

Flight and echolocation in the ecology and evolution of bats

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Bats (Order Chiroptera) are a diverse group presenting variations on a single basic theme: a flying mammal. Today, 927 species of bats are classified in two suborders: the Megachiroptera of the Old World tropics, and the cosmopolitan Microchiroptera (Box 1). Although most bats are insectivorous, they show an impressive diversity of feeding habits, including frugivores, nectar-feeders (nectarivores), those that prey on small vertebrates (including fish), and three species of vampires that eat only blood.

Several life history features distinguish chiropteran species from other small mammals: smaller size, longer lifespans, lower rates of predation, smaller litter sizes, longer gestation periods and slower growth¹. Many of these characteristics may be linked to flight and echolocation, the two basic attributes of the Microchiroptera.

The coupling between echolocation and flight in bats

Some of the work on bat flight has examined the relationship between wing morphology, foraging behaviour and flight style^{2,3} (Box 2). Similarly, the study of echolocation in bats has shown a close match between the type of echolocation and the ecological features of bats, particularly their diet and foraging strategy^{4,5} (Box 3). In spite of the clear relationship between flight and echolocation, until recently, few researchers have integrated both into ecological studies⁶. Even then, flight and echolocation have been viewed as traits that could evolve independently, albeit constrained by ecological requirements because some combinations of wing morphology and echolocation system are more adaptive than others.

Both flight and echolocation are energetically expensive⁷⁻⁹, so a flying, echolocating animal could face severe constraints unless it reduces energy expenditure somehow. Echolocation adds no extra cost to flying European pipistrelles, even though, when roosting, these bats expend 0.067 joules per echolocation pulse⁸. Since echolocating bats searching for airborne targets produce an echolocation pulse every 50 to 300 milliseconds (ms), the sound production side of echolocation could be expensive. Sound emission is synchronized with exhalation and with the upstroke phase of the wingbeat cycle, coinciding with the greatest force pulling the wing, and with contractions of the abdominal muscles, which exert pressure on the diaphragm^{9,10}. This synchronization of wingbeat and vocalization reduces the cost of echolocation associated with pulse production, at least in bats emitting high intensity calls. An analysis of the scaling of wingbeat frequency and echolocation pulse repetition rate with body mass (using data from field studies)

Flight and echolocation are key characters distinguishing most bats from other mammals. The number of ecological niches for bats is limited by the concurrent constraints of the mammalian physiology and reproductive system and the high cost of flight and echolocation. The recent discovery of a biomechanical coupling between echolocation and flight highlights the need to incorporate both characters as parts of a single adaptive complex in future research on the ecology and evolution of bats.

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showed that most insectivorous bats searching for airborne prey produce one or fewer echolocation pulses per wingbeat¹¹. Gleaning bats emit several echolocation calls per wingbeat, but their calls are of lower intensity, and presumably of lower energetic cost.

The discovery of the coupling of echolocation, respiration, and flight in bats that feed on airborne prey obliges us to reconsider the impact of echolocation and flight on the ecology, behaviour and evolution of bats¹². Here, we focus on the role of flight and echolocation in determining the size and morphology of the Microchiroptera, the structuring of their communities, and their origin and evolution. An additional comparison with the Megachiroptera provides a perspective on the relative

impact of flight and echolocation on the appearance and behaviour of bats.

Size and shape in bats

Morphology of bats

Ecomorphology – the analysis of size and shape in plants and animals to infer ecological features – has been successfully applied to the study of bats¹. Ecomorphological research assumes that organisms are shaped by the concurrent effects of their ecological requirements and their evolutionary backgrounds. Bats provide obvious examples, such as the elongated muzzles of nectarivores, the reduced postcanine dentition of vampires, or the ways in which flight and echolocation affect the appearance of their wings and faces.

Species in six families of echolocating bats have noseleaves, conspicuous facial ornaments projecting upwards from the nostrils¹³ (Fig. 1d–1f). Experiments with the short-tailed fruit bat have shown that the noseleaf helps in the transmission of echolocation signals¹⁴. In phyllostomids, species that use echolocation for detecting prey (insectivores and some carnivores) have more developed noseleaves than frugivores, nectarivores and vampires, all species that rely on echolocation mostly for orientation¹³. Despite this correlation between diet and noseleaf morphology, the connection to echolocation and foraging behaviour is not clear¹⁵. The pinnae (external ears) of some bats also reflect echolocation (Fig. 1). A comparative study of 47 species demonstrated three patterns of ear shape¹⁶. In high-duty-cycle bats (Box 3) and some free-tailed bats, the pinnae are mechanically tuned to the sound frequency dominating the echolocation calls. In comparison, the large ears of gleaning bats are most sensitive to lower frequency sounds (<10 kHz), such as those associated with prey movement or prey calling¹⁷ (Fig. 1c). Finally, the pinnae of bats using broadband

Box 1. Common and scientific names of bats mentioned in the text

Order Chiroptera

Suborder Megachiroptera

Pteropodidae

Egyptian fruit bat (*Rousettus aegyptiacus*)

Indian flying fox (*Pteropus giganteus*)

Suborder Microchiroptera

Superfamily Emballonuroidea

Craseonycteridae

Bumblebee bat (*Craseonycteris thonglongyai*)

Emballonuridae

Blackhawk bat (*Saccolaimus peli*)

Superfamily Rhinolophoidea

Hipposideridae

Commerson's leaf-nosed bat (*Hipposideros commersoni*)

Megadermatidae

Ghost bat (*Macroderma gigas*)

Rhinolophidae

Horseshoe bats (*Rhinolophus* spp.)

Superfamily Phyllostomoidea

Mormoopidae

Parnell's moustached bat (*Pteronotus parnellii*)

Phyllostomidae

Bennett's spear-nosed bat (*Mimon bennettii*)

Big-eyed bat (*Chiroderma villosum*)

Greater spear-nosed bat (*Phyllostomus hastatus*)

Linnaeus' false vampire bat (*Vampyrum spectrum*)

Little long-eared bat (*Micronycteris megalotis*)

Long-tongued bat (*Glossophaga soricina*)

Short-tailed fruit bat (*Carollia perspicillata*)

Superfamily Vespertilionoidea

Molossidae

European free-tailed bat (*Tadarida teniotis*)

Underwood's mastiff bat (*Eumops underwoodi*)

Vespertilionidae

European pipistrelle (*Pipistrellus pipistrellus*)

Giant house bat (*Scotophilus nigrita*)

Mexican long-eared bat (*Plecotus mexicanus*)

Naked bat (*Cheiromeles torquatus*)

Western pipistrelle (*Pipistrellus hesperus*)

echolocation calls, like those of non-echolocating pteropods, show no evidence of mechanical tuning to any sound frequencies.

The relationship between wing morphology and diet, foraging strategy and other ecological features has been studied by Norberg and her collaborators^{2,3} (Box 1). If echolocation and flight are parts of a single adaptive complex, wing morphology and echolocation features should correspond, as is the case with carnivorous bats¹⁸. A combination of morphological characters (large body mass, low wing loading, low aspect ratio) and echolocation calls (short duration, low intensity and high sound frequency) distinguishes

Box 2. Size and shape of bat wings

Chiropteran wings can be described quantitatively by three parameters, wing loading, aspect ratio and wing tip index². **Wing loading** ($WL = W/S$, where W is the bat's weight, and S is the area of the wing elements) measures the force per unit area that wings must support during flight. The **aspect ratio** ($AR = b/c$, where b is the wing span, and c is the mean width of the wing elements) measures the shape of the wings by quantifying their relative length. **Wing tip indices** measure the shape of the tips of the wing; high values of the indices correspond to wings with rounded or squarish tips, whereas low values are typical of more-pointed wings.

The type of flight and foraging habitat of bats correspond closely to the size and shape of the wing elements³. For example, free-tailed bats (Molossidae), which are fast fliers and forage in open areas, have wings that are relatively small (i.e. with a high wing loading) and long (i.e. with a high aspect ratio). Conversely, gleaners (species that prey on insects or small vertebrates that they capture from a surface) possess wings that are large (low wing loading) and relatively short (low aspect ratio). They can fly slowly within vegetation, carrying heavy weights.

bats that feed on small vertebrates from other species. None of these features by itself, however, clearly discriminates carnivores from other bats¹⁸.

The diversity of the behaviour, ecology and morphology of echolocating bats presents excellent opportunities for further comparative studies, and the detailed phylogenies available for some groups will make it possible to place such studies in an evolutionary context. For example, molecular data show that the subfamily Phyllostominae, which traditionally includes all of the phyllostomid gleaners, is polyphyletic¹⁹. If so, then gleaning and the associated morphological, behavioural and echolocation traits may have evolved several times in this family, and the similarities between species could be examples of convergence rather than of parallel evolution.

Why are bats so small?

Bats are small mammals (Fig. 2), ranging in adult mass from 2 g (bumblebee bat) to 1500 g (Indian flying fox). Winged vertebrates can attain larger sizes, as indicated by birds and pterosaurs, showing that flight alone does not limit body size in bats. Why are bats so small? Variation among feeding and taxonomic groups of bats suggests that the answer reflects present ecological factors and historical evolutionary constraints, particularly factors associated with flight and echolocation.

Aerial-feeding insectivorous bats are particularly small, with most species weighing less than 30 g as adults, and with only four species (naked bat, blackhawk bat, giant house bat and Commerson's leaf-nosed bat) weighing more than 100 g. The morphological constraints imposed by the agility necessary for capturing flying insects might limit the size attainable by aerial insectivores. Bats with low wing loading are more manoeuvrable and, because wing loading is proportional to mass^{1/3} for similarly shaped bats, smaller animals have lower wing loading than larger ones. This relationship implies that smaller bats should be more efficient at capturing airborne prey, and could explain why aerial insectivorous bats and birds tend to be small².

The effective range of echolocation may also constrain the size of bats using this behaviour to search for, detect and assess airborne targets²⁰. Larger insectivorous bats tend to use echolocation calls dominated by lower frequency sounds, which are well suited for detecting large targets but not small ones. Furthermore, larger sized bats have higher wing loading so they are not manoeuvrable or agile enough to respond to and capture small prey detected at short range. The combination of mechanical constraints associated with flight and the operational range of echolocation might limit the size of aerial insectivorous bats²⁰.

The coupling of flight and echolocation imposes yet another constraint to body size¹¹. Because echolocation call-emission and wingbeat are synchronized, and because larger bats have lower wing-beat frequencies owing to allometric constraints, larger bats have lower call-repetition rates than smaller individuals. In the extreme case, a very low pulse-repetition rate would impair the ability of a very large bat to detect flying insects¹¹. Therefore, there should be a limit to the size of aerial insectivorous bats imposed by the mechanics of flight and the efficiency and energetic cost of echolocation¹¹.

These theories for small size in insectivorous bats are supported by field data on echolocation and behaviour of bats^{11,20}. In general, smaller bats produce higher frequency echolocation calls, allowing them to detect and track both small and large insects^{11,21}. Larger bats, in contrast, depend on large insects for food. Commerson's leaf-nosed bat, for example, uses echolocation calls that are dominated by 60 kHz

sounds in order to detect and track its prey, usually large (10–15 g) flying dung beetles²². An exception to the rule is the naked bat, an insectivore that produces echolocation calls at sound frequencies higher than expected for a bat of its size, and that can feed on small insects, despite its very large size (170 g) and high flight speed²³.

Other large insectivorous bats can escape from energetic constraints by feeding on large moths. Moths are among the largest insects, but many have ears sensitive to sounds in the 20–60 kHz range (the bandwidth most often used by echolocating bats, particularly those broadcasting high-intensity calls while searching for airborne prey). These moths are capable of avoiding predation by bats by hearing their echolocation calls^{24,25}. There are two ways to thwart this hearing-based defence. First, the European free-tailed bat uses echolocation calls with peak energy in the 11–12 kHz range, sounds below the frequencies to which moths' ears are most sensitive. This bat feeds heavily on moths because the insects detect it when it is too late to evade the attack²⁶. Second, the short and weak echolocation calls of gleaner bats make them less conspicuous to insects with hearing-based defences^{11,27}. Gleaners range in size from about 6 g (e.g. the little long-eared bat) to over 150 g (ghost bat, Linnaeus' false vampire), and some take much larger moths than aerial-feeders of equivalent size²⁸.

Bat communities and faunas

A current topic in ecology is the relative role of local (ecological) and regional (historical) factors in determining the composition and structure of biotic communities. The analysis of echolocation data and wing morphology provides important clues for understanding the forces that shape bat assemblages, where differences in these features between species reflect different strategies of resource use. There is a close relationship between morphology and diet in some communities of insectivorous bats¹, and a case of partitioning of sonar frequencies, presumably associated with a partitioning of feeding resources, has been reported for an assemblage of Malaysian rhinolophids²⁹.

Using bivariate plots of wing loading versus aspect ratio (see Box 2), McKenzie and Rolfe³⁰ identified distinct guilds in Australian woodland bat communities. Species that flew in the same stands tended to have different morphologies, indicating ecological displacement reflected by foraging behaviour and habitat selection. A new dimension to the study of bat communities was added by including echolocation call data^{6,31}, which permitted a better understanding of the mechanisms allowing the coexistence of insectivorous bats. Aldridge and Rautenbach⁶ viewed flight and echolocation as manifestations of the same adaptive complex and found significant correlations between wing morphology (as measured by wing loading, aspect ratio and wing-tip index; see Box 2) and type of

Box 3. Echolocation in bats

All microchiropterans and one pteropodid (Egyptian fruit bat) orient by echolocation, and some microchiropterans also use echolocation to detect, track and assess airborne targets. Egyptian fruit bats use tongue clicks to generate echolocation sounds, while microchiropterans use vocalizations produced in the larynx to generate tonal signals showing structured changes in frequency over time. Most bats use ultrasonic (>20 kHz) echolocation calls that, because of their wavelengths, provide better resolution of target detail. Some bats, usually larger species, use echolocation calls that are audible to humans (<20 kHz).

Echolocation signals can be broadband or narrowband. Broadband or FM (frequency modulated) calls span a range of sound frequencies (bandwidths up to 100 kHz), while narrowband or CF (constant frequency) calls are almost pure tones, with bandwidths of <5 kHz. Microchiropterans that hunt airborne prey use a combination of broad- and narrowband calls. Some bats use high intensity, energetically expensive echolocation calls (>110 dB SPL at 10 cm); others, the 'whispering bats' use calls of lower intensity (60 db SPL at 10 cm).

The 130 species of horseshoe and Old World leaf-nosed bats and Parnell's moustached bat emit echolocation calls separated by brief periods of silence – a high-duty-cycle system with calls produced over 50% of the time. The remaining echolocating microchiroptera and Egyptian fruit bats produce echolocation calls separated by long periods of silence – a low-duty-cycle system with calls produced 20% of the time.

echolocation calls (as measured by the characteristic frequencies and the 'shape' in a sonagram). They identified four groups of insectivorous bats based on correlated features of foraging behaviour, echolocation calls and wing morphology.

Evidence of the role of regional factors in shaping bat communities is revealed by morphological structure, as well as by taxonomic and trophic composition, which show that local assemblages of New World bats are random subsamples of the whole neotropical fauna. This applies when the local faunas of eastern Brazil and the Yucatan peninsula in Mexico are compared with regional pools, the South American bat fauna and the fauna of south-eastern Mexico, respectively^{32,33}. Bivariate plots of aspect ratio and wing-tip indices demonstrate more morphological overlap within neotropical assemblages than in Old World communities³⁴. Additionally, neotropical communities are characterized by

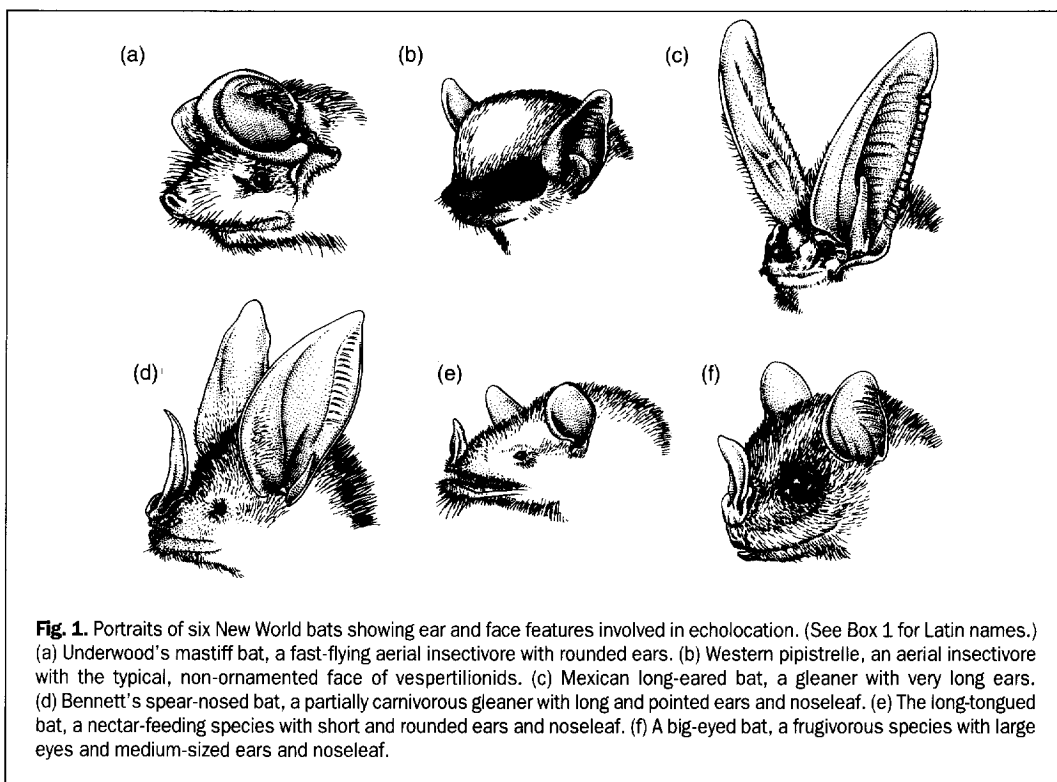


Fig. 1. Portraits of six New World bats showing ear and face features involved in echolocation. (See Box 1 for Latin names.) (a) Underwood's mastiff bat, a fast-flying aerial insectivore with rounded ears. (b) Western pipistrelle, an aerial insectivore with the typical, non-ornamented face of vespertilionids. (c) Mexican long-eared bat, a gleaner with very long ears. (d) Bennett's spear-nosed bat, a partially carnivorous gleaner with long and pointed ears and noseleaf. (e) The long-tongued bat, a nectar-feeding species with short and rounded ears and noseleaf. (f) A big-eyed bat, a frugivorous species with large eyes and medium-sized ears and noseleaf.

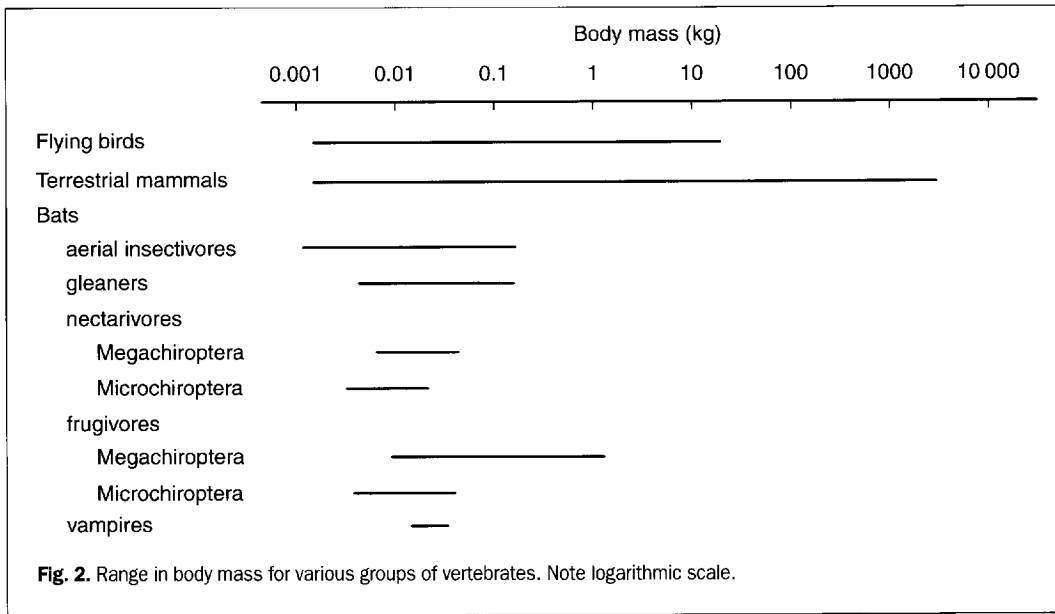


Fig. 2. Range in body mass for various groups of vertebrates. Note logarithmic scale.

the high diversity of 'whispering bats' (mainly phyllostomids) that have radiated to include gleaning, plant-visiting and haematophagous species. The situation suggests the importance of the history of invasions of the New World by bats and supports the idea that the composition and structure of bat communities are determined primarily by regional, historical factors more than by local interactions¹.

The origin and evolution of bats

The evolution of flight and echolocation

Recently, two theories about the evolution of flight and echolocation in Microchiroptera have been proposed, the flight-first and echolocation-first theories, which agree that

bats arose from gliding, nocturnal insectivores that echolocated using the echoes of short, broadband clicks produced at low-duty cycles (Fig. 3, Box 3). The theories differ in the proposed sequence and timing of the evolution of flight and echolocation.

The flight-first theory² proposes that bats evolved from primitive climbing insectivores that ate arthropods, which were located and captured on the substrate. The immediate ancestors of bats developed gliding for transportation and used echolocation in orientation. Even after the evolution of flight, lack of manoeuvrability precluded the capture of airborne prey. Improved manoeuvrability was followed by the perfection of echolocation for detecting, tracking and assessing airborne targets. The combination of echolocation and manoeuvrability opened new niches for bats, and promoted their adaptive radiation.

The echolocation-first theory³⁵ argues that the ability to use echolocation to detect, track and evaluate flying insects evolved before flight with the appearance of the stronger signals necessary to increase the effective range of echolocation. This theory proposes that gliding protobats hunted from perches, using echolocation to detect airborne prey that was captured in the air.

Both theories are coherent with current knowledge on echolocation and flight. However, the mechanical coupling of flight and echolocation would support the flight-first hypothesis, as it implies that sophisticated echolocation could have evolved only as a system linked to a well-developed flight mechanism. The fossil record provides no evidence in favour of either theory, as the oldest bat fossils from the Eocene show wing morphology and basi-cranial structure that suggest fully developed flight and echolocation capabilities³⁵.

Are megachiropterans 'bats'?

Pteropodids (with the exception of Egyptian fruit bats) do not echolocate and have simple ears and faces that lack conspicuous ornamentations such as noseleaves. As frugivores and nectarivores, megachiropterans are the Old World equivalents of some phyllostomids, although they differ in appearance, echolocation ability and

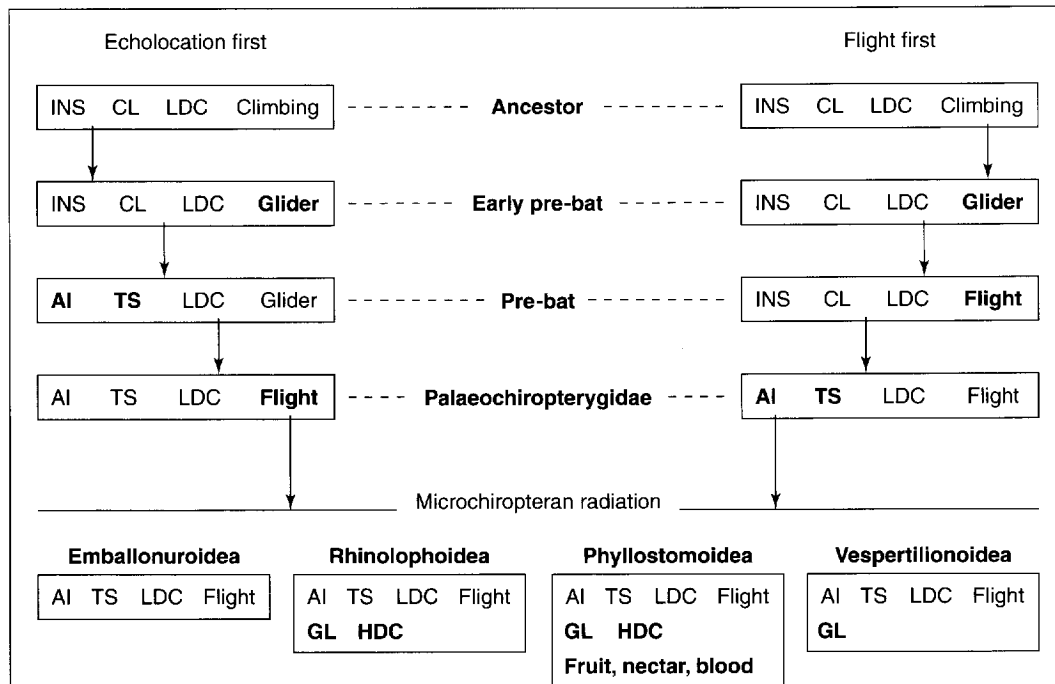


Fig. 3. Evolution of echolocation and flight in the Microchiroptera according to the echolocation-first (left) and flight-first (right) hypotheses. Both theories consider an insectivorous, climbing ancestor that, through a series of evolutionary events, gave rise to a stage corresponding to the Palaeochiropterygidae, a fossil family from the Eocene. The subsequent microchiropteran radiation gave rise to the four modern subfamilies: Emballonuroidea, Rhinolophoidea, Phyllostomoidea, Vespertilionoidea. Diet: INS, non-flying insects; AI, airborne insects; GL, insects or small vertebrates captured from surfaces (gleaning). Type of echolocation sound: CL, clicks; TS, tonal signals. Duty cycle: LDC, low-duty cycle; HDC, high-duty cycle. Symbols in bold indicate the origin of new traits.

size. Both nectar-feeding pteropodids and phyllostomids are small, with adult masses of <50 g. The small size in nectarivorous bats can be explained by energetic constraints related to a diet of nectar and pollen, and by the type of foraging behaviour shown by these bats. While some phyllostomids can hover, the flower-visiting megachiropterans tend to hang while feeding. Hovering would be too expensive for a large bat, and flowers simply could not support the weight of a very large pteropodid^{2,7}.

The largest fruit-eating bats are pteropodids, and many of them are at least twice as large as the biggest fruit-eating phyllostomid, the greater spear-nosed bat (150 g). This difference in size suggests that echolocation might also represent a size-constraint for non-insectivorous bats. However, very little is known about the role of echolocation in the lives of phyllostomids⁵, so it is not clear why phyllostomid frugivores are so much smaller than their pteropodid counterparts.

But are megachiropterans 'bats' like the microchiropterans? Pettigrew has proposed a diphyletic origin of bats, with megachiropterans being the sistergroup of primates, rather than of microchiropterans³⁶. The conventional view has been that mega- and microchiropterans are sistergroups that diverged very early in their evolutionary history³⁷. Neither theory on the evolution of flight and echolocation addresses directly the question of the monophyly or diphyly of bats, and in fact both theories could be adjusted to any of the two scenarios of the early evolution of bats. If both suborders evolved from a common ancestor, then flight has appeared in mammals only once. In this case, according to the echolocation-first theory, echolocation was lost early in the megachiropteran line and evolved later in the genus *Rousettus*. According to the flight-first theory, echolocation would have been lost in all megachiropterans, except Egyptian fruit bats, which would have retained the primitive system based on clicks. If bats are diphyletic, flight appeared twice in the evolution of mammals and echolocation may have evolved independently in the Microchiroptera and the Megachiroptera.

The controversy regarding the mono- or diphyly of bats remains open. Because morphological and molecular data have led to contrasting conclusions^{36,37}, only a thorough analysis could tell whether megachiropterans are true 'bats'.

Perspectives

Flight and echolocation have a considerable impact on the ecology of bats. If body size is constrained by the energetic needs imposed by flight and echolocation, then these two features indirectly affect all aspects of the ecology of bats, because body mass is strongly correlated with most life history parameters of vertebrates. Recent discoveries, such as the presence of folivory in bats despite the energetic constraints limiting the evolution of leaf-eating in flying animals³⁸, and Barclay's³⁹ theory of calcium as a limiting resource for the reproduction of flying animals, particularly insectivorous bats, show that our understanding of how flight and echolocation affect the ecology and evolution of bats is still rudimentary. Future research should take into account that the lives of bats cannot be understood without considering the effects of flight and echolocation.

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Evolution of genital masculinization: why do female hyaenas have such a large ‘penis’?

Laurence G. Frank

Why would evolution create a reproductive organ so hazardous that 9–18% of females die during their first birth, and those that survive lose over 60% of their first-born young^{1,2}? Since Aristotle, natural historians and scientists have been challenged to explain the extraordinary genitalia of the female spotted hyaena (*Crocuta crocuta*). Although disparate mammalian taxa show some degree of clitoral enlargement³, in none is it so fully masculinized as in this species. The female has no external vagina; rather, the urogenital canal traverses the hypertrophied clitoris, which resembles a penis in size, shape and erectile ability (Fig. 1). The glans clitoridis differs from the glans penis in being blunt rather than pointed and lacking a distinct constriction at the base⁴. In place of the vulva is a scrotum-like sac, filled with fat and connective tissue. Internally, however, the gross anatomy of the female reproductive tract is unexceptional. The female mates and gives birth through the peniform clitoris. In the prepubertal clitoris, the urogenital canal is only slightly larger than that of the penis. At puberty, however, the female canal enlarges and becomes elastic⁵ to allow mating, which is facilitated by a pair of robust retractor muscles⁶ that enable the female to retract the phallus upon itself, much as one pushes up a shirt sleeve, forming a hole which permits the male to achieve intromission.

Since 1877, anatomical studies have disproved the ancient belief that the spotted hyaena is hermaphroditic, bearing

In place of a ‘normal’ external vagina, female spotted hyaenas bear a fully erectile, penis-sized clitoris through which they mate and give birth. Early hypotheses on the evolution of this organ have focused on its signal function, because the erect phallus is used by both sexes as part of submission or appeasement displays. However, a quite different hypothesis is suggested by recent data on the ecological function of female aggressiveness, and on the role of androgens in the development of aggressiveness and male genital development. In this view, the female phallus may have originated as an unselected side effect of selection for androgen-mediated bellicosity, a major advantage in the extraordinarily competitive hyaena social system.

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both sexes simultaneously or sequentially⁷. Because neither soft anatomy nor behavior leave a fossil record, we do not know when masculinized females first evolved from a more prosaic ancestor. Several hypotheses have been proposed to explain the adaptive function of the bizarre female genitalia, but none is supported by data.

Field studies on the reproductive payoffs of female social rank lead to the hypothesis that the modern spotted hyaena is the result of selection for aggressive females in an exceptionally competitive social system. Laboratory studies on the hormonal basis of hyaena masculinization suggest that prenatal androgen exposure is responsible for both the aggressive nature of females, and their male-like anatomy. In this view, masculinized genitalia originated as an unselected by-product of prenatal androgens. Resolution of the endocrine mechanisms underlying female masculinization may

identify the mutational events responsible for this unusual suite of characters.

Hyaena ecology and social organization

Anatomical masculinization in the female spotted hyaena is associated with a social system characterized by near-absolute female dominance over males. Females are much more aggressive than males, dominating them in nearly all social situations⁸ such that even the lowest ranking females are able to displace the highest ranking adult males. Females