

BEHAVIOR OF SCANDINAVIAN BATS DURING MIGRATION AND FORAGING AT SEA

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We studied bats migrating and foraging over the sea by direct observations and automatic acoustic recording. We recorded 11 species (of a community of 18 species) flying over the ocean up to 14 km from the shore. All bats used sonar during migration flights at sea, often with slightly lower frequencies and longer pulse intervals compared to those used over land. The altitude used for migration flight was most often <10 m above sea level. Bats must use other sensory systems for long-distance navigation, but they probably use echoes from the water surface to orient to the immediate surroundings. Both migrant and resident bats foraged over the sea in areas with an abundance of insects in the air and crustaceans in the surface waters. When hunting insects near vertical objects such as lighthouses and wind turbines, bats rapidly changed altitude, for example, to forage around turbine blades. The findings illustrate why and how bats might be exposed to additional mortality by offshore wind power.

Key words: bats, behavior, Chiroptera, flight altitude, foraging, migration, sea, sonar

Although we know a lot about bird migration, bats differ enough from birds to justify additional and different study designs. How bats fly during migration and how they cope with the energetic challenges of migration are virtually unknown.

The fact that some bats fly across areas of open sea is well known. Bats have been recorded on remote islands such as Iceland, the Faroe Islands, and also on ships and oil rigs in the North Sea (e.g., Baagøe and Bloch 1993; Koopman and Gudmundsson 1966; Petersen 1994; Russ et al. 2001; Skiba 2007; Stansfield 1966; Vauk 1974; Walter et al. 2007). Recoveries of ringed or banded bats (Gerell 1987) show that some bat species from the Scandinavian Peninsula hibernate on the European continent and therefore must migrate across large stretches of open sea. Ahlén (1997a) found large numbers of bats migrating from specific departure points along the coast of southern Sweden. Observations of migrating bats occurred at a number of localities where the bats do not occur in summer (Ahlén 1997b, 2006; Baagøe 2001, 2007c, 2007e). An investigation on bats in the context of existing and planned offshore turbines (Ahlén et al. 2007) gave us the

opportunity to survey for bats at sea on a scale not undertaken before. We provide a short description of these findings, specifically as they relate to migration behavior and other bat activity at sea.

MATERIALS AND METHODS

Our study took place in coastal areas and islands of the Scandinavian Peninsula and islands of southern Sweden and Denmark (approximately 54°–57°N and 11°–19°E; Fig. 1) from July to October of 2005, 2006, and 2008. We surveyed for bats on the islands of Gotland, Öland, Bornholm, Falster, Lolland, Saltholm, and Peberholm, and over the water of the Öresund, Kattegat, and Baltic Sea. Surveys also occurred from ships using strong spotlights. The distance from the nearest coast to observation sites at sea extended out to 14.2 km in Kalmarsund, 11.8 km in Öresund, 19.1 km in Kattegat, and 9.1 km at Bornholm. We used 38 nights for studies from boats (and some small islands) and made observations 4 h from sunset.

We recorded flying bats in a variety of ways, including portable incandescent spotlights and a Raytheon Palm IR PRO infrared thermal imaging camera (Raytheon Co., Waltham, Massachusetts) for visual observations, as well as both handheld and automated ultrasound detectors (Pettersson D920, D240×, and D1000×; Pettersson Elektronik AB, Uppsala, Sweden) to monitor echolocation calls. BatSound

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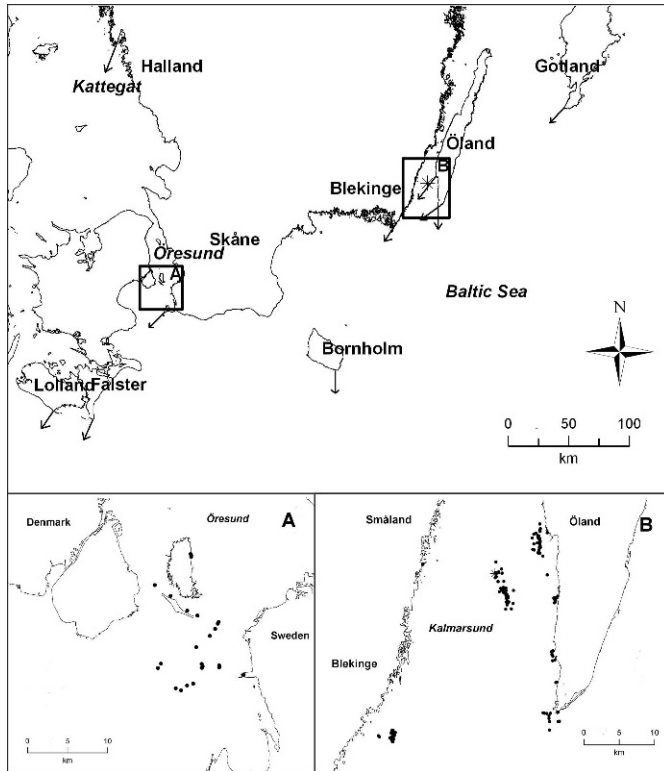


FIG. 1.—Areas in the southern Baltic Sea, Öresund, and Kattegat where observations of bats were made, showing departure sites on land (arrows) and squares A and B for the enlarged detail maps below of A) Öresund and B) Kalmarsund (B) with observation sites at sea (dots). Utgrunden lighthouse in Kalmarsund is marked by an asterisk.

software (Pettersson Elektronik AB, Uppsala, Sweden) was used to analyze echolocation calls and generate species identification following Ahlén and Baagøe (1999). We measured pulse frequency at maximum amplitude and interval length by the distance between corresponding points on sound pulses.

We tracked the flight routes and altitudes of some bats over water using a tracking radar system installed at Utgrunden lighthouse between Öland and the Swedish mainland (Ahlén et al. 2007). These observations were carried out during 18 nights from July to October in 2005 and 2006. The radar system consistently detected the largest species (*Nyctalus noctula*), but not smaller species (Ahlén et al. 2007). We used a global positioning system (RPDA 560; Andres Industries, Berlin, Germany) to record the precise coordinates of all observations.

Previous studies have attempted to locate coastal points in southern Sweden (Ahlén 1997a) and Denmark (Baagøe 2001, 2007c, 2007e) where bats depart land on migration. We identified departure points by direct observations of bats leaving land, by detecting accumulations of bats in coastal areas during poor weather (e.g., high winds or rain), and recording species not belonging to the summer fauna of the area. Activity and species composition of bats at departure points were assessed using spotlights and bat detectors. We also made observations from ships positioned offshore from known departure sites as well as other areas to determine

whether there were flyways over the sea. We recorded bats over the open sea in connection with a monitoring study at 2 groups of offshore wind turbines, some sea areas planned for construction of wind farms, and adjoining areas. We placed automated bat detectors on offshore wind turbines to remotely record echolocation calls. We also received reports on bats observed coming in from the sea by a network of ornithologists watching birds at the coasts in spring (Baagøe 2001).

It is not always possible to differentiate migration and commuting flight from foraging flights because bats sometimes combine the 2 flight styles. However, in most cases we could easily identify foraging flight by behavior and feeding buzzes. We define migratory or commuting flight as direct flight without foraging behavior.

We quantified the presence of insects at and over the water surface by subjectively estimating their abundance as not present, present in low numbers, or present in high abundance. Samples of both flying insects and crustaceans in the sea surface waters were taken by nets at the spots where we saw bats gaffing in the sea surface. Crustaceans were easily observed because they were so numerous that they almost covered large areas of the sea surface. Insects and crustaceans were identified by specialists at the Ecological Research Station on Öland (Uppsala University).

RESULTS

Arrival of bats in spring.—In spring, migrating bats arrive in the study area from southern latitudes at many coastal sites ranging from Lolland in the southwest to the east coast of Gotland. Widespread observations showed that northward migrating bats are widely dispersed and do not arrive in concentrated flyways. The distance from Gotland southwest to the German coast is about 400 km, whereas the nearest distances from Gotland and Öland to the Polish coast are 225 and 170 km, respectively. *Pipistrellus nathusii*, a common migrant over the southern Baltic Sea, flies at about 20 km/h (Baagøe 1987) meaning that migration flights would take 9–20 h. This is longer than the duration of the dark hours of night.

Departure points in autumn.—We identified a number of departure points where bats left land to migrate over the sea (Fig. 1). Accumulations of presumably migrating bats were found at other sites where we could not directly record departures from the coast. Migration activity observed at departure points differed between years and lasted from mid-August to early October. Peak activity varied with species, but usually occurred near the end of August. The maximum number of accumulating bats observed by using spotlights at departure points was assessed at approximately 250 individuals at the southern tip of Öland, but normally the size of the swarms ranged from a few to 20 individuals. In 2005 and 2006, we made 8,524 observations of 14 different species of bats over land at departure points (Table 1). Some of these species made no attempts to leave land and were never

TABLE 1.—Species of bats observed over the open sea and at departure points from land in Sweden and Denmark during 2005, 2006, and 2008. A total of 4,051 observations of 11 bat species were made out at sea and 3 additional species were observed at departure sites in the southern Baltic Sea areas, the Öresund, and in Kattegat.

Species observed	No. observations	Migratory or resident	Hunting mode
Out at sea			
<i>Myotis daubentonii</i>	93	Resident	Surface gaffer, aerial hawk
<i>Myotis dasycneme</i>	118	Migratory	Surface gaffer, aerial hawk
<i>Pipistrellus nathusii</i>	112	Migratory	Aerial hawk
<i>Pipistrellus pipistrellus</i>	5	Migratory	Aerial hawk
<i>Pipistrellus pygmaeus</i>	179	Partially migratory	Aerial hawk
<i>Nyctalus leisleri</i>	12	Migratory	Aerial hawk
<i>Nyctalus noctula</i>	277 (+2,989 by radar)	Migratory	Aerial hawk
<i>Eptesicus nilssonii</i>	112	Resident	Aerial hawk
<i>Eptesicus serotinus</i>	113	Partially migratory?	Aerial hawk
<i>Vespertilio murinus</i>	40	Migratory	Aerial hawk
<i>Plecotus auritus</i>	1	Resident	Gleaner, aerial hawk
Total	4,051		
Additional species only observed at departure sites 1993–2008			
<i>Myotis brandtii/mystacinus</i>			
<i>Myotis nattereri</i>			
<i>Barbastella barbastellus</i>			

recorded at sea. During the day, some bats were found roosting in houses, trees, and in small caves and crevices in rocky terrain near the takeoff points.

Flyways on land.—Flyways with many passing bats leading to departure points were found using automated bat detectors and visual observations. Bats often followed linear landscape features such as coastlines, forest edges, and in open country, stone dikes, or tree rows. On Gotland, flyways led to the west side of the southernmost point of the island (Hoburgen), and on Öland to the southernmost tip (Ottenby) and to a 2nd point on the western coastline where it makes an eastward bend (Eckelsudde). The same flyways and departure points were used between years.

Bat species found at sea.—During 2005 and 2006, we made 4,051 observations and documented 10 different species over the sea in the southern Baltic Sea and in Öresund between Denmark and Sweden. Additional observations were made off the northern coast of Bornholm in 2008 and an 11th bat species (*Plecotus auritus*) was recorded off the west coast of Sweden. This means that out of a total of 18 species of bats known for this part of Europe no less than 11 species were found at sea.

Flyways over the sea.—We observed greater levels of bat activity at sea adjacent to known departure points, consistent with there being flyways. We could identify to species >90% of all bats recorded with automated detectors on turbines and in most cases differentiate passing from foraging bats. Automated detectors recorded bats at all 12 offshore wind turbines monitored. The largest bat species in the study area, the noctule (*N. noctula*), could be tracked on radar (Fig. 2). Medium-sized *Vespertilio murinus*, observed from the boat, was detected by radar only on a few occasions. No other species we observed were simultaneously detected by radar. When leaving the coast, bats usually flew alone or in loose (scattered) groups of 2 or 3 individuals. We never observed groups that we considered flocks.

Sonar used at sea.—All bats recorded at sea by visual and acoustic monitoring generally used normal echolocation calls. Most were aerial hawking species with loud quasi-constant-frequency (QCF) or constant-frequency (CF) elements. *Myotis daubentonii* and *M. dasycneme* were recorded to hunt over and gaff prey from the water surface, and both species use frequency-modulated (FM) calls.

All QCF species exhibited changes in frequencies and interval lengths of calls compared to calls recorded over land. The frequency of QCF or CF pulses were usually near or slightly below the lower frequency range for the species compared to frequencies used over land, and call pulse

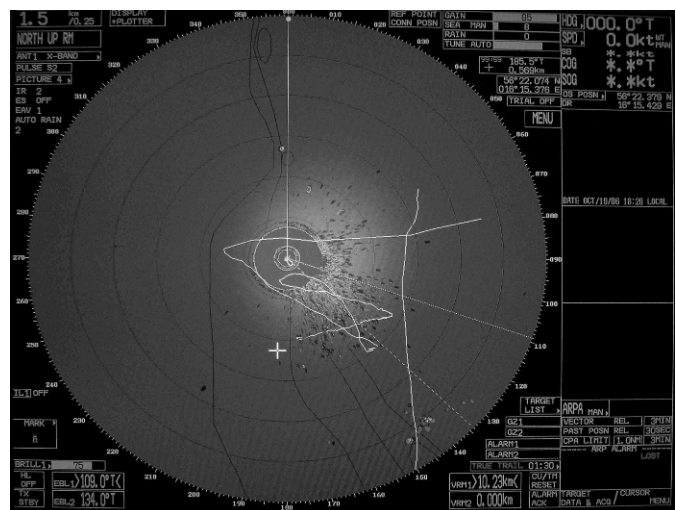


FIG. 2.—The radar screen at Utgrunden lighthouse (center) showing routes of 2 passing bats (*Nyctalus noctula*) on 19 October 2006 at 1820 h. Both individuals came from the northeast (upper right) and disappeared into the south–southwest and south. One just passed and the other obviously searched for insects. The radius of the radar-swept area is 1.5 km.

intervals were somewhat extended. For example, typical calls used on land by *Eptesicus nilssonii* have peak energy (amplitude) at 29–30 kHz, but in open areas or over lakes it can range as low as 26–27 kHz. Over the ocean, calls from 26 to 27 kHz were common. Pulse intervals of *E. nilssonii* on land are about 200 ms in straight flight, but often extended to about 220 ms over the sea. Similar changes were noted for *Eptesicus serotinus*, with slightly lower frequencies and extended intervals compared to the most common calls over land. The observed differences were so small that they did not change the possibilities for acoustic species identification. When *M. dasycneme* flew over the sea, it regularly used the diagnostic calls that we have described with extended QCF parts in the middle of pulses similar to when over large lakes and fiords.

Flight altitude at sea.—All migrating bats observed over the sea flew at relatively low altitudes. Even the normally high-flying *N. noctula* flew lower than 10 m above the surface. Radar observations confirmed that most migrating *N. noctula* flew low, although a few flew >40 m high. Bats changed altitude rapidly when they were near tall vertical obstacles such as ships, bridges, and wind turbines. At the Utgrunden lighthouse, we found that bats always avoided an area around the lighthouse when a navigation radar was on. This confirms the aversive effect of electromagnetic radiation reported by Nicholls and Racey (2007, 2009). We observed *N. noctula* to change altitude quickly, moving from low over the water surface to the top of a nearby wind turbine within a few minutes.

Foraging at sea.—We regularly documented bats foraging over the ocean in almost all survey areas. Foraging behavior was especially common in areas with high abundance of insects in the air or crustaceans on the water surface. The abundance of prey at sea varied with area. We observed *M. daubentonii* and *M. dasycneme* touching the water surface, presumably gaffing prey, where net samples collected no insects but an abundance of crustaceans in the sea surface. We assume that these bats were feeding on the crustaceans. There was no apparent correlation between insect abundance and sea-bottom structure or distance from coast. Insect abundance was probably related to wind conditions and water currents. During periods with low easterly winds, insects of many kinds drifted over the water surface. On these occasions, insect density increased as we moved south and passed the tip of Öland at Ottenby. Insects included chironomids of marine origin but also terrestrial insects probably flying or drifting from the Baltic Republics or Russia.

Migrating bats took advantage of the presence of abundant prey and foraged for shorter or longer periods depending on prey availability. The abundance of food offshore already was used by many bat species in midsummer, well before the onset of the migration period. Bats apparently flew long distances from the coast to forage. Radar data showed *N. noctula* foraging at sea and repeatedly returning to the same land areas again before dawn.

At 1 departure site, Hoburgen on Gotland, bats of several species were seen landing on the almost vertical cliffs facing the sea, where they crawled around and fed on night-active



FIG. 3.—*Eptesicus nilssonii* searching for night-active invertebrates on vertical cliffs at Hoburgen, Gotland. A number of bat species are able to feed in this way before they take off from land. At sea, bats also hunt insects at wind power turbines near the blades and on the vertical tower sides. Photo: Ingemar Ahlén.

invertebrates that emerged from crevices (Fig. 3). We also observed bats attempting to land on the surfaces of offshore wind turbines, either to glean insects or in attempts to roost.

Roosting at sea.—Roosting occurred along flight routes on structures such as wind turbines, ships, and probably bridges and lighthouses. At a group of wind turbines 5.8 km offshore, we observed individual bats (*Pipistrellus pygmaeus*, *P. nathusii*, and probably *Nyctalus leisleri*) roosting for several days and regularly foraging over the surrounding waters. Some of these bats flew around turbines emitting territorial or mating calls. Service technicians found bats roosting in the nacelles of turbines. We also observed bats of several species foraging and emitting mating calls at coastal points and small islands where they have not been recorded during the breeding season, such as on the island of Saltholm.

DISCUSSION

Our studies on migration and activities of bats at sea have resulted in information about the behavior and distribution patterns of migratory bats, including regular occurrences of many species travelling over open water, seasonal differences in the distribution of migrating bats, and detailed observations of flight behavior, echolocation calls, and roosting and feeding habits of bats at sea. Eleven of 18 species occurring in the region were detected at departure points and out at sea, suggesting that migration and foraging over marine environments are common.

Pipistrellus pygmaeus was the most numerous bat found at departure sites and over the ocean. This is surprising because it is not considered to be migratory in Scandinavia and because this species has not been recorded on the island of Bornholm in the middle of the southern Baltic Sea (Baagøe 2001, 2007d).

The vast majority of migrating bats flew rather low above the surface of the sea. This is surprising in comparison with

bird migration, which generally occurs at higher altitudes. Even species of bats that often fly high and fast such as *N. noctula* and *V. murinus* mostly migrated <10 m above the sea surface. Observations of birds using a thermal camera at Falsterbo in Sweden (Zehnder et al. 2001) revealed *N. noctula* foraging at altitudes up to 1,200 m high (Ahlén et al. 2007). Bats must use systems of orientation other than echolocation for long-distance navigation (Holland et al. 2006; Neuweiler 2000) but we argue that bats migrating over the sea fly low to detect the water surface by echolocation to remain oriented. It is also possible that lower wind speeds at the low altitudes are favored by bats (Ahlén et al. 2007). Our methods of observation (spotlights, radar, and thermal imaging) permitted us to detect bats flying as high as about 100 m, yet with the exception of bats investigating turbines and other structures, they rarely occurred at such heights. Examination of our data does not support the idea that bats migrate at higher altitudes over the open sea. However, although bats normally fly low over the sea while migrating and commuting, they may change altitude in response to flight height of their prey.

All bats observed flying over the sea echolocated. We made nearly 1,000 such observations, radar observations excluded, and never observed a bat that was not echolocating. This is a strong indication that bats migrating at sea normally use echolocation. All QCF bats of northern Europe have species-specific ranges of frequencies for the intense QCF “tail” of calls used during commuting or search phase flight. In general, these species use QCF tails near the lower limit of their frequency range and all northern European species use longer intervals when flying in completely open environments well away from clutter (Ahlén and Baagøe 1999; Kalko and Schnitzler 1993; Schnitzler and Kalko 1998). We also observed this over the open sea, which is the most open and clutterless environment encountered by bats. The slight modification of call parameters used at sea toward the lowest frequencies and longest intervals between echolocation pulses might be due to the lack of obstacles and the need to orient in relation to the water surface.

Myotis daubentonii and *M. dasycneme* hunt over the sea in fiords, along coasts, and in archipelagos (Ahlén 1997b, 2006; Baagøe 2001, 2007a, 2007b), but our data showing that at least 10 species, both migratory and resident, regularly forage far out at sea are novel. Particularly surprising was the degree to which migrants take advantage of invertebrate prey in marine environments. In some areas at sea, prey availability is extremely high and is easily accessible because of complete lack of clutter. We observed bats feeding on an abundance of prey items never seen in terrestrial habitats, such as insects and spiders and probably also marine crustaceans. Similarly, in inland areas, one of us (IA) has found that most species of bats regularly switch to foraging over large lakes during longer drought periods when the terrestrial food supply is limited.

Further and more quantitative studies are needed to understand the dynamics of bat foraging and prey availability at sea, as well as detailed investigations into how far from the coast and how regularly and during which periods this phenomenon occurs. We have interviewed members of ship

crews and learned that they often see large numbers of (sometimes terrestrial) insects in the air or on the sea surface at long distances west of the European and African continents. We hypothesize that invertebrates at sea are an underappreciated, yet potentially critical food resource for migrating bats.

The finding that bats sometimes land on artificial structures at sea suggests they use behaviors rarely observed on land. Our observations have implications for the problems concerning bats and wind turbines. Because bats generally migrate at low altitudes, we expect that accidents with wind turbines are probably not frequent during migration itself. It is when bats stop over and forage for insects that are accumulated around the wind turbines that accidents become more likely. During certain weather conditions insects are attracted to turbines and other objects at sea such as ships, lighthouses, and bridges. The problem is likely to be most serious when wind turbines are located in areas where many bats are passing and foraging. This can be in sea areas just offshore from important departure points but it can also be in areas on land with landscape structures and habitats that attract or funnel large numbers of breeding or migrating bats.

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