

INTRODUCTION

Ecomorphology and sensory biology of bats

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Abstract

This special issue of The Anatomical Record is inspired by and dedicated to Professor Kunwar P. Bhatnagar, whose lifelong interests in biology, and long career studying bats, inspired many and advanced our knowledge of the world's only flying mammals. The 15 articles included here represent a broad range of investigators, treading topics familiar to Prof. Bhatnagar, who was interested in seemingly every aspect of bat biology. Key topics include broad themes of bat development, sensory systems, and specializations related to flight and diet. These articles paint a complex picture of the fascinating adaptations of bats, such as rapid fore limb development, ear morphologies relating to echolocation, and other enhanced senses that allow bats to exploit niches in virtually every part of the world. In this introduction, we integrate and contextualize these articles within the broader story of bat ecomorphology, providing an overview of each of the key themes noted above. This special issue will serve as a springboard for future studies both in bat biology and in the broader world of mammalian comparative anatomy and ecomorphology.

KEYWORDS

Chiroptera, development, echolocation, functional morphology, olfaction

1 | THE CRYPTIC WORLD OF BATS

This special issue of The Anatomical Record celebrates Prof. Kunwar P. Bhatnagar, his lifelong dedication to science, and his fascination with bats. With over 1400 species and a distribution spanning every continent except Antarctica, bats (order Chiroptera) are the second most speciose order of mammals (Altringham, 2011; Simmons & Cirranello, 2023). When first categorized as mammals in 1758, fewer than 10 species of bats had been formally described (Neuweiler, 2000). The early scarcity of published information on bats may be attributed to their nocturnal habits and the aptitude of most species to roost in places largely inaccessible to researchers (but see Rocha et al., 2021 for a review of cultural knowledge about bats). However, by the end of the 20th century, more than 900 species of bats had been described, along with a vast amount of information about their anatomy,

behavior, ecology, and evolution (Altringham, 2011). This explosion of published information resulted from decades of field and lab research across the globe aided by technological advances (e.g., Bumrungsri et al., 2006). For example, the pace of publication increased rapidly with the adoption of the Japanese mist-net during the 1950s by ornithologists and mammalogists (Genoways et al., 2020), which enabled the capture of bats for detailed in vivo and postmortem study.

In their morphology, habits, and sensory abilities, bats are specialized to live in vastly different habitats and climates. As such, they are a favorite subject to investigators with an interest in ecomorphology, the study of how organisms function within their environment and how their morphology reflects their ecological adaptations (Wainwright & Reilly, 1994). Further, based on their ubiquity and diverse ecological roles, bats serve as quintessential indicators of ecosystem health (Russo

et al., 2021). Kunwar Bhatnagar was a pioneer in quantitative methods and studies of ecomorphology (e.g., Bhatnagar & Kallen, 1974a; and see Smith, 2023), and had a special interest in bat sensory systems (e.g., Bhatnagar & Kallen, 1975; Cooper & Bhatnagar, 1976; Hope & Bhatnagar, 1979; Meisami & Bhatnagar, 1998). In his autobiography (recently published by his daughter, Dr. Divya Cantor), he lists bat collecting sites in India, Thailand, and North America (Cantor, 2022); there he sought bats not only in their iconic setting, the cave (Figure 1), but also in ancient castles and forts.

In this special issue, contributors offer a glimpse into the many adaptations of the first and only flying mammals. The researchers revisit some territory that was very familiar to Prof. Bhatnagar, from bat brain morphology (Reep & Bhatnagar, 2000) to anatomy of gliding mammals (Bhatnagar & Wible, 1994), and bat reproductive biology

(e.g., Bhatnagar, 1978; Krishna & Bhatnagar, 2011; Rehorek et al., 2010; Singh et al., 2005). High-resolution computed tomography is employed by Manguerra and Orliac (2023) to study virtual endocasts of bats, a potentially more efficient route to explore a topic that previously required intricate dissection (Reep & Bhatnagar, 2000). The authors pave a path forward for future investigators to identify neurological and vascular structures that may be observed in chiropteran endocasts. Also in this issue, Wible (2023) investigates the ear region in *Cynocephalus volans*, the Philippine flying lemur (a gliding mammal also studied by Bhatnagar & Wible, 1994). The author documents many unusual basicranial features that may help to clarify relationships of the order Dermoptera with other groups such as primates. Finally, Rodriguez et al. (2023) study an integumentary gland in bats of the family Molossidae. The authors found immunohistochemical evidence

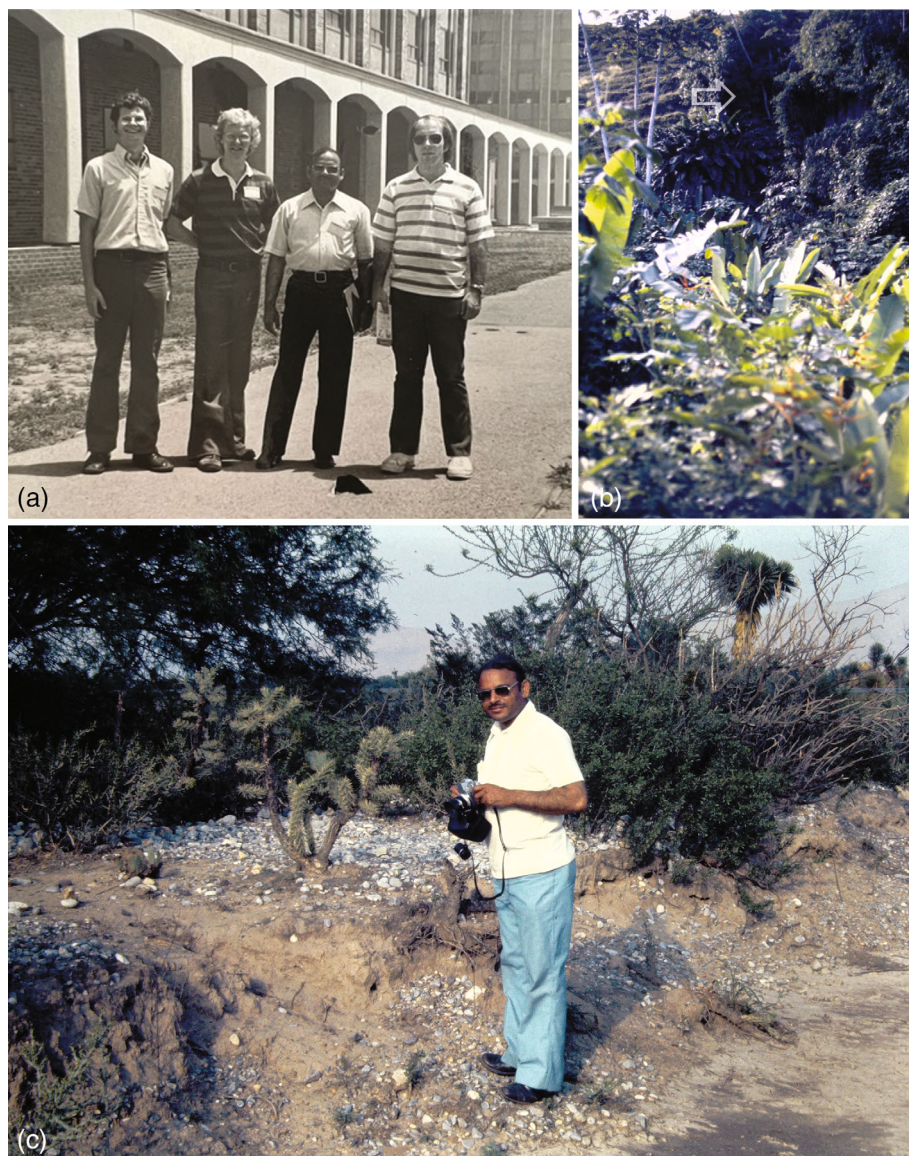


FIGURE 1 (a) Leon Kundrotas, Greg Cooper, Dr. Bhatnagar, and Barry Spoonamore at Texas Tech University, in 1974 on the way to Mexico and their field work in the bat (murciélagos) caves of the Yucatan. (b) Entrance to a cave (open arrow). (c) Prof. Kunwar Bhatnagar.

for mechanoreceptors in the gland, and suggest the exocrine gland may be activated by mechanoreceptors involved in reproductive behavior.

Below, we continue with the numerous themes Prof. Bhatnagar contemplated, and which this special issue demonstrates continue to hold interest for many investigators.

2 | LIFE HISTORY OF BATS: STRATEGIES FOR A MOST SPECIALIZED EXISTENCE

Mammals that are born relatively large compared to maternal mass, and in small litters, are considered precocial. This is in contrast to altriciality, the presumed ancestral mammalian state. The altricial condition is typified by larger litters of relatively small and poorly developed offspring (e.g., in skeletal maturity and muscular mass; Derrickson, 1992; Grand, 1992). However, altriciality and precociality are considered to be end-points along a spectrum (Starck & Ricklefs, 1998), and some mammals, such as primates and bats, have a blend of attributes that render them intermediate, or “semi-precocial” (Grand, 1992; Martin, 1990). Precociality is only considered an evolutionary advantage for larger-bodied mammals, and perhaps for this reason small mammals are more frequently altricial than larger mammals (Hennemann, 1984).

Among small mammals, bats truly stand out with their large young, requiring a relatively prolonged gestation. Even small-bodied bats have relatively lengthier gestation periods than most other similarly sized mammals (Altringham, 2011). This prolonged prenatal period partially explains the large relative size of neonatal bats, ranging from 12% to 43% of maternal weight (Grunstra et al., 2019; Kurta & Kunz, 1987).

Several factors have been suggested for the large size of newborn bats, and some of these also relate to their small litter sizes (most have one per litter) and may be important for similar reasons. One explanation focuses on maternal limitations: since many bat mothers fly with their young pups attached, there must be a limit on the number of offspring a bat mother can carry during flight (Altringham, 2011). Other explanations focus on maturation of the young bat, which must swiftly develop the capacity to fly (Kurta & Kunz, 1987). A simpler explanation is possible; for at least some species, larger newborn pups have greater survivability. Notably, these explanations are not mutually exclusive, so it is difficult to tease out causative factors in the development of bat pups and how that relates to maternal size and condition.

Whereas they may be relatively large at birth, bat pups are very heterogeneous in the degree of somatic and

neural development. For example, they are notably altricial in their wing development, whereas their hindlimbs at birth are highly developed (Farnum et al., 2008; Koyabu & Son, 2014; Kunz & Robson, 1995). Essentially, bats may prioritize development of the hind limb to facilitate gripping the mother as she flies (Kunz & Robson, 1995; Reyes-Amaya et al., 2017; Schutt et al., 1999), a fascinating contrast to marsupials that accelerate fore limb development as an adaptation to grip the mother and crawl to the teat (reviewed in Smith & Keyte, 2020). It is also known that some bats are born neurally precocious (Grand, 1992), but a broader perspective on bat development is still lacking. In this issue, Smith et al. (2023) study the relative degree of somatic and neural development in a newborn vampire bat (*Desmodus rotundus*) relative to its mother. Using diffusible iodine-based contrast-enhanced computed tomography scans of the two preserved specimens, the authors reconstructed and volumetrically measured masticatory and limb muscles, as well as endocranial volume at both ages. In addition, they assess skeletal and dental maturation of the newborn. In comparing the two ages, Smith et al. (2023) find that the newborn has far better developed musculature of the leg, including the digital flexor musculature, compared to the forearm. In addition, ossification of leg and foot bones is nearly complete, whereas none of the carpals or secondary ossification centers in the forearm and hand have commenced ossification in the newborn. Muscles involved in biting (temporalis and masseter) are poorly developed, although crown mineralization of the incisors (important for piercing prey skin) is well-progressed in the newborn. Impressively, the endocranial volume of the newborn is 74% of that in the adult. Smith et al. conclude that in *Desmodus* the young exist in “condition III” at birth, regarding maturational characteristics discussed by Grand (1992); that is, they possess a relatively large brain and weak musculature. For *Desmodus*, the slow prenatal somatic development for most of the body is matched with prolonged dependency of the young (Greenhall et al., 1983), and the advanced neural development is undoubtedly associated with the extremely gregarious nature of vampire bats, which are notable for their intracolony altruism (Hermanson & Carter, 2020; Wilkinson, 1984) and other highly social behaviors, including play (Park, 1990).

We are beginning to more clearly see the interface of ecology and ontogeny through studies of bats. Prolonged gestation is strongly suggested as an explanation for a relatively large brain in bats (Jones & MacLarnon, 2004); although the relative size of the neonatal brain remains unknown for most bat species, some authors infer many bats (perhaps especially smaller bats) are born with relatively large brains (Grunstra et al., 2019). If true,

prioritizing brain development may facilitate learning to navigate in three dimensions and socialization (as may be important to *Desmodus*—Smith et al., 2023). More work on relative neonatal brain size across a broad spectrum of bats, perhaps based on an endocast volume proxy, may reveal if the pace of brain development varies among bats having different diets, foraging/hunting strategies, or group sizes.

A topic that has been better studied with respect to ecological adaptations is the development of the masticatory apparatus. In this issue, Stanchak et al. (2023) track measurements of muscular and skeletal morphology and size in a cross-sectional age sample of a species of insectivorous bat (*Eptesicus fuscus*). With increasing postnatal age, they report profound increases in masticatory muscle volume and related surface area for attachment sites in the skull. Their data highlight dramatic ontogenetic changes in skull shape, particularly within the first 20 days post-birth. These changes include the development of the sagittal crest, the lateral expansion of the skull dome and zygomatic arches, and the rostral movement of the mandibular tooth row as the molars erupt and develop. Together with accelerated growth, these morphological changes seem to prepare the neonate feeding apparatus to transition from suckling milk to an insect-based diet—which starts around 25 days of age—by partly enabling a previously reported allometric increase in bite force (Santana & Miller, 2016). Yet, much remains to be understood about how internal muscle architecture and jaw movement dynamics develop in young insectivorous bats to fully understand their dramatic ontogenetic change in feeding performance and diet.

3 | GLIDING AND FLIGHT

The first recognized bat skeletons that appear in the Eocene fossil record had a suite of morphological features indicating already well-developed flight capabilities (e.g., Rietbergen et al., 2023), suggesting that discovery of more fossils is needed to understand the evolution of flight in bats. Indeed, the fossil record of bats is extremely poor (Eiting & Gunnell, 2009; and see Teeling et al., 2005), highlighting the need to study modern species using diverse techniques that allow us to gain insights into evolutionary patterns and processes in this group.

In the absence of fossils constituting stages that may presage flight adaptations, scenarios for flight evolution have been proposed and tested using extant mammals as models, often involving intermediate stages resembling gliding locomotion (e.g., Bishop, 2008; Burtner et al., 2023). In this issue, Berghäuser et al. (2023)

examined cortical bone thickness of the glenoid fossa in arboreal climbing versus aerial (gliding) squirrels. They found no significant difference in thickness between locomotor groups, suggesting that no biomechanical adaptation in terms of bone robusticity has evolved to resolve landing forces at the end of a glide. Instead, the authors suggest behavioral changes, such as adjustments in landing posture, may help deal with these forces. The findings of Berghäuser et al. (2023) also offer indirect support to the hypothesis that bats evolved from gliding mammals, as they demonstrate that gliding does not require major changes to bone architecture, such as increased robusticity. Thus, hypothetical gliding ancestors to bats could have had gracile, lightweight limb skeletons similar to extant flying squirrels, and would have been ideally positioned to evolve further modifications allowing flight (Rickman et al., 2023).

Two contributions in this special issue offer more insights into specialized membranous forelimbs of bats, which are key adaptations for flight (but, see other suggested functions in bat ancestors [Anderson & Ruxton, 2020; Speakman, 2001]). The profound specialization of the bat forelimb is visible at embryonic stages, in which the handplate dwarves the footplate in size (Giannini et al., 2006). The embryonic precursor gives rise to adult wings with specialized flight musculature and integumentary expansions that form the wing. In a study of the brachial plexus in bats, Toledo et al. (2023) note that the range in number of contributing ventral rami (“roots”) is greater in bats than in most mammals. The authors discuss the possibility that the specialized flight musculature may relate to the inclusion of more nerve roots. They observe that the cutaneous components of the plexus may also explain an expanded range of roots, based on derivation from an expanded range of embryonic somites, which go on to form the disproportionately large fore limbs. Additional neural specializations serve the wings: a distribution of fine hairs, previously suggested to sense airflow during flight (Sterbing-D’Angelo & Moss, 2014), but only studied to date in a few bat species. In this issue, Rummel et al. (2023) studied the sensory hair distribution in 17 bat species. The authors describe distinctive clustering of the sensory hairs in some species, with the higher density along the proximal wing. In addition, sensory hairs appear to be localized near internal wing structures such as muscles within wing membranes, in some but not all species. Rummel et al. suggest that in species in which the hairs associate with muscles, they may transmit sensory information that would be transmitted muscle spindles in most skeletal muscle, but which appear to be lacking in the intramembranous wing muscles. These findings build on prior studies of bat wing microanatomy,

revealing the wing membrane provides a dynamic alternative to feathered flight (Cheney et al., 2015, 2022).

4 | DIET

Bats are fodder for much research on ecomorphology relating to diet. Prior research has spanned a broad range of topics, including how mechanical properties of food may influence dental microanatomy (e.g., Dumont, 1995), craniodental form (e.g., Gregorin & Ditchfield, 2005; Nogueira et al., 2009; Santana et al., 2010, 2012) or feeding behavior (e.g., Dumont & O'Neal, 2004), and how flight may constrain the morphology of the skull (Dumont, 2007), to name a few topics.

Previous work on bat dietary ecomorphology has revealed tight links between craniodental form and function and specialized diets, particularly in the context of dietary adaptive radiations such as that experienced by the family Phyllostomidae (e.g., Arbour et al., 2019; Dumont et al., 2012; Rossoni et al., 2017). It is less clear, however, how the morphologies of less specialized species, such as omnivores, are able to meet the functional requirements of their eclectic diets. In this issue, Quinche et al. (2023) describe how the skull shape, palate, and tongue anatomy of an omnivorous phyllostomid, *Phyllostomus discolor*, compares to those of more specialized species. *P. discolor* includes a high amount of nectar in its diet when compared to its congeners, which it combines with insect prey and fruit. Using a combination of micrographs and electron microscopy, Quinche et al. describe features of the tongue of *P. discolor* that enable it to collect nectar from flowers, and that are shared with specialized nectar feeding glossophagines (Phyllostomidae: Glossophaginae) and distantly-related nectarivorous pteropodids. For example, the body of the tongue exhibits abundant hair-like papillae that become larger and denser toward the middle region of the lingual body. These papillae likely contribute to nectar collection by increasing the lingual surface area and thus enhancing nectar adhesion. Nevertheless, the skull shape of *P. discolor* lacks the extreme elongation observed in nectar specialists and is rather more similar to that of closely-related omnivorous/carnivorous species. The authors view the combination of these morphological features in *P. discolor* as a compromise—a skull shape allowing the processing of a diverse solid diet, along with tongue adaptations that are critical for nectar collection in the form of elongated papillae.

Most bats consume at least some insects, and many bats are dependent on insects for all dietary needs. Bats are considered to fulfill a critical role as natural checks on insect populations (Ramírez-Francel et al., 2022), and

estimates of their monetary value (e.g., in lieu of pesticides) are immense (Ricucci & Lanza, 2014). As discussed in this issue by Paksuz (2023), a potential cost of insectivory is water loss, since insects have far lower water content than other food. In a histological study, Paksuz (2023) identifies microanatomical features of the kidneys in the insectivorous bat *Myotis myotis* that mitigate this potential water loss, such as a relatively large medullary region, where water is reclaimed and urine is concentrated.

5 | SPECIAL SENSES

Bats are notably reliant on sound for communication, passive listening of prey sounds, and—in most species—for the specialized use of echolocation in navigation and hunting. A strong reliance on hearing and echolocation may be reflective of an adaptation for nocturnality, which typifies the vast majority of extant bats. In modeling for the common ancestor of bats, Thiagavel et al. (2018) assert that the eyes of ancestral bats were small, too small to aid in visual pursuit of aerial insects, and that these bats were small, volant, and already capable of laryngeal echolocation. Further, these authors observe that among extant bats, those with the most sophisticated echolocation abilities have the smallest eyes, suggesting that extant bats bear the stamp of a trade-off of vision and specialization for echolocation.

In their auditory senses, bats are similar to other mammals in certain respects. Across mammals, smaller species tend to have a greater sensitivity to high frequency sounds, and bats, as expected from their relatively small size, are in keeping with this trend (Heffner, 2004; Heffner et al., 2003). In this issue, Dickinson et al. (2023) investigate osteological features of the inner and middle ear of phyllostomid bats based on micro computed tomographic scan data. Their findings show ear ossicles have a strong negative allometric relationship to body size; this may be reflective of a general trend for sensory structures, which do not relate to body size in the same way musculoskeletal structures do (see further discussion in Eiting et al., 2023 and Smith & Bhatnagar, 2004). More interestingly, trends in inner ear morphology potentially reveal ecological adaptations. For example, Dickinson et al. found that the complexity (spirality) of the cochlea is not predicted by body mass, and instead varies according to wing aspect ratio and therefore potentially with adaptation to flight in different habitats. In addition, some measurements of malleus dimensions were explained by diet, whereas some measurements of the incus were explained by call frequency, and not solely body size. These osteological features offer possible

ecological correlates that could be explored functionally in extant bats, or measured in fossil bats to make inferences about their ecology.

For a more complete picture of the sensory world of bats, a more thorough understanding of less studied senses may be beneficial, an avenue explored by several investigative teams in this issue. One important sense for most mammals is olfaction, and bats are no exception. Olfaction is used by many species of bats for foraging, mother-pup recognition, and even sexual selection (Hodgkison et al., 2013; Kunz & Hood, 2000; Voigt et al., 2008). In fact, studying olfactory structures (including the vomeronasal system) in bats was a keen interest of Prof. Bhatnagar, as exemplified by his early and many publications on the subject (e.g., Bhatnagar & Kallen, 1974a, 1974b, 1975; Bhatnagar & Smith, 2007; Meisami & Bhatnagar, 1998). An article in this special issue by Yohe and Krell (2023) dives into the olfactory system of bats through a genetic lens, thus linking detailed microanatomical work of Prof. Bhatnagar and colleagues with newer approaches to investigate ecomorphology. Yohe and Krell point out that modern genetic studies have uncovered intriguing links between genes related to the main and accessory olfactory systems and their phylogenetic distribution, often with a mismatch between these senses and what is known about the ecology of the species. Thus, they point out, there is an ever-apparent need to continue the detailed, comparative anatomical, functional, and ecological work that Prof. Bhatnagar would have enjoyed.

Numerous researchers have explored dietary correlates of olfactory anatomy in bats (e.g., Barton et al., 1995; Eiting et al., 2014; Frahm & Bhatnagar, 1980; Hall et al., 2021). The ethmoid bone, whose internal projections (turbinates) bear the majority of olfactory epithelium, is greatly variable in bats (Allen, 1882; Bhatnagar & Kallen, 1974b; Curtis et al., 2017, 2020; Eiting et al., 2014; Ito et al., 2021; Smith et al., 2012, 2021). Some of this variation reflects dietary adaptations, and this is most clearly manifested when examining bats broadly. For example, Bhatnagar and Kallen (1974a) revealed that frugivorous bats have larger olfactory bulbs and a greater number of olfactory foramina in the cribriform plate compared to insectivorous bats. A similar result was presented by Barton et al. (1995) who found frugivorous bats have relatively larger olfactory bulbs than non-frugivorous bats. In this issue, the validity of olfactory bulb volume as a proxy for olfactory abilities is supported by Eiting et al. (2023), who used statistical methods to take phylogenetic relationships into account, which is a method not available to Prof. Bhatnagar in his early comparative work. In their neuroanatomical study, Eiting et al. specifically find that frugivorous bats have relatively more olfactory sensory

neurons (within olfactory epithelium) and glomeruli within the olfactory bulb, compared to insectivorous bats. These structures are key players in the early neuronanatomical olfactory pathway, and they relate directly to computational processing capabilities in the olfactory system.

Across bats, the anatomy of the nasal region has long been known to vary greatly (e.g., Allen, 1882), and dietary correlates are less clear. For example, the size of the olfactory recess, the cul-de-sac that houses most of the olfactory epithelium in many mammals (Craven et al., 2010), does not covary with other anatomical features that are proxies for “olfactory reliance” in phyllostomid bats (Eiting et al., 2014). Further, Eiting et al. (2015) found that nasal airflow patterns in phyllostomids cannot be related to dietary specialization. Extreme variation in nasal anatomy, even seen at the family level, emphasizes the multifunctionality of the mammalian snout. Beyond olfaction, the snout or midface functions to condition inspired air, facilitate feeding (via dental morphology and/or snout shape), and in many bats acts in echolocation (Curtis et al., 2020; Santana, 2018; Santana et al., 2011; Smith et al., 2021). As of this date, we are far from a complete understanding of how these factors may result in midfacial variation in bats.

One contribution to bat olfactory anatomy in this special issue provides further insights. Hand et al. (2023) describe a fossil rhinonycterid bat from the early Miocene. Fossil rhinonycterids were very diverse, and they reveal morphological diversity exceeding that of the living species. One likely trend is a reduction in number and size of ethmoturbinates in this group. Combined with the observations of variable olfactory anatomy in other bat families, this finding is consistent with a hypothesis that ancestral bats had well-developed olfactory anatomy, and all extant families are undergoing adaptive changes to the midface that broadly reflect constraint on visual system and selection for anatomy facilitating echolocation (Thiagavel et al., 2018).

The continued internal exploration of bat sensory systems will eventually allow a comprehensive picture of sensory ecomorphology in bats. As of now, the majority of our understanding is centered on auditory specialization and vision, and phylogenetic analyses suggest that echolocation is an ancestral feature of bats, and with a trade-off for reduced vision (Thiagavel et al., 2018); within bat families, there are “über” specialists in echolocation who appear to have the most extremely diminutive visual systems (Arbour et al., 2021; Thiagavel et al., 2018). This raises the question, are other sensory systems facilitated or constrained in bats? Regarding the olfactory apparatus of the midface, is it also diminished as a consequence of specialization for echolocation? This remains unclear due

to the relative deficiency of information on olfactory anatomy compared to some other senses.

6 | THE FLIGHT PATH CONTINUES

Prof. Kunwar Bhatnagar's dedication to science and his wide-ranging biological interests entailed decades of inquiry, often in collaboration, and inspired many to pursue similar paths. This special issue reveals the complex picture of bat biology that long interested him, including fascinating flight adaptations such as rapid fore limb development, ear specializations relating to echolocation, and enhanced senses that allow bats to exploit nocturnal niches in virtually every part of the world.

AUTHOR CONTRIBUTIONS

Timothy D. Smith: Conceptualization; writing – original draft; writing – review and editing. **Sharlene E. Santana:** Conceptualization; writing – original draft; writing – review and editing. **Thomas P. Eiting:** Conceptualization; writing – original draft; writing – review and editing.

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