexually dimorphic traits in bats, and many more odorous structures exist than originally thought. Moreover, soft tissues and odours can be cryptic to human perception (Voigt 2014). These difficulties presumably influenced Darwin's original perception in the first edition of *The Descent of Man and Selection in Relation to Sex*: "Hardly a single species amongst the Chiroptera (…) presents well-developed secondary sexual differences" (Darwin 1871). Dobson's (1873, 1878) and Darwin's (1874) later contributions correct this impression and formally recognise the existence of marked differences in glands and odours between sexes in bats.

Information value of odours

Glands and non-glandular odour-producing structures are mostly developed, exhibited, and functional in adult male bats during the mating season, and are underdeveloped or entirely absent in females and young males (Quay 1970, Schmidt 1985, Bloss 1999, Krutzsch 2000). In some species, males produce greasy, oily, sebaceous odoriferous exudates (Heideman et al. 1990, Brooke & Decker 1996, Krutzsch 2000) to attract females, to mark their territories, and to mark themselves or females, presumably in order to defend and enhance their breeding success (Krutzsch 2000). This suggests that odours might be important to female bats for mate selection and thus play a critical role in reproductive behaviour (Schmidt 1985).

According to Penn and Potts (1998), odours could serve as effective indicators of an individual's health and fitness, because they are direct signals that are often more labile to changes in health status than morphological traits. For example, parasitic infection can abolish the attractiveness of male scent: female mice *Mus musculus* are more attracted to the odour of uninfected males than to that of males experimentally infected with parasitic protozoans or nematode worms (Kavaliers & Colwell 1993, 1995, Ehman & Scott 2002, Kavaliers et al. 2003, González-Quiñonez et al. 2011). Female birds can increase the resistance of their progeny to parasites and reduce their own risk of contracting contagious diseases or parasites only by avoiding infected males (Hamilton & Zuk 1982, Moller et al. 1999). Females of the long-nosed bat *Leptonycteris curasoae* are attracted

to the odour of male dorsal patches (Muñoz-Romo et al. 2011b), and evidence indicates significant relationships between the presence of the patch and low ectoparasite loads (Muñoz-Romo & Kunz 2009) and between symmetry of patches and low ectoparasite loads (Muñoz-Romo et al. 2011a).

Unconventional sexually dimorphic traits

Recognising a set of unconventional traits to include in studies establishing patterns of sexual dimorphism in bats would allow us to reach a different perspective to compare and even validate consistency in studies of patterns of sexual dimorphisms based on conventional traits (e.g. body mass, canine length; Andersson 1994). For example, non-sexually dimorphic fringe-lipped bats, *Trachops cirrhosus* (Willig & Hollander 1995), are likely to appear as one of the most sexually dimorphic species when male forearm crust size and odour are taken into consideration (Flores & Page 2017, Muñoz-Romo et al. 2020).

Traits reviewed here could serve as good candidates to estimate the strength of precopulatory sexual selection. Measures of sexual dimorphism such as forearm crust size, gular gland volume, dorsal patch size, length of interaural crests, area of collar, and area of epaulettes could be used as indicators of direct male competition, instead of relative body mass, canine length or other cranial and skeletal characters. Promoting the study of sexual dimorphism based on unconventional traits (e.g. soft tissue, odorous surfaces) and the development of procedures and methods to measure variation in these less-studied traits is likely to uncover unprecedented patterns of sexual selection and dimorphism.

The enormous variety in sexually dimorphic odorous structures among 70% of chiropteran families suggests that there are remarkable differences in the production and use of odours, and that these are likely to be critical to sexual interactions (Schmidt 1985, Krutzsch 2000). Bats may have evolved the great diversity we document here in odorous displaying structures as a result of their unique combination of life-history traits. First, being nocturnal, bats are less able to attract mates effectively by displaying visual traits, which lack efficacy in the absence of light. Second, odours do not constrain the ability to manoeuvre in flight in the way that some visual features can. We believe that these key factors – nocturnality and powered flight – combined with the foundation of glandular traits that is common to mammals, together promoted the evolution of the great diversity of odorous displaying structures we find in the order Chiroptera. While we have identified many of these fascinating traits here, we expect that many more sexual dimorphisms in odour-producing structures may yet be discovered.

Dobson (1873) was the first naturalist to realise and formally recognise the importance of rigorously studying the unconventional traits he found to be sexually dimorphic in bats. He published a whole chapter entitled 'On secondary sexual characters in the Chiroptera' (1873), completely based on describing soft tissue. In the first lines of this pioneering study, Dobson wrote: "The study of sexual dimorphism in bats deserves urgent attention". As we have shown here, we now have numerous examples of striking sexual dimorphisms in bats, providing unequivocal evidence that Darwin and Dobson were indeed correct, that "…several species in this order present well-marked secondary sexual differences" (Dobson 1873). Nearly a century and a half after Dobson's paramount contribution, the study of odorous traits in bats remains indispensable. Our review details the extraordinary sexual dimorphism that has been observed in Chiroptera to date, identifying target body parts where sexually dimorphic traits are likely to be found. Future investigation should consider the importance of the timing of secondary sexual trait observations, involve behavioural studies including testing female preference, and include chemical analyses. Detailed analyses of soft tissue in museum specimens are also warranted.

ACKNOWLEDGMENTS

REFERENCES

Adams DM, Li Y, Wilkinson GS (2018) Male scent gland signals mating status in greater spear-nosed bats, *Phyllostomus hastatus*. *Journal of Chemical Ecology* 44: 975–986.

Adams DM, Nicolay C, Wilkinson GS (2020) Patterns of sexual dimorphism and mating systems. In: Fleming TH, Dávalos L, Mello M (eds) *Phyllostomid Bats, a Unique Mammalian Radiation*, 221–236. Chicago University Press, Chicago, USA.

Andersson MB (1994) *Sexual Selection*. Princeton University Press, Princeton, New Jersey, USA.

Angulo S, Ríos J, Díaz M (2008) *Sphaeronycteris toxophyllum* (Chiroptera: Phyllostomidae). *Mammalian Species* 814: 1–6.

Aufdermaur E, Haffner M, Ziswiler V (1995) Microscopic-anatomical investigations on the anorectal region of pipistrelle bats *Pipistrellus pipistrellus* (Schreber, 1774) (Mammalia, Chiroptera). *Revue Suisse de Zoologie* 102: 103–108.

Baskaran S, Kaliraj P, Maruthupandian J, Marimuthu G, Elangovan V (2015) Influence of rain on activity of the Indian flying fox *Pteropus giganteus*. *Indian Journal of Science* 15: 6–12.

Begum KM, Alexander KM (1993) Specialized skin glands of behavioral relevance in the microchiropteran bat, *Megaderma lyra*. *Bat Research News* 34: 11–12.

Behr O, von Helversen O (2004) Bat serenades - complex courtship songs of the sac-winged bat (*Saccopteryx bilineata*). *Behavioral Ecology and Sociobiology* 56: 106–115.

Bergmans W (1977) An annotated inventory of three small collections of Nigerian Microchiroptera (Mammalia, Chiroptera). *Zeitschrift fur Saugetierkunde* 42: 279–289.

Best TL, Hunt JL, McWilliams LA, Smith KG (2002) *Eumops auripendulus*. *Mammalian Species* 708: 1–5.

Best TL, Kiser WM, Freeman WM (1996) *Eumops perotis*. *Mammalian Species* 534: 1–8.

Blaustein A (1981) Sexual selection and mammalian olfaction. *American Naturalist* 117: 1006–1010.

Bloss J (1999) Olfaction and the use of chemical signals in bats. *Acta Chiropterologica* 1: 31–45.

Bloss J, Acree TE, Bloss JM, Hood WR, Kunz TH (2002) Potential use of chemical cues for colony-mate recognition in the big brown bat, *Eptesicus fuscus*. *Journal of Chemical Ecology* 28: 819–834.

Bouchard S (2001) Sex discrimination and roostmate recognition by olfactory cues in the African bats, *Mops condylurus* and *Chaerephon pumilus* (Chiroptera: Molossidae). *Journal of Zoology (London)* 254: 109–117.

Bradbury JW (1977a) Social organization and communication. In: Wimsatt WA (ed.) *Biology of Bats*, vol III, 1–72. Academic Press, New York, USA.

Bradbury JW (1977b) Lek mating behavior in the hammer-headed bat. *Zeitschrift für Tierpsychologie* 45: 225–255.

Brennan PA, Kendrick KM (2006) Mammalian social odours: attraction and individual recognition. *Philosophical Transactions of the Royal Society* 361: 2061–2078.

Brooke AP, Decker DM (1996) Lipid compounds in secretions of fishing bat, *Noctilio leporinus* (Chiroptera: Noctilionidae). *Journal of Chemical Ecology* 22: 1411–1428.

Buchler ER (1980) Evidence for the use of a scent post by *Myotis lucifugus*. *Journal of Mammalogy* 61: 525–528.

Caspers BA, Schroeder FC, Franke S, Streich JW, Voigt CC (2009) Odour-based species recognition in two sympatric species of sac-winged bats (*Saccopteryx bilineata*, *S. leptura*): combining chemical analyses, behavioural observations and odour preference tests. *Behavioral Ecology and Sociobiology* 63: 741–749.

Clutton-Brock TH (1989) Mammalian mating systems. *Proceedings of the Royal Society of London (B)* 236: 339–372.

Dalquest WW (1950) The genera of the chiropteran family Natalidae. *Journal of Mammalogy* 31: 436–43.

Dapson RW, Studier EH, Buckingham MJ, Studier AL (1977) Histochemistry of odoriferous secretions from integumentary glands in three species of bats. *Journal of Mammalogy* 58: 531–535.

Darwin C (1871) *The Descent of Man and Selection in Relation to Sex*, 1st ed. John Murray, London, UK.

Darwin C (1874) *The Descent of Man and Selection in Relation to Sex*, 2nd ed. International Science Library, H. L. Fowle, New York, USA.

Dechmann DKN, Safi K (2005) Studying communication in bats. *Cognitie, Creier, Comportament (Cognition, Brain, Behavior)* IX: 479-496.

Desai I, Pandya H, Pratyush P, Suresh B (2012) Some observations on the population of naked-rumped tomb bat (*Taphozous nudiventris cretzschmar*) at the Maharaja Sayajirao University of Baroda campus, Gujarat. *Cibtech Journal of Zoology (online)* 1: 2319–3883.

Dobson GE (1873) On secondary sexual characters in the Chiroptera. *Proceedings of the Zoological Society of London*, 241–252.

Dobson GE (1878) *Catalogue of the Chiroptera in the Collection of the British Museum*. Taylor & Francis, London, UK.

Dunn LH (1934) Notes on the little bulldog bat, *Diras albiventer minor* (Osgood), in Panama. *Journal of Mammalogy* 15: 89–99.

Ehman KD, Scott ME (2002) Female mice mate preferentially with non-parasitized males. *Parasitology* 125: 461–466.

Eisenberg JF, Kleiman DG (1972) Olfactory communication in mammals. *Annual Review of Ecology and Systematics* 3: 1–32.

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215–223.

Faulkes CG, Elmore JS, Baines DA, Fenton B, Simmons NB, Clare EL (2019) Chemical characterisation of potential pheromones from the shoulder gland of the Northern yellow-shouldered-bat, *Sturnira parvidens* (Phyllostomidae: Stenodermatinae). *PeerJ* 7: e7734.

Fenton MB, Eger JL (2002) *Chaerephon chapini*. *Mammalian Species* 662: 1–2.

Fenton MB, Taylor PJ, Jacobs DS, Richardson EJ, Bernard E, Bouchard S et al. (2002) Researching little-known species: the African bat *Otomops martienseni* (Chiroptera : Molossidae). *Biodiversity and Conservation* 11: 1583–1606.

Flores V, Mateo JM, Page RA (2019) The role of male forearm crust odour in fringe-lipped bats (*Trachops cirrhosus*). *Behaviour* 156: 1–24. https://doi. org/10.1163/1568539X-00003573.

Flores V, Page RA (2017) Novel odorous crust on the forearm of reproductive male fringe-lipped bats (*Trachops cirrhosus*). *Journal of Mammalogy* 98: 1568–1577.

Gannon MR, Willig MR, Jones JK Jr (1989) *Sturnira lilium*. *Mammalian Species* 333: 1–5.

Gaona O, Cerqueda-García D, Falcón LI, Vázquez-Domínguez G, Valdespino-Castillo PM, Neri-Barrios CX (2019) Microbiota composition of the dorsal patch of reproductive male *Leptonycteris yerbabuenae*. *PLoS One* 14: e0226239.

Giannini NP, Barquez RM (2003) *Sturnira erythromos*. *Mammalian Species* 729: 1–5.

González-Quiñonez N, Fermin G, Muñoz-Romo M (2014) Diversity of bacteria in the sexually selected epaulettes of the little yellow-shouldered bat *Sturnira lilium* (Chiroptera: Phyllostomidae). *Interciencia* 39: 882–889.

González-Quiñonez N, Pirela A, de Jesús R, Muñoz-Romo M (2011) Female mice preference: does *Trypanosoma cruzi* affect males' scent? *Interciencia* 36: 764–767.

Goodwin GG (1928) Observations on *Noctilio*. *Journal of Mammalogy* 9: 106.

Goodwin GG, Greenhall AM (1961) A review of the bats of Trinidad and Tobago. *Bulletin of the American Museum of Natural History* 122: 191–301.

Gutierrez M, Aoki A (1973) Fine structure of the gular gland of the free-tailed bat, *Tadarida brasiliensis*. *Journal of Morphology* 141: 293–306.

Haffner M (1995) The possibilities of scent marking in the mouse-eared bat *Myotis myotis* (Borkhausen, 1797) and the noctule bat *Nyctalus noctula* (Schreber, 1774) (Mammalia, Chiroptera). *Zeitschrift für Säugertierkunde* 60: 112–118.

Haffner M (2000) Structure and function of pilosebaceous units on the heads of small mammals (Insectivora, Chiroptera, Rodentia). *Acta Zoologica (Stockholm)* 81: 195–203.

Hall LS (1989) 40. Rhinolophidae. In: Walton DW, Richardson BJ (eds) *Fauna of Australia, Volume 1B: Mammalia*, 1–15. Australian Government Publishing Service, Canberra, Australia.

Hall LS, Gordon G (1982) The throat pouch of the yellow-bellied bat, *Taphozous flaviventris*. *Mammalia* 46: 247–252.

Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? *Science* 218: 384–387.

Harrison A, Davies DV (1949) A note on epithelial structures in Microchiroptera. *Journal of Zoology (London)* 119: 351–357.

Häussler U (1989) Male social behaviour in *Molossus molossus* (Molossidae). In: Hanák V, Horácek I, Gaisler J (eds) *European Bat Research 1987*, 125–130. Charles University Press, Prague, Czech Republic.

Heideman PD, Erickson KR, Bowles JB (1990) Notes on the breeding biology, gular gland and roost habits of *Molossus sinaloae* (Chiroptera: Molossidae). *Zeitschrift für Säugertierkunde* 55: 303–307.

Herreid CF (1960) Comments on the odors of bats. *Journal of Mammalogy* 41: 396.

Hickey MBC, Fenton MB (1987) Scent-dispersing hairs (osmetrichia) in some Pteropodidae and Molossidae (Chiroptera). *Journal of Mammalogy* 68: 376–384.

Hill JE (1974) A new family, genus, and species of bat (Mammalia: Chiroptera) from Thailand. *Bulletin of the British Museum of Natural History Zoology* 27: 301–336.

Hill JE, Smith JD (1984) *Bats: a Natural History*. University of Texas Press, Austin, Texas, USA.

Höller VP, Schmidt U (1993) Olfactory communication in the lesser spear-nosed bat, *Phyllostomus discolor* (Chiroptera, Phyllostomidae). *Zeitschrift für Säugertierkunde* 58: 257–265.

Hood CS, Smith JD (1984) Histology of a sexually dimorphic integumentary gland in *Macroglossus lacochilus* (Chiroptera: Pteropodidae). *Journal of Mammalogy* 65: 1–9.

Horst R (1966) Observations on the gular gland of *Molossus rufus nigricans*. *Anatomical Record* 154: 465.

Hunt JL, McWilliams LA, Best TL, Smith KG (2003) *Eumops bonariensis*. *Mammalian Species* 733: 1–5.

Hurtado N, Arias E, Pacheco V (2014) Redescription of *Mimon koepckeae* (Chiroptera: Phyllostomidae). *Zoologia* 31: 377–388.

Jennings JB, Best TL, Burnett SE, Rainey JC (2002) *Molossus sinaloae*. *Mammalian Species* 691: 1–5.

Johansson BG, Jones TM (2007) The role of chemical communication in mate choice. *Biological Reviews of the Cambridge Philosophical Society* 82: 265–289.

Jones JK, Hood CS (1993) Synopsis of South American bats of the family Emballonuridae. Biological Reviews. *Occasional Papers of the Museum Texas Tech University* 155: 1–32.

Kavaliers M, Colwell DD (1993) Aversive responses of female mice to the odors of parasitized males: neuromodulatory mechanisms and implications for mate choice. *Ethology* 95: 202–212.

Kavaliers M, Colwell DD (1995) Odours of parasitized males induce aversive responses in female mice. *Animal Behaviour* 50: 1161–1169.

Kavaliers M, Fudge MA, Colwell DD, Choleris E (2003) Aversive and avoidance responses of female mice to the odors of males infected with an ectoparasite and the effects of prior familiarity. *Behavioral Ecology and Sociobiology* 54: 423–430.

Knörnschild M (2014) Vocal production learning in bats. *Current Opinion in Neurobiology* 28: 80–5. https://doi.org/10.1016/j.conb.2014.06.014.

Krutzsch PH (2000) Anatomy, physiology and cyclicity of the male reproductive tract. In: Crichton EG, Krutzsch PH (eds) *Reproductive Biology of Bats*, 91–155. Academic Press, San Diego, California, USA.

Krutzsch PH, Crichton EG (1987) Reproductive biology of the male little mastiff bat, *Mormopterus planiceps* (Chiroptera: Molossidae), in Southeast Australia. *The American Journal of Anatomy* 178: 352–368.

Krutzsch PH, Fleming TH, Crichton EG (2002) Reproductive biology of male Mexican free-tailed bats (*Tadarida brasiliensis mexicana*). *Journal of Mammalogy* 83: 489–500.

Kurta A, Frick WF, Fenton MB, Campbell P, McCracken GF, Timm RM, Genoways HH (2020) Obituary: Thomas Henry Kunz (1938–2020). *Journal of Mammalogy* 101. https://doi.org/10.1093/jmammal/gyaa100

Langevin P, Barclay RMR (1990) *Hypsignathus monstrosus*. *Mammalian Species* 357: 1–4.

Leong TM, Teo SC, Lim KKP (2009) The naked bulldog bat, *Cheiromeles torquatus* in Singapore – past and present records, with highlights on its unique morphology (Microchiroptera: Molossidae). *Nature in Singapore* 2: 215–230.

Lily D (2005) *Scent gland histology, biochemistry and chemical signaling during the mating behaviour of three species of Temple bats*. PhD thesis, Manonmanium Sundaranar University, Tirunelveli, Tamilnadu, India.

Lily D, Vanitharani J (2005) Chemical signaling in *Hipposideros speoris*. *Journal of Theoretical and Experimental Biology* 1: 183–192.

Lloyd BD (2001) Advances in New Zealand mammalogy 1990–2000: short-tailed bats. *Journal of the Royal Society of New Zealand* 31: 59–81.

Lu D, Zhou CQ, Liao WB (2014) Sexual size dimorphism lacking in small mammals. *North-Western Journal of Zoology* 10: 53–59.

Lundberg K, Gerell R (1986) Territorial advertisement and mate attraction in the bat *Pipistrellus pipistrellus*. *Ethology* 71: 115–124.

Mainoya JR (1979) Spermatogenic and frontal sac gland activity in *Triaenops persicus* (Chiroptera: Hipposideridae). *African Journal of Ecology* 17: 127–129.

Mainoya JR, Howell KM (1977) Histology of the frontal sac in three species of leaf-nosed bats (Hipposideridae). *African Journal of Ecology* 15: 147–155.

Mainoya JR, Howell KM (1979) Histology of the neck 'glandular' skin patch in *Eidolon helvum*, *Rousettus aegyptiacus*, and *R. angolensis* (Chiroptera: Pteropodidae). *African Journal of Ecology* 17: 159–164.

McCracken GF, Wilkinson GS (2000) Bat mating systems. In: Crichton EG, Krutzsch PH (eds) *Reproductive Biology of Bats*, 321–362. Academic Press, San Diego, California, USA.

McPherson FJ, Chenoweth PJ (2012) Mammalian sexual dimorphism. *Animal Reproduction Science* 131: 109–122.

McWilliam AN (1988) Social organisation of the bat *Tadarida* (*Chaerephon*) *pumila* (Chiroptera: Molossidae) in Ghana, West Africa. *Ethology* 77: 115–124.

McWilliam AN (1990) Mating system of the bat *Miniopterus minor* (Chiroptera: Vespertilionidae) in Kenya, East Africa: a lek? *Ethology* 85: 302–312.

McWilliams LA, Best TL, Hunt JL, Smith KG (2002) *Eumops dabbenei*. *Mammalian Species* 707: 1–3.

Moller AP, Christe P, Lux E (1999) Parasitism, host immune function, and sexual selection. *Quarterly Review of Biology* 74: 3–20.

Müller-Schwarze D (1983) Scent glands in mammals and their functions. In: Eisenberg JF, Kleiman DG (eds) *Advances in the Study of Mammalian Behavior*, 150–197. Special Publication 7, The American Society of Mammalogists, Lawrence, Kansas, USA.

Muñoz-Romo M, Burgos J, Kunz TH (2011a) The dorsal patch of males of the Curaçaoan long-nosed bat, *Leptonycteris curasoae* (Phyllostomidae: Glossophaginae) as a visual signal. *Acta Chiropterologica* 13: 207–215.

Muñoz-Romo M, Burgos J, Kunz TH (2011b) Smearing behaviour of male *Leptonycteris curasoae* (Chiroptera) and female responses to the odour of dorsal patches. *Behaviour* 148: 461–483.

Muñoz-Romo M, Flores V, Ramoni-Perazzi P, Page RA (2020) The crust of a male: does size matter when females are fertile? *Behavioral Ecology and Sociobiology* 74: http://dx.doi.org/10.1007/s00265-020-02914-0.

Muñoz-Romo M, Kunz TH (2009) Dorsal patch and chemical signaling in males of the long-nosed bat, *Leptonycteris curasoae* (Chiroptera: Phyllostomidae). *Journal of Mammalogy* 90: 1139–1147.

Muñoz-Romo M, Nielsen LT, Nassar JM, Kunz TH (2012) Chemical composition of the substances from dorsal patches of males of the Curaçaoan long-nosed bat, *Leptonycteris curasoae* (Phyllostomidae: Glossophaginae). *Acta Chiropterologica* 14: 213–224.

Murray KL, Fleming TH (2008) Social structure and mating system of the buffy flower bat, *Erophylla sezekorni* (Chiroptera, Phyllostomidae). *Journal of Mammalogy* 89: 1391–1400.

Myers P (1981) Observations on *Pygoderma bilabiatum* (Wagner). *Zeitschrift für Säugetierkunde* 46: 146–151.

Mykytowycz R, Goodrich BS (1974) Skin glands as organs of communication in mammals. *Journal of Investigative Dermatology* 62: 124–131.

Nanayakkara RP, Vishvanath N, Kusuminda TGT (2012) Re-discovery of pouch bearing sheath tailed bat *Saccolaimus saccolaimus* Temminck (Chiroptera: Emballonuridae) from Sri Lanka after 75 years. *Asian Journal of Conservation Biology* 1: 134–137.

Nassar JM, Salazar V, Quintero A, Stoner K, Cabrera A, Gómez M, Jaffé K (2008) Seasonal sebaceous patch in the nectar-feeding bats *Leptonycteris curasoae* and *L. yerbabuenae* (Phyllostomidae: Glossophaginae): phenological, histological, and preliminary chemical characterization. *Zoology* 111: 363–376.

Ober HK, Braun de Torrez EC, Gore JA, Bailey AM, Myers JK, Smith KN, McCleery RA (2016) Social organization of an endangered subtropical species, *Eumops floridanus*, the Florida bonneted bat. *Mammalia* 81: 375–383. https://doi.org/10.1515/mammalia-2015-0183

Olson SH, Bounga G, Ondzie A, Bushmaker T, Seifert SN, Kuisma E, Taylor DW, Munster VJ, Walzer C (2019) Lek-associated movement of a putative Ebolavirus reservoir, the hammer-headed fruit bat (*Hypsignathus monstrosus*), in northern Republic of Congo. *PLoS One* 14: e0223139.

Penn D, Potts WK (1998) Chemical signals and parasite-mediated sexual selection. *Trends in Ecology and Evolution* 13: 391–396.

Peterson RL (1965) *A Review of the Bats of the Genus Ametrida, Family Phyllostomidae*. Royal Ontario Museum Life Sciences 65, Toronto, Canada.

Quay WB (1970) Integument and derivatives. In: Wimsatt W (ed.) *Biology of Bats*, vol II, 1–56. Academic Press, New York, USA.

Racey PA (2009) Reproductive assessment of bats. In: Kunz TH, Parsons S (eds) *Ecological and Behavioral Methods for the Study of Bats*, 247–264, 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Ralls K (1976) Mammals in which females are larger than males. *The Quarterly Review of Biology* 51: 245–276.

Ralls K (1977) Sexual dimorphism in mammals: avian models and unanswered questions. *American Naturalist* III: 917–938.

Rasweiler JJ (1992) Reproduction biology of the female black mastiff bat, *Molossus molossus*. In: Hamlett WC (ed.) *Reproductive Biology of South American Vertebrates*, 262–283. Springer-Verlag, New York, USA.

Rehn JAG (1901) A study of the genus *Centurio*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 53: 295–302.

Rehorek SJ, Smith TD, Bhatnagar KP (2010) The orbitofacial glands of bats: an investigation of the potential correlation of gland structure with social organization. *The Anatomical Record* 293: 1433–1448.

Rodríguez-Herrera B, Sánchez-Calderón R, Madrigal-Elizondo V, Rodríguez P, Villalobos J, Hernández E, Zamora-Mejías D, Gessinger G, Tschapka M (2020) The masked seducers: lek courtship behavior in the wrinkle-faced bat *Centurio senex* (Phyllostomidae). *PLOS ONE* 15: e0241063. http://dx.doi.org/10.1371/journal.pone.0241063.

Rosevear DR (1965) *The Bats of West Africa*. Trustees of the British Museum (Natural History), London, UK.

Safi K, Kerth G (2003) Secretions of the interaural gland contain information about individuality and colony membership in the Bechstein's bat. *Animal Behaviour* 65: 363–369.

Schmidt U (1985) The bats: order Chiroptera. In: Brown RE, MacDonald DW (eds) *Social Odours in Mammals*, 217–234. Clarendon Press, Oxford, UK.

Scully WMR, Fenton MB, Saleuddin ASM (2000) A histological examination of the holding sacs and glandular scent organs of some bat species (Emballonuridae, Hipposideridae, Phyllostomidae, and Molossidae). *Canadian Journal of Zoology* 78: 613–623.

Simmons NB, Cirranello AL (2020) *Bat Species of the World: a Taxonomic and Geographic Database*. https://batnames. org. Accessed on 31/7/2020

Snow JL, Jones JK, Webster WD (1980) *Centurio senex*. *Mammalian Species* 138: 1. http://dx.doi.org/10.2307/3503871.

Spencer HJ, Flick BH (1995) Secretion of marking fluid from the penis of the spectacled flying fox, *Pteropus conspicillatus*. *Bat Research News* 36: 112.

Studier EH, Lavoie KH (1984) Microbial involvement in scent production in noctilionid bats. *Journal of Mammalogy* 65: 711–714.

Tavares VC, Tejedor A (2009) The forelimb swellings of *Pygoderma bilabiatum* (Chiroptera: Phyllostomidae). *Chiroptera Neotropical* 15: 411–416.

Toth CA, Parsons S (2013) Is lek breeding rare in bats? *Journal of Zoology* 291: 1–9.

Turcios-Casco MA, Medina-Fitoria A, Portillo-Álvarez LR (2020) First record of the pale-face bat (*Phylloderma stenops*, Phyllostomidae) in the Caribbean lowlands of Gracias a Dios in eastern Honduras. *Caribbean Journal of Science* 50: 16–22.

Valdivieso D, Tamsitt JR, Valdivieso D (1964) The histology of the chest gland of the pale spear-nosed bat. *Journal of Mammalogy* 45: 536–539.

Vanitharani J, Vijaya M, Lily M (2007) Scent gland and chemical signaling in *Cynopterus sphinx* (short-nosed fruit

bat) during breeding season. *Journal of Theoretical and Experimental Biology* 3: 67–75.

Vilar EM, Nunes H, Nascimento JL, Estrela PC (2015) Distribution extension of *Ametrida centurio* Gray, 1847 (Chiroptera, Phyllostomidae): first record in the Brazilian Atlantic Forest. *Check List* 11: 1503.

Voigt CC (2005) The evolution of perfume-blending and wing sacs in emballonurid bats. *Chemical Signals in Vertebrates* 10: 93–100.

Voigt CC (2014) Sexual selection in neotropical bats. In: Macedo RH, Machado G (eds) *Sexual Selection - Perspectives and Models from the Neotropics*, 409–432. Elsevier, Amsterdam, the Netherlands.

Voigt CC, Caspers B, Speck S (2005) Bats, bacteria, and bat smell: sex-specific diversity of microbes in a sexually selected scent organ. *Journal of Mammalogy* 86: 745–749.

Voigt CC, von Helversen O (1999) Storage and display of odour by male *Saccopteryx bilineata* (Chirotera, Emballonuridae). *Behavioral Ecology and Sociobiology* 47: 29–40.

Vonhof MJ, Kalcounis MC (1999) *Lavia frons. Mammalian Species* 614: 1–4.

Walton DW, Siegel NJ (1966) The histology of the pararhinal glands of the pallid bat, *Antrozous pallidus. Journal of Mammalogy* 47: 357–360.

Werner HJ, Dalquest WW (1952) Facial glands of the tree bats, *Lasiurus* and *Dasypterus. Journal of Mammalogy* 33: 77–80.

Werner JO, Dalquest WW, Roberts JH (1950) Histological aspects of the glands of the bat, *Tadarida cyanocephala* (Le Conte). *Journal of Mammalogy* 31: 395–399.

Werner HJ, Lay DM (1963) Morphologic aspects of the chest gland of the bat *Molossus ater. Journal of Mammalogy* 44: 552–555.

Wickler W, Seibt U (1976) Field studies on the African fruit bat *Epomophorus wahlbergi* (Sundevall), with special reference to male calling. *Zeitschrift für Tierpsychologie* 40: 345–376.

Wilkins KT (1989) *Tadarida brasiliensis. Mammalian Species* 331: 1–10.

Willig MR, Hollander RR (1995) Secondary sexual dimorphism and phylogenetic constraints in bats: a multivariate approach. *Journal of Mammalogy* 76: 981–992.

Wood WF, Szewczak JM (2007) Volatile antimicrobial compounds in the pelage of the Mexican free-tailed bat, *Tadarida brasiliensis mexicana. Biochemical Systematics and Ecology* 35: 566–568.

Wood WF, Walsh A, Seyjagat J, Weldon PJ (2005) Volatile compounds in shoulder gland secretions of male flying foxes, genus *Pteropus* (Pteropodidae, Chiroptera). *Zeitschrift für Naturforschung* 60: 779–784.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Glands and non-glandular odour-producing structures commonly observed in bats.
Appendix S2. Adult males of: a) the common noctule *Nyctalus noctula*; b) the black-winged little yellow bat *Rhogeessa tumida*.
Appendix S3. a) Adult male buffy flower bat *Erophylla sezekorni*; b) detail of the wet postorbital glandular area.
Appendix S4. Frontal gland in an adult male Commerson's roundleaf bat *Macronycteris commersoni*, in natural state (a) and everted by researcher (b).