

Evolution of nocturnality in bats: Potential competitors and predators during their early history

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Despite their taxonomic and ecological diversity, modern bats (Order Chiroptera) are almost exclusively nocturnal. This behaviour is too ubiquitous to be explained by common patterns of temporal variation in availability of their diverse food sources or by the risk of hyperthermia when flying during the day. Other explanations for bat nocturnality include competition and increased predation risk from birds during the day. In the early and mid Eocene, the known bat fauna consisted of several insectivorous species of sizes similar to those of the modern European assemblage. This fauna was contemporaneous with several species of predatory birds, including owls (Strigiformes), hawks (Accipitridae), falcons (Falconidae) and rollers (Coraciiformes), which were the same size as modern predators on bats. Predation risk could therefore have been a significant factor preventing the early bats from becoming diurnal. Competition from aerial insectivorous birds, however, was less likely to have been significant for bats during the early Eocene, since very few such groups, mainly small Aegialornithidae, were present, with most of the major groups of aerial insectivores evolving later.

ADDITIONAL KEY WORDS:—Bat evolution · Eocene · insectivory · bird evolution · competition · predation.

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INTRODUCTION

The bats (Order Chiroptera) comprise the second largest order of mammals, with nearly a thousand (977) species (Corbet & Hill, 1991). Despite their taxonomic and ecological diversity, it is remarkable that almost all the bats are

exclusively nocturnal. Exceptions are few, occurring for example on some oceanic islands (e. g. Moore, 1975; Cox, 1983), and occasionally in temperate areas (Speakman, 1990).

The nocturnal activity patterns of bats do not always coincide with peak availability of food. For instance, fruits, which are eaten by many Old World fruit bats (Pteropidae) and Neotropical leaf-nosed bats (Phyllostomidae), are presumably just as available in daylight as during the night. Likewise, the activity of insects, at least at high latitudes in temperate areas, is usually highest during the late afternoon or early in the evening before it gets dark and before the bats start to fly (Rydell, 1992; Speakman, 1995). Nocturnality in bats is too ubiquitous in such a diverse group of animals to be explained by coincident temporal variations in the availability of the diverse food sources.

Other functional explanations of nocturnality in bats have focused on three potential disadvantages for bats that fly in daylight (Speakman, 1991a, 1995): First, bats that fly in daylight may face the risk of hyperthermia, because they may be unable to dissipate the endogenous heat generated in flight at generally higher daytime temperatures, at the same time as they receive radiant heat from the sun (Thomas *et al.*, 1991). Second, the insectivorous bats may be prevented from entering the diurnal niche by competition from aerial insectivorous birds (Thomas *et al.*, 1991; Tugendhat, 1966). Third, bats flying in daylight may be particularly susceptible to predation by avian predators (Speakman, 1993), possibly because bats are relatively slow fliers compared to aerial insectivorous birds (like swallows and swifts). Furthermore, most bats rely on echolocation, which, in comparison with vision, is more directional, has a shorter range and may therefore be less suitable for detection of approaching predators (Speakman, 1993). This latter argument cannot, however, apply to the Old World fruit bats (Megachiroptera), which are mostly visually oriented and non-echolocating and which comprise 17% of the current bat species (Corbet & Hill, 1991).

From a thermophysical model, Speakman (1995) has suggested that overheating may be a problem for very large bats (>90g) that fly in tropical or subtropical areas, but not, generally, for smaller bats or for any bat in overcast weather or above about 40° latitude. Hence, bat nocturnality seems to be too widespread to be explained by this hypothesis alone. Moreover, the hyperthermia hypothesis hinges critically upon the low albedo of bat wings (Speakman & Hays, 1992), and this morphological trait must be explained by other hypotheses. For example, Thomas *et al.* (1991) argued that competition with aerial insectivorous birds restricted bats to the nocturnal niche, where dark wings were advantageous to avoid predation. Hence, the problem of overheating then reinforced this restriction.

The evidence for the competition and predation hypotheses is equivocal. Current bats are sometimes observed in antagonistic interactions with insectivorous birds and they also become prey of diurnal avian predators (Speakman, 1991b). Current predation and competition may, however, bear little relation to the situation faced by bats during the early phase of their evolution, when different predators and competitors may have been present and the susceptibilities of the bats themselves may have been different too. In this paper we review the competitive and predatory environment faced by bats in Europe today, and compare this with the likely situation during the early history of the bats.

COMPETITIVE AND PREDATORY ENVIRONMENT OF BATS AT PRESENT

The risk of being taken by an avian predator is about two orders of magnitude higher for a small bat that flies during the day, compared to one that flies during the night (Speakman, 1991a). This indicates that predation risk may be a main factor currently restricting bats to the nocturnal niche. The most important avian predators of bats today are several species of owls, e.g. barn owls (*Tyto alba* L.) and tawny owls (*Strix aluco* L.) (e.g. Gillette & Kimbrough, 1970; Krzanowski, 1973; Ruprecht, 1979; Bekker & Mostert, 1991; Speakman, 1991b) and also the tropical bat hawks, (*Machaerhamphus* spp.), which are specialized bat predators (Black *et al.*, 1979).

The greatest threats to bats that fly in daylight do not come from owls and bat hawks, however, since these birds are mostly nocturnal or crepuscular, but from diurnal raptors, like small hawks (Accipitridae) and falcons (Falconidae). Some other diurnal birds like small gulls (Laridae) and crows (Corvidae) can also be important predators in daytime (Gillette & Kimbrough, 1970; Speakman, 1991b). Regardless of systematic affinity, most birds that prey on bats are relatively small members of their families; nine of the thirteen species known to feed on bats in Europe have body lengths between 25 and 40 cm (Fig. 1).

Most insectivorous birds that have been observed to interact antagonistically with daylight flying bats in Europe, and therefore may be considered to be potential competitors of bats, are either swallows (Hirundinidae) or swifts (Apodidae) (e.g. Tugendhat, 1966), which are 13–22 cm in body length. There is no evidence that perching insectivorous birds, like flycatchers or bee-eaters for example, interact antagonistically with bats or compete with them.

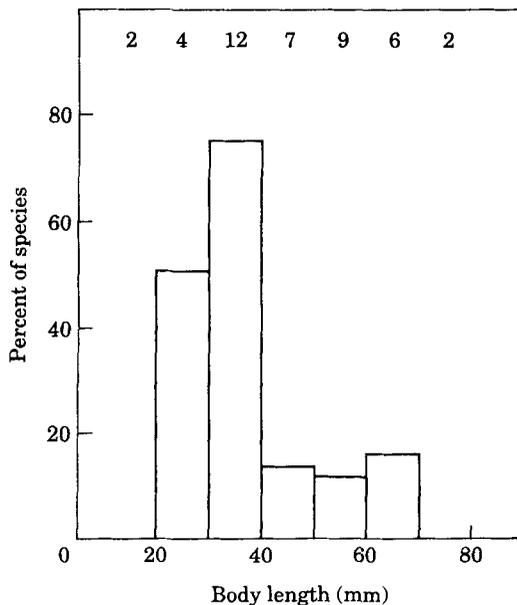


Figure 1. Frequency (%) of predatory land birds of Western Europe ($n = 42$) in different size classes that are known to prey on bats. The total number of species in each size class are indicated above the bars. Included are owls (Strigidae), hawks (Accipitridae), falcons (Falconidae), gulls (Laridae) and corvids (Corvidae). Evidence of predation on bats are from Speakman (1991a,b) and references therein.

THE OLDEST KNOWN BATS

The oldest known bats consist of fragmentary remains of *Icaronycteris* Jepsen (Icaronycteridae), *Archaeonycteris* Revilliod and *Palaeochiropteryx* Revilliod (Palaeochiropterygidae) from the late Palaeocene (MP7) of France and Belgium (Stucky & McKenna, 1993). The oldest complete bat fossil is *Icaronycteris index* Jepsen from the early Eocene (Wind River Formation) of Wyoming (Jepsen, 1966, 1970). Of slightly younger age (mid Eocene) is the rich fossil bed of the Messel Formation in Germany, where several hundred bat specimens, comprising seven species in three microchiropteran genera, have been found (Habersetzer & Storch, 1987, 1989; Habersetzer *et al.*, 1992). The bat species described from Messel and some of their morphological characteristics, together with those of *Icaronycteris index*, are given in Table 1.

Icaronycteris, as well as the Messel bats, all belong to extinct families, but bats that can be assigned to recent families (Emballonuridae, Rhinolophidae, Vespertilionidae and Molossidae) also appeared already in the mid or late Eocene (Stucky & McKenna, 1993). The oldest described Old World fruit bat, or megachiropteran, *Archaeopterus transiens* Mesch., dates from the mid Oligocene (Habersetzer & Storch, 1987), but a recent find of a single tooth from late Eocene deposits of Thailand suggests that the group may be older (Ducrocq *et al.*, 1992).

The excellent state of preservation of *Icaronycteris index* and the Messel bats has permitted detailed analysis of their wings, basicranial features and the inner ear. In several species of the Messel bats, even the stomach contents are preserved and have been analysed. The wing forms of these bats indicate that their flight was already well developed, although some of them still retained some primitive features. According to Jepsen (1970), "*Icaronycteris index* was a true flier although it lacked many of the advanced specializations of some extant bats". Primitive characters also include a large number of teeth and a claw on the index finger (Jepsen, 1966). In the Messel bats, characteristics like size, wing loading and aspect ratio differed considerably among the three genera (Table 1). *Archaeonycteris trigonodon* Revilliod and *A. pollex* Storch & Habersetzer were intermediate in size and showed 'primitive' characters like *Icaronycteris*, with

TABLE 1. Six species of middle Eocene bats from Messel, Germany, and some of their (measured or estimated) characteristics together with those of *Icaronycteris index* from the early Eocene of the Wind River Formation, Wyoming. Data from Habersetzer & Storch (1987), Storch & Habersetzer (1988) and Habersetzer *et al.* (1992).

Bat species	Forearm (mm)	Body mass (g)	Wing loading (N/m ²)	Aspect ratio
<i>Icaronycteris index</i> (n = 2)	46-48	12-15	8.8-9.1	6.0-6.2
<i>Archaeonycteris trigonodon</i> (n = 3)	52-58	18-27	9.6-12.1	5.8-6.2
<i>A. pollex</i> (n = 1)	61	33	11.7	5.5
<i>Palaeochiropteryx tupaiodon</i> (n = 3)	39-46	7-10	6.9-9.1	6.1-6.9
<i>P. spiegelii</i> (n = 2)	43-49	10-13	8.0-9.7	6.2-6.6
<i>Hassianycteris messelensis</i> (n = 2)	64-72	32-37	15.3-15.5	6.9-7.3
<i>H. magna</i> (n = 1)	81	65	21.3	7.6

a claw on the index finger and an unspecialized wing form. *Palaeochiropteryx tupaiodon* Revilliod and *P. spiegelii* Revilliod, in contrast, were more advanced. They were small bats with wing forms indicative of slow and highly manoeuvrable flight, suitable for exploitation of structurally complicated habitats. *Hassianycteris messelensis* Smith & Storch, *H. magna* Smith & Storch and *H. revilliodi* (Russel & Sigé) were large species adapted for fast flight in the open air (Habersetzer & Storch, 1987, 1989; Storch & Habersetzer 1988, Norberg, 1989). The diversity in flight styles among the Messel bats, as indicated by their sizes and wing forms, was comparable to that of modern bat faunas (Habersetzer & Storch, 1989; Norberg, 1989). The Eocene bats were on average larger than current European bats, but all species except one fall within the size extremes of the latter assemblage (Fig. 2).

Icaronycteris and *Palaeochiropteryx* share several basicranial features and a relatively large cochlea with the echolocating Microchiroptera, but not with other mammals including the mostly non-echolocating Megachiroptera. This suggests that an echolocation capability was developed in the Eocene bats (Novacek, 1985). There is no evidence of an 'acoustical fovea', as in extant rhinolophids, hipposiderids and mormoopids, however (Habersetzer & Storch, 1989), which indicates that these bats did not employ narrowband echolocation in its most sophisticated form, as would have been required for efficient echolocation close to vegetation (Neuweiler, 1989).

Analysis of stomach contents of the Messel bats has shown that *P. tupaiodon* fed almost exclusively on moths, mostly primitive families of Microlepidoptera, while *P. spiegelii* also fed on caddis-flies (Trichoptera). In the stomachs of *Hassianycteris* spp. and *Archaeonycteris* spp., beetle remains, probably from dung beetles (Scarabaeidae), were also found (Richter & Storch, 1980). Most extant representatives of these insect families are nocturnal.

Hence, by the early and mid Eocene, all the known microchiropterans were probably nocturnal and insectivorous, and had already become more or less specialized and diversified for sustained flight and echolocation in various aerial niches, which can still be recognized today.

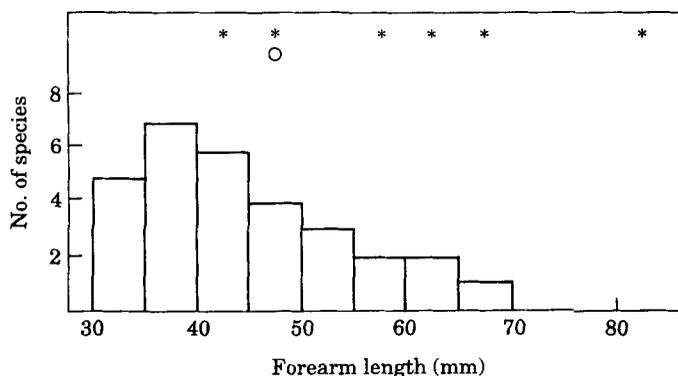


Figure 2. Size distribution (forearm lengths) of the Messel bats (asterisks) and *Icaronycteris index* (circle) in comparison with that of the current European bat fauna. Measurements are from Jepsen (1966), Habersetzer & Storch (1987), Storch & Habersetzer (1988) and Schober & Grimmberger (1987).

FOSSIL RECORDS OF POTENTIAL COMPETITORS

To be able to exclude the Messel bats, for example, from the diurnal insectivore niche by competition, the potential competitors must clearly have been capable of sustained flight and insect capture on the wing. Regardless of whether the competition mechanism included aggression (contest competition) or not (scramble competition), the potential competitors would also have needed to be common and sympatric with the bats. Hence, the only likely candidates for competitors are found among small birds, like hirundines and apodids, or, if it is assumed that the bats evolved during the Mesozoic (see below), possibly among the smaller Pterosaurs.

We examined the fossil record for evidence of representatives of the Hirundinidae or Apodidae and other, ecologically similar but extinct, bird families, during the Palaeocene and early Eocene. Passerines, including the Hirundinidae, did not appear before the Oligocene, and most modern forms did not appear until the Miocene and Pliocene (Olson, 1985). The hirundines, therefore, could not have influenced the early evolution of bats. The true swifts (Apodidae) apparently originated during the late Eocene (Unwin, 1993), but the earliest swift-like birds (Apodiformes), the extinct Aegialornithidae, appeared in the early Eocene and may have been aerial insectivores (Peters, 1992). The oldest representative of this family is *Primapus lackii* Harrison & Walker from the London Clay (Harrison & Walker, 1975). A similar form also occurs in the Green River Formation in Wyoming (Olson, 1985), and four individuals of another species *Aegialornis szarskii* Peters of the same family have been found in the Messel Formation (Peters, 1985). The first representatives of the Apodiformes were hence contemporaneous with *Icaronycteris* and the Messel bats.

There are two reasons why we suspect that the Aegialornithidae of the early and mid Eocene did not, however, affect the behaviour of the early bats. First, the abundance of bats among the Messel fossils, for example, exceeds that of the Aegialornithidae by two orders of magnitude, suggesting that these birds were uncommon compared to the bats, at least in that place. Second, early and mid Eocene aegialornithids were all very small (size of medium to large hummingbirds; *A. szarskii* from Messel was about 7 cm long), and probably also less specialized for sustained flight than extant swifts (Peters, 1992). Hence, these birds were probably too small to be significant contest competitors and not abundant enough to be significant scramble competitors of the Eocene bats.

POTENTIAL PREDATORS OF EARLY BATS

The fossil history of the owls (Strigiformes) goes back to the Palaeocene (Rich & Bohaska, 1976), from which two families (Sophiornithidae and Ogygoptingidae) are known (Unwin, 1993). Several owl families, including the Tytonidae, are known from the Eocene (Olson, 1985). The hawks (Accipitridae) and the falcons (Falconidae) both first appeared in the early Eocene deposits of southern England (Upper Bracklesham Beds and London Clay, respectively; Unwin, 1993). Indeed, one species of owl, *Palaeoglaux* sp., which is small (size of a little owl), but may in fact have been diurnal (since it had ornamental feathers), as well as a small, yet undescribed, hawk, which can be classified with the Accipitridae, have been found in the Messel deposits (Peters, 1992).

Hence, the predatory bird fauna was diverse already in the early Eocene, and may, therefore, have been a factor influencing the behaviour of the early bats.

The gulls (Laridae) and the corvids did not appear until the Oligocene and Miocene, respectively (Olson, 1985). On the other hand, some species of roller-like birds (Coraciiformes) could have been predators on Eocene bats. This group included the majority of the tree living birds in the early Tertiary, at least in the northern hemisphere. One group of roller-like birds (the 'Primobucconidae'), which had shortened digits and long, sharp claws, reminiscent of those of raptors and owls, has been suggested as being predatory (Peters, 1992). Several such birds have been found in Messel, as well as in the Green River Formation of Wyoming and elsewhere in North America (Olson, 1985; Peters, 1992). From published photographs of two such birds from Messel (Peters, 1992), it appears that at least these two were about 25 cm long, and hence of a size suitable for predation on bats.

MESOZOIC BIRDS AND PTEROSAURS

So far we have assumed that the bats radiated after the Cretaceous/Tertiary boundary, along with the other major mammalian groups, and in response to the vacation of niches by the dinosaurs (Eisenberg, 1981). However, it remains possible that bats evolved during the Mesozoic, because there was no obvious insectivorous dinosaur which could have restricted the evolution of bats from terrestrial or arboreal mammals (e.g. Weishampel *et al.*, 1990). Therefore, it is appropriate to examine the possibility that potential competitors and predators for bats existed during the Mesozoic.

The earliest birds, such as *Archaeopteryx lithographica* Meyer, descended from small theropod dinosaurs during the late Jurassic (Ostrom, 1976), and may have been insectivorous. Truly flying birds existed at least in the early Cretaceous (Unwin, 1988), but it is not clear if any Mesozoic birds were aerial predators or insectivores (Olson, 1985).

The small and presumably insectivorous pterosaurs, such as *Pterodactylus*, *Anurognathus*, *Sordes* and *Batrachognathus* for example (the Rhamphorhynchoidea), represent either late Triassic or Jurassic lineages, which became extinct before the Cretaceous. The subsequent Cretaceous pterosaurs (Pterodactyloidea) were all large, mostly fish catching, filter feeding or perhaps scavenging, forms (Wellnhofer, 1991). Therefore, it is unlikely that the Pterosaurs or early birds could have interfered with the evolution of bats, unless the bats radiated already during the middle of the Mesozoic era or earlier. In that case, small Pterosaurs could have been significant competitors or predators. These arguments, of course, imply that the aerial insectivore niche was either unfilled or non-existent during the Cretaceous period.

CONCLUSIONS

The presence of owls, small hawks, falcons and predatory roller-like birds during the early Eocene may have prevented the early bats from taking advantage of the diurnal insectivore niche. The predation hypothesis may therefore explain why bats did not evolve diurnal activity patterns. Assuming that the apparent absence of aerial insectivorous birds in the Palaeocene and

early Eocene, with the exception of the small Aegialornithidae, is real, and not an artefact of an incomplete fossil record or of a lag in the description of existing fossils, the competition hypothesis seems unlikely to be a general explanation for bat nocturnality.

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