Experimental evidence of light disturbance along the commuting routes of pond bats (*Myotis dasycneme*)

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Abstract: A population of pond bats (*Myotis dasycneme*) inhabits a network of foraging areas and separate male, female-breeding and temporary colonies. These are interconnected by commuting routes which are also used for foraging. The functioning of these networks is crucially important for the conservation of the species. Observations and anecdotal evidence suggest that light may be an important source of disturbance along commuting routes and potentially affect the connectivity of the networks. The disturbing effects of light on pond bats were experimentally studied by placing a strong lamp (1000 W) along existing pond bat commuting routes. Each experimental site had specific characteristics which allowed us to explore the interacting effects of light disturbance and the environment. The number of passing bats, the percentage of feeding buzzes relative to total commuting calls and flight patterns were compared between dark control nights and experimentally illuminated nights. There were no clear effects of experimental light on the number of passing bats nor did more bats use an alternative commuting route when just one of two possible routes was lit. However, light did reduce the percentage of feeding buzzes by more than 60%, although the abundance of insect food tended to increase. It was observed that light disturbs the flight patterns of pond bats. When approaching the beam of light, between 28% and 42% of pond bats turned before continuing on their normal commuting route. Virtually all pond bats (96%) turned when the light was erected on an existing barrier and they had to fly straight into the beam of light. These disturbing effects also seemed to occur at low levels of light intensity. This study is the first known experimental evidence on the disturbing effects of light on pond bat behaviour along commuting routes and raises many questions, especially as to whether these disturbing effects will have fitness consequences.

Keywords: ecological connectivity, conservation, illumination, foraging, turning behaviour.

Introduction

The pond bat (*Myotis dasycneme*) is insectivorous. In the Netherlands, where an important part of the European population is located (Limpens et al. 1999), this species mainly forages in open landscapes, rich in water and particularly over fresh water lakes and marshy areas (Kapteyn 1995, Limpens et al. 1997). Colonies are typically found in buildings such as churches and houses, which can be up to 20 km away from their foraging areas (Kapteyn 1995, Haarsma 2003, Van de Sijpe et al. 2004). Colonies of males and females are typically separated during the breeding season (Voûte 1972, Limpens et al. 1997, Haarsma 2002). Colonies of reproductive females are used for different lengths of time; some for the entire summer, others for much shorter periods. In addition some temporary colonies are only used for a few days or weeks. The main foraging areas, male, female and temporary colonies are interconnected by fixed commuting routes. These are also used for foraging and can be seen as part of the bats' foraging areas. Commuting routes often follow watercourses (such as canals) and sometimes are partly over land along linear landscape elements, such as rows of trees (Verboom et al. 1999, Van de Sijpe et al. 2004).

The connectivity of this network of colonies and foraging sites is essential for the survival of a pond bat population (Limpens et al. 1999). The connectivity is highly dependent on the existence of undisturbed commuting routes that connect the different elements of the network. In addition to barriers that may be created along these commuting routes, such as roads (Bach et al. 2004), a common threat may be the disturbing effects of light.

Only a few studies have addressed the possible disturbing effects of light on bat behaviour. As light attracts insects, there may be an interaction between the effects of increased food availability and the disturbing effects of light. Studies performed in Sweden and England showed that an increased insect abundance observed under street lights offers preferred feeding sites for just a restricted number of bat species (Rydell 1992, Blake et al. 1994). Only fast-flying bat species that use long-distance sonar, such as noctule bat (*Nyctalus noctula*), parti-coloured bat (*Vespertilio murinus*), northern bat (*Eptesicus nilssonii*) and occasionally common pipistrelle (*Pipistrellus pipistrellus*) were observed foraging under street lights. By contrast, slow-flying species such as *Myotis spp*. and brown long-eared bat (*Plecotus auritus*) were observed to avoid these lit areas. Species from this last group are thought to be more vulnerable to avian predators in lit areas, and therefore avoid such sites (Speakman 1991, Rydell et al. 1996). In addition to these species-specific responses to light at feeding sites, there are indications that the effects of light are dependent on the time of year (Rydell 1991), weather conditions (Blake et al. 1994) or that they may differ between foraging sites and commuting routes, as has been suggested for common pipistrelle (Verboom 1998). In addition, there are several field observations and anecdotal evidence that suggest that light has disturbing effects on a number of bat species (for example Alder 1993, Shirley et al. 2001). However, these studies did not establish any direct relation between light and the disturbing effects on bat behaviour, and factors other than light could potentially explain the effects on bat behaviour.

Knowledge on the potentially disturbing effects of light on bat behaviour is highly relevant. Most bat species have a high status of legal protection in EU countries (in the framework of the Habitats Directive) and effects that negatively impact on bats may be illegal. Equally, the amount of artificial light has increased substantially during recent decades (Longcore & Rich 2004) and this may be undermining conservation efforts for several bat species.

In this study we experimentally manipulated light levels by placing a strong lamp along existing commuting routes of pond bats in the Netherlands and measured the effects on bat numbers and behaviour. This is the first study we are aware of that experimentally studies the disturbing effects of light on bats and constitutes an important first step in increasing knowledge in this field.

Methods

Experimental set-up

To study the effects of light on the number and behaviour of pond bats a series of experiments was carried out, in which sites along commuting routes were experimentally illuminated. Depending on the study site (see below), the lamp was placed perpendicular to, or against, the flight direction of commuting pond bats. Data was collected on the number of passing bats and flight direction and since the commuting routes of pond bats are also important as foraging sites, the number of feeding buzzes (foraging calls). To investigate the possible disturbing effects of light, these measurements were collected on experimentally illuminated nights and compared with dark control nights before and after the experimental lighting.

For experimentally lightning we used a 1000 W halogen lamp connected to a generator for power supply. This lamp produced a beam of light ranging between 1-30 Lux with a range of approximately 10 m (N. Goossens & H. Toorman, unpublished data; photo 1). For comparison, natural

Photo 1. Experimental lighting consisted of a 1000 W halogen lamp, producing a beam of light between 1-30 Lux, with a diameter of approximately 10 m which was placed along the waterside of a commuting route of pond bats. *Photograph: N. Goossens.*

values of light intensity during moonlit nights can reach up to 0.12 Lux (van der Vegte 2005). At 10 m distance from the lamp slightly elevated levels of light intensity were measured, whereas 15 m from the lamp the values returned to the normal background values.

The lamp was placed on the banks of canals known to be commuting routes for pond bats. The generator was always placed more than 30 m away, to prevent any noise disturbance. All experiments were carried out between the 11th July and the 12th August 2005, during the period when pond bats are reproducing, giving birth and lactating (Limpens et al. 1997, Krapp 2001).

Study sites

All the study sites were located in the province of Friesland in the Netherlands (figure 1). Since the number of pond bats using the commuting routes at each location is highly dependent on the size of the nearest colony, and as each experimental location had its specific characteristics, the results from these locations were initially analysed separately. Experimental illumination was carried out at four locations, near the villages of Tjerkwerd, Warga, Allingawier and Workum. At Tjerkwerd illumination was applied on four nights. At Warga, Allingawier and Workum illumination was applied on just one night. The experimental set-up differed between the sites. Three types of experiments were performed:

1) Experiment monitoring an alternative route: light perpendicular to the assumed flight path

This experiment was carried out in Tjerkwerd where there is a colony of more than 175 pond bats (based on counts of swarming bats in 2005)

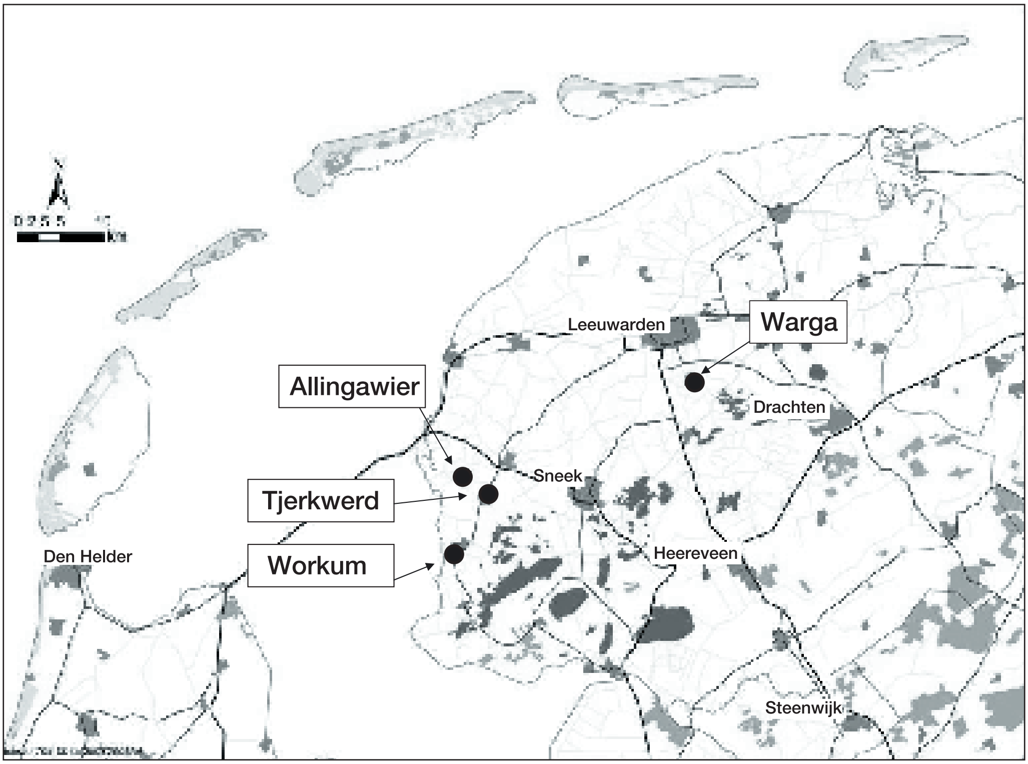

Figure 1. Locations of experiments.

located in the village church. The foraging areas of these bats are mainly situated along the Ijsselmeer Lake. Bats follow two alternative commuting routes to reach the foraging areas; via the 'Van Panhuys' and 'Workumertrekvaart' canals. Both are large canals approximately 15 m wide and the banks are mainly vegetated with common reed (*Phragmites australis*). The main experiment was carried out at this location. Experimental light was applied over four nights. It was placed on the waterside, perpendicular to the flight direction of the bats. Bat numbers and behaviour on the experimentally lit nights were compared to four dark control nights, immediately before and after the experimental nights. The experiment was carried out between the 11th and the 22nd July 2005 (period 1) and repeated between the 1st and the 12th of August 2005 (period 2). Light was applied to just one of the alternative commuting routes (the Workumertrekvaart). In this way we studied whether lighting one commuting route would increase the number of bats using the alternative, unlit, commuting route.

2) Short experiment with light perpendicular to the flight path

This experiment was carried out in Warga, which has a colony of more than 118 pond bats (based on counts of swarming bats in 2005) located in a house inside the village. The main foraging areas are situated on open water in the 'Oude Venen' marsh land area. Bats follow the 'Meanewei', a small canal approximately 7 m wide, to these foraging areas. The banks along this canal are vegetated with common reed and bushes of willow (*Salix cinerea* and *Salix alba*). On this site during light was applied for just one night. Bat numbers and behaviour on the experimentally lit night were compared to those in two dark control nights, immediately before and after the experimental night. The light was placed on the waterside perpendicular to the flight direction of the bats.

3) Short experiment with light pointing towards the flight path

This experiment was carried out in Allingawier and Workum. Pond bats observed in Allingawier most likely originate from the colony in the church at Tjerkwerd (over 175 individuals), approximately 4 km away from Allingawier. While following the Van Panhuys canal to foraging sites along the banks of Lake IJsselmeer they pass the village Allingawier. On this site light was applied on one night and the effects compared to two control dark nights immediately before and after the experimental night. The experimental light was placed under the bridge just north of Allingawier against the flight direction of the bats, with passing bats having to fly straight into the light.

Workum has a colony of more than 220 pond bats (based on counts of swarming bats in 2005) located in a house in the centre of the village. Bats reach their foraging areas on Lake IJsselmeer by following the 'It Soal' canal. A large sluice on the border of the village regulates the water level in this canal (approximately 7 m wide) and provides a barrier that bats have to cross on their route. Because of nearby houses, there is already much artificial light on this site. Here night light was applied on one night and compared to two control dark nights immediately before and after the experimental night. The light was placed on top of the sluice against the flight direction of the bats, with bats having to fly straight into the light.

Data collection

The number of passing bats was determined using D200 Petterson's heterodyne bat detectors. These detectors lower the frequency of bats' sonar so that it is within audible range for humans so they can observe and monitor bats (Limpens 1993). The bat detectors were connected to sound-controlled recorders which started recording the moment that bats passed. The detectors and recorders were placed inside waterproof PVC pipes placed on a Styrofoam disc and floated on the canals in front of the experimental light. After each night, the tapes with the recorded bat sounds were removed and then analysed in the lab.

Pond bats typically produce sounds ranging between 25 and 60(-80) kHz, with a clear peak at 35 kHz. While commuting from their colony to the foraging areas, pond bats produce commuting calls that can be characterized as steep FM-type (frequency modulating) pulses, sometimes alternating with long-range sonar (QCF type calls), the latter with a clear peak frequency at 35 kHz, a unique characteristic of the species (Limpens et al. 1997 & 1999). Foraging behaviour can acoustically be distinguished from these commuting calls. During foraging, the bats emit feeding buzzes, consisting of a series of short, quick pulses (Britton et al. 1997, Siemers et al. 2005). All the tapes recorded during the experimentally lit and dark control nights were analysed by experienced observers. The number of individual passing bats was determined by counting the commuting calls. The number of feeding buzzes relative to the number of commuting calls was used as an estimate of the amount of foraging behaviour. All the observations were carried out between 11:00 PM and 01:00 AM, the observed peak in commuting behaviour at these locations. The peak of commuting behaviour shifted during the experimental period, related to sun-set, although remained within this time range.

During the nights with experimental light, additional data were gathered on the behaviour of passing bats, always by the same two observers. These two observers, with D200 Petterson bat detectors stood, close to the experimental light. One observed the bats flying in the beam of light with high levels of light intensity (1-30 Lux), 10 m radius from the lamp. The second observed the bats approaching the beam of light at a distance of 15 m from the lamp, where the light intensity was slightly above natural levels (0.12-1 Lux, see 'Experimental set-up'). For each approaching bat it was noted whether they turned away from, or flew straight on through, the beam of light.

In addition to data on the number of bats and their behaviour, data on insect abundance were collected to test for the possible effects of the experimental light in attracting insects. A strip of 'Yellow-sticky-traps' was attached to each floating PVC pipe, encircling it. These sticky-traps have an adhesive yellow surface of 10x30 cm traps insects landing on the surface. They are used as a method to determine insect abundance (see for example Heinz et al. 1992). After each night, the total number of insects per species per sticky trap was determined.

Statistical analyses

Differences in number of passing pond bats and the amount of foraging (percentage of feeding buzzes relative to total commuting calls) at the Workumertrekvaart and Van Panhuys canal during dark and light nights were tested using One-way ANOVA followed by Tukey multiple comparison tests for the two separate experimental periods. The overall effects of light for both experimental periods combined on the two canals were tested using univariate GLM using period and experimental manipulation as the fixed factors. The overall effects of light on the number and percentage foraging bats at the other three locations were tested in combination using One-way ANOVA followed by the Tukey-test.

Results

Experiment monitoring alternative routes with light perpendicular to flight path

During nights with experimental light, there was no observed reduction in the number of pond bats passing along the Workumertrekvaart canal (figure 2). While there was a tendency towards a lower number of passages during the illuminated nights in period 1 (the 11th to the 22nd July 2005), these differences were not significantly different ($F_{2,7}$=0.50, P=0.63). In period 2 (the 1st to the 12th of August 2005), a higher number of pond bats was observed during the nights with experimental light, although this also did not differ significantly from the dark control nights ($F_{2,11}$=1.30, P=0.32). Combining both periods, the number of passing pond bats did not differ between dark control nights and experimentally illuminated nights ($F_{2,19}$=0.102, P=0.904). Experimental lighting along the Workumertrekvaart canal did not result in a higher number of pond bats using the alternative commuting route along the Van Panhuyskanaal in either period (period 1: $F_{2,6}$=1.70, P=0.30: period 2; $F_{2,11}$=0.72, P=0.51, see figure 2). The number of passing pond bats was either in the middle of the range (in period 1) or lower than those in the control nights (period 2). When both periods were combined, there was no overall effect of experimental lighting on the number of passing bats along the Van Panhuyskanaal. The detailed observations of flight behaviour during nights with experimental light showed that a high proportion (36-42%) of bats observed near the beam of light turned when they approached the lamp, before continuing along the same commuting route (table 1). Of these turning bats, the majority (54-89%) turned before the beam of light, compared to 11-47% that turned when in the beam of light. Bats that passed the light tried to evade the beam by flying around it at a large distance or flying partly overland.

Light, foraging behaviour and insect abundance

Foraging behaviour was significantly lower during the experimentally illuminated nights than during the dark control nights in period 1 ($F_{2,7}$=6.32, P=0.043, figure 3). This pattern was broadly repeated in period 2, but due to a high variation in the proportion of feeding buzzes recorded, there was no significant difference between the proportion of feeding buzzes on the lit and on the dark control nights ($F_{2,11}$=0.77, P=0.49). In the first period the amount of feeding buzzes was 69 to 84% lower during nights with experimental light than on dark control nights. This decrease in the proportion of feeding buzzes occurred despite an increase in the abundance of insect food. In both periods, more

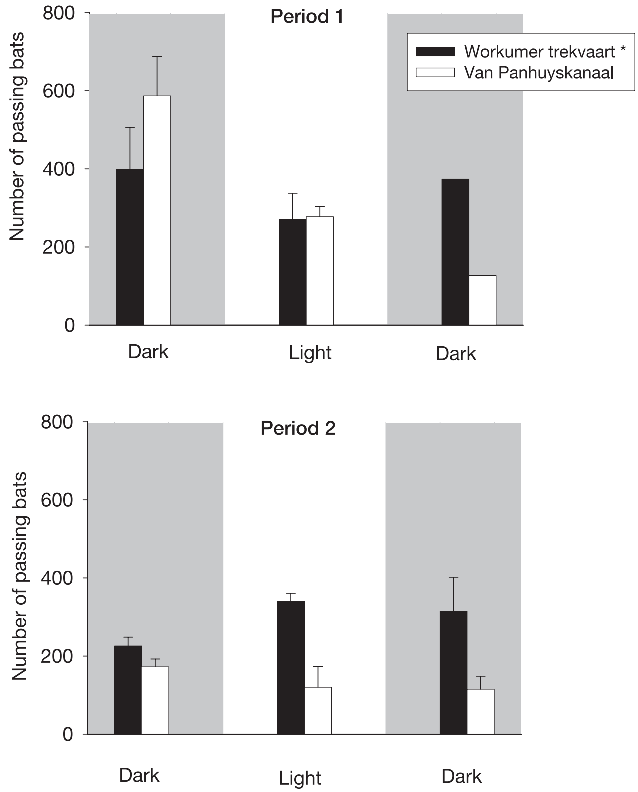

Figure 2. Number of passing pond bats on two alternative commuting routes during four nights with experimental light compared to four dark control nights before and after the experimental lighting. Experimental lighting was only carried out along the Workumertrekvaart canal (marked with an asterisk). Data were collected in two periods: from the 11th to the 22nd of July 2005 (period 1) and the 1st to the 12th of August 2005 (period 2).

Table 1. Percentage of turning pond bats in and before the light beam - based on the number of passing bats for which this could be observed. Turning bats were sub-divided into those that turned before the beam of light (15 m from the light source) and in the beam of light (less than 10 m from the light source). Numbers from the Workumertrekvaart canal refer to averages of four nights with experimental light, with standard errors in brackets.

Location	Number of nights with light	Number of passing bats	% turning	% turning before light	% turning in light
Workumer-trekvaart					
Period 1	4	271 (67)	36 (8)	89 (26)	11 (26)
Period 2	4	340 (21)	42 (3)	54 (12)	47 (12)
Workum	1	170	96	57	43
Warga	1	177	28	86	14
Allingawier	1	-	-	-	-

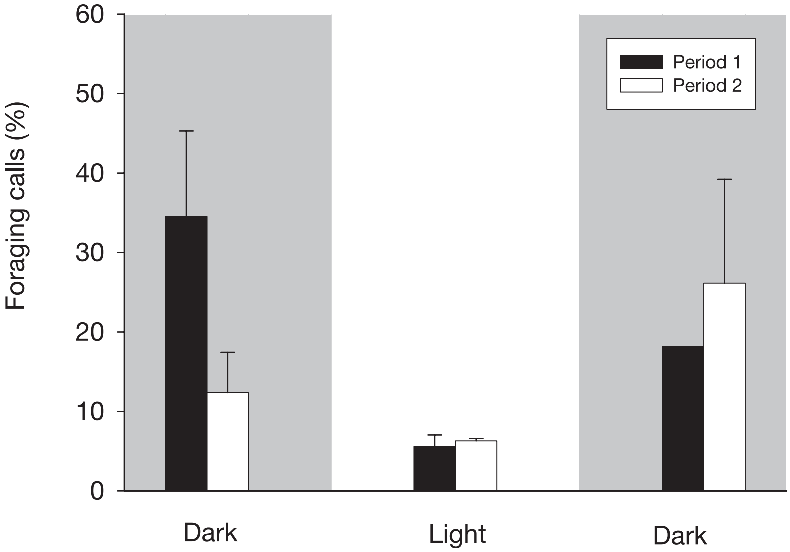

Figure 3. Amount of foraging, expressed as the percentage of feeding buzzes relative to commuting calls, during four nights with experimental light compared to four dark control nights along the Workumertrekvaart canal before and after the experimental lighting. Periods as in figure 2.

insects, mainly of the order Diptera, were caught on the Yellow-sticky-trap during the nights with experimental light than on the dark control nights (table 2). However, due to a high variation in the number of insects caught per night, these differences were not significant, either for each period separately or for both periods combined ($F_{2,24}$=1.83, *P*=0.19).

Short experiments with light perpendicular to or pointing towards flight path

Experimental lighting during one night did not reduce the number of passing pond bats at the three selected different locations (figure 4). The number of passing bats during illuminated nights was higher than observed on the two dark control nights at Warga and Allingawier and approximately the same as on the control nights at Workum. Hence, there were no clear differences between the position of the lamp and the effect on the number of passing pond bats. Combining the results of all three locations, there was no overall significant effect of light on the number of passing pond bats ($F_{2,8}$=0.071, *P*=0.93).

Table 2. Average total number of insects recorded on Yellow-sticky-traps. Count taken during four dark control nights before experimental lighting, four nights with experimental lighting and four dark control nights after experimental lighting. Numbers refer to the averages of the four night periods, with standard errors in brackets.

Location	Number of insects in dark	Number of insects in light	Number of insects in dark
Workumertrekvaart			
Period 1	2.3 (1.4)	23.3 (14.5)	3.8 (2.5)
Period 2	4.8 (4.4)	5.5 (4.2)	3.3 (1.8)

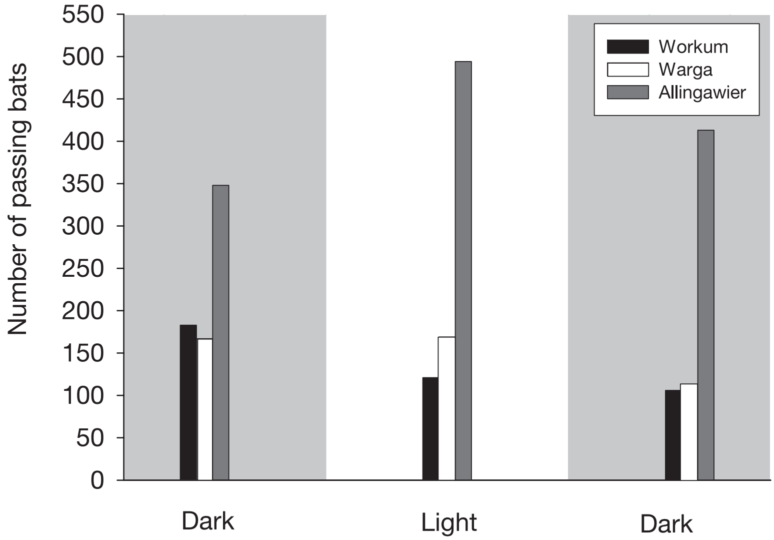

Figure 4. Number of passing pond bats during one night of experimental lighting and two dark control nights at three different locations. At Workum and Allingawier the light was pointing towards the flight direction: in Warga it was pointing perpendicular to the flight path.

However, more detailed observations of flight and foraging behaviour suggested that the position of the lamp did have an effect. Observation of flight behaviour during nights with experimental light showed that a high proportion of the bats turned when they approached the lamp (table 1). Virtually all (96%) the bats turned when they had to fly straight into the beam of light and over an existing barrier (Workum). Again, the majority of the turning bats at these sites, 57-86%, turned before entering the beam of light compared to 14-43% which turned when in the beam of light. At Allingawier no data on flight behaviour could be collected due to bad weather conditions preventing observation of animals during the lit night.

The proportion of feeding buzzes during the one night of experimental light was reduced by more than 39% (Warga) and 96% (Workum) compared to the dark control nights. Only at Allingawier there was no clear reduction in foraging behaviour, where the amount of feeding buzzes during the night with experimental light was somewhere between that on the two dark control nights. The largest reduction in foraging behaviour was observed when the light was placed on an existing barrier in the flight direction of the pond bats (Workum).

Discussion

This study is the first we are aware of to demonstrate experimentally that light along the commuting routes of pond bats, which are also used as foraging areas, has disturbing effects on their behaviour. Although we did not find changes in the number of passing pond bats as a result of experimental illumination, the amount of foraging behaviour decreased (despite higher availability of insect food) and a high proportion of pond bats turned when approaching the light. These changes in behaviour are likely to result in negative effects on individuals by increasing their energy expenditure during the energy-demanding reproductive period.

Disturbing effects of light on bat behaviour

Commuting routes of pond bates are used for commuting between colonies and foraging areas, but much foraging behaviour is also observed (Verboom 1998, Verboom et al. 1999). These routes therefore can be seen as part of the bats' foraging areas. Placing a light source along existing commuting routes clearly disturbed the behaviour of commuting pond bats. Foraging behaviour, expressed as the percentage of feeding buzzes, was reduced by 49-84% during the four nights along Workumertrekvaart with experimental light compared to nights without light. The illumination tended to increase insect abundance and hence food abundance, an effect also observed in several other studies (Rydell 1992, Blake et al. 1994). There was an increase in the number of insects of the order Diptera, especially mosquitoes, which constitute an important part of the diet of pond bats (Britton et al. 1997, Van de Sijpe et al. 2004). Despite increased food abundance, foraging behaviour did not increase, further illustrating the disturbing effects of light. It may be that pond bats do not profit from the increased food supply due to a higher risk of predation when foraging in illuminated conditions (Speakman 1991, Rydell et al. 1996). Commuting routes are an important part of pond bats' foraging areas, and illuminating them reduces the suitable foraging area for this species. This may have negative effects on individuals by decreasing their food intake. This may be especially harmful during their relatively short energy-demanding reproductive period (Duverge et al. 2000, O'Donell 2002). The present study demonstrated this effect by placing just one lamp along a commuting route. If we extrapolate these observed effects, placing a row of lamps along an existing commuting route may lead to a considerable reduction in foraging area of this species. In addition to less foraging behaviour close to the lamp, a high proportion (28-96%) of bats turned when approaching the beam of light. The position of the light seemed important, the highest proportion of bats (96%) turned when the light was placed on top of an existing barrier and they had to fly straight into the beam of light. The finding that most turning bats (54-89%) turned before reaching the beam of light suggests that these disturbing effects operate at low levels of light intensity. The highest proportion of bats turned between 15 and 10 m distance from the light source at light levels of approximately 0.6-3.2 Lux. This indicates that light levels slightly above natural light values, (for example moon-lit nights can be 0.12 Lux - van der Vegte 2005), along commuting routes may have disturbing effects. As flight is energy-consuming for bats (Salcedo et al. 1995, Henry et al. 2002), a high amount of light-induced turning along a commuting route may increase their energy expenditure by increasing their flight distances. The combined effects of this and a lowered food intake (discussed above) may cause problems at periods of high energy demand, especially among lactating females, during their reproductive period. If these disturbing effects take place at a large scale, they may have negative effects on the fitness of individual bats.

No effects of light on number of bats

Although this study clearly showed that light did disturb bat behaviour it did not find that lighting had any effect on the number of passing pond bats. There are several possible explanations for this not occurring, despite the clear disturbing effects of the light on bat behaviour. Firstly, the light source used, a lamp of 1000 W, may not be sufficiently disturbing to prevent bats from using the commuting route. This lamp provided light levels ranging between 1 and 30 Lux within a 10 m range of the lamp. These values close to the lamp are clearly above the maximum natural levels of light at night (see van der Vegte 2005). The lamp's range of 10 m fully illuminated the width of the smaller canals used in the experiment, but left several metres virtually unlit on the larger canals (approximately 15 m wide). Bats could have evaded the beam of light by flying on the unlit opposite site of the wider canals or by flying partly overland, behaviour that was observed during the experiments. Pond bats are already known to use commuting routes that are, partly, overland (Limpens et al. 1997, Haarsma 2003). Other studies indicate that bats evade light sources by flying at a distance around them (Alder 1993).

Another possible explanation is that the majority of the pond bats that turned in the proximity of the light turned again and flew straight through the light beam at a second attempt and so continued along the same commuting route. This would explain why the total number of passing bats during dark and illuminated nights was unaffected by the light. Pond bats are known to be habitual in their use of colony sites, commuting routes and foraging sites (Kapteyn 1995, Limpens et al. 1997) and hence are not likely to rapidly respond to changes which make a commuting route less attractive. As most experimental sites were located near colonies of reproducing females, the majority of passing bats most likely consisted of (lactating) females at the end of their reproductive season and with high energy demands (Duverge et al. 2000). For these individuals, the extra costs involved in choosing an alternative commuting route may not outweigh the negative effects of light applied during these experiments, so they continued along the known commuting route. Field observations of turning bats support this idea that a large number of bats did eventually pass the beam of light.

Focus of future research

This study clearly shows that light clearly does disturb the behaviour of pond bats and raises several questions for further study. As only one lamp, with one level of light intensity, was used in the present study it is not known what the effect of multiple light sources would be. It may be such that these effects are cumulative, and that the effect of several light sources along a commuting route would be much larger than the sum of individual light sources. In addition, the intensity or the colour of the light may have different effect on bats (see for example Rydell 1992 and Blake et al. 1994). A useful next step would be to establish a dose-effect relation between light level and type and the number of passing bats and their behaviour. The disturbing effects of light may also be lessened by habituation. In the present study, with short experimental periods of four nights of lighting, no habituation effect was discovered. However, it is unclear how long-term exposure of light along a commuting route will affect the behaviour of bats. It could lead to the use of an alternative commuting route (see for example Alder 1993) or to habituation to the new situation.

Another important question is whether and how these disturbing effects might affect the population level of pond bats. Several other studies have shown that disturbances that lead to an increase in energy expenditure can result in negative effects on a species' reproductive output. This has been demonstrated in detail for (among others) arctic breeding geese (Madsen 2001, Drent et al. 2003), where disturbing the geese at staging sites along their migration route eventually led to a decline in the population (Klaassen et al. 2006). To further quantify the disturbing effects on the fitness of individual bats and population size, further research into the energy cost of flying and detailed measurements on the reproductive output of individually marked females would be required.

In addition to these questions that are relate specifically to pond bats, the disturbing effects of light on other species of bats also warrant further study. While increased light levels may disturb the behaviour of some bat species, several species may benefit from increased lighting at their foraging areas (Rydell 1992, Blake et al. 1994). This may result in increased food competition for the light-sensitive species and could be an additional factor in the decline of some bat species (Arlettaz et al. 2000).

Despite the many questions that still need to be answered before we fully understand the effects of light on (pond) bats, this study is an important first step in this direction. Further development of our knowledge on the disturbing effects of light could play an essential role in contributing to the conservation of bats. As bats are often dependent on urban areas (at least for part of their life cycle), good spatial planning of light along commuting routes could prevent a growing conflict of interests and maintain suitable habitats for bats.

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Samenvatting

Experimenteel bewijs van lichtverstoring langs vliegroutes van meervleermuizen (*Myotis dasycneme*)

Een populatie van meervleermuizen (*Myotis dasycneme*) bestaat uit een netwerk van foerageergebieden, van elkaar gescheiden mannen-, vrouwen- en tijdelijke verblijven, onderling verbonden door vliegroutes. Een goed functionerend netwerk is essentieel voor het behoud van deze soort. Verschillende waarnemingen en anekdotisch bewijs suggereren dat licht een belangrijke verstoringsbron kan zijn langs bestaande vliegroutes. Verlichting die wordt ge-plaatst nabij vliegroutes kan de connectiviteit van een netwerk aantasten. De verstorende effecten van verlichting op meervleermuizen zijn in deze studie experimenteel onderzocht door het plaatsen van een sterke lichtbron (1000 W) langs bestaande vliegroutes. Elke experimentele plek had zijn eigen specifieke kenmerken waardoor we in staat waren om de interactie tussen lichtverstoring en de omgeving te exploreren. Het aantal passerende vleermuizen, het percentage ‘vangstbuzzen’ (foerageergeluiden) en het vliegpatroon werd vergeleken tussen donkere controle nachten en experimenteel verlichte nachten. In tegenstelling tot onze verwachting was er geen duidelijk effect van verlichting op het aantal passerende vleermuizen. Ook gebruikte geen groter aantal vleermuizen een alternatieve onverlichte route als twee mogelijke vliegroutes bestonden en langs slechts één vliegroute verlichting werd aangebracht. Echter, verlichting verminderde het percentage vangstbuzzen met meer dan 60% ten opzichte van controle nachten. Deze vermindering van foerageergedrag trad op ondanks dat het aanbod van insecten, geschikt als voedsel, de neiging had toe te nemen. Daarnaast werden verstorende effecten van verlichting op het vliegpatroon van vleermuizen waargenomen. Tussen 28 en 42% van de meervleermuizen keerde om bij het naderen van de lichtbundel alvorens door te vliegen op hun normale vliegroute. Vrijwel alle meervleermuizen (96%) keerden om als de verlichting was aangebracht op een bestaande barrière en de vleermuizen recht tegen het licht in moesten vliegen. Deze verstorende effecten traden al op bij lage waarden van lichtintensiteit die slechts iets boven natuurlijke waarden van lichtintensiteit ’s nachts lagen. Dit suggereert dat meervleermuizen erg gevoelig zijn voor verhoogde waarden van lichtintensiteit. Hoewel nog veel vragen onbeantwoord zijn, vooral of deze verstorende effecten zullen leiden tot effecten op de fitness van individuen, demonstreert deze studie voor het eerst experimenteel de verstorende effecten van verlichting op het gedrag van meervleermuizen.

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