

Group size and dispersal ploys: an analysis of commuting behaviour of the pond bat (*Myotis dasycneme*)

A.-J. Haarsma and H. Siepel

Abstract: Like most bat species, the pond bat (*Myotis dasycneme* (Boie, 1825)) lives in roosts more or less in the centre of their foraging habitat and are considered central-place foragers. Commuting routes, or flyways, between roosts and hunting areas have an essential ecological function for bats. We summarize the results of research performed on the commuting routes of pond bats between 2002 and 2009. We give, among others, a description on how bats disperse, how to recognize a commuting route, and details about the effort needed to make a complete survey of one commuting route. Furthermore, we make a relation between number of animals on the route and size of their respective roost. The results suggest pond bats are not completely reliant on waterways for reaching their foraging habitat; they use directional dispersal, following commuting routes over waterways in combination with shortcuts over land. These results provide information that can be used to better understand how bats use their commuting routes. Also, the knowledge can be applied to survey work.

Key words: movement, dispersal mechanism, exit count, Chiroptera, pond bat, *Myotis dasycneme*, population size, survey method.

Résumé : À l'instar de la plupart des espèces de chauves-souris, les murins des marais (*Myotis dasycneme* (Boie, 1825)) vivent dans des dortoirs situés à peu près au centre de leur habitat d'alimentation et retournent à ces lieux centraux entre les épisodes de quête de nourriture. Les voies de déplacement, ou de vol, entre les dortoirs et les zones de chasse ont une fonction écologique essentielle pour ces animaux. Nous présentons un sommaire des résultats de recherches effectuées sur les voies de déplacement de murins des marais de 2002 à 2009. Nous décrivons, entre autres, la dispersion des murins, comment reconnaître une voie de déplacement et des détails concernant l'effort nécessaire pour effectuer une enquête exhaustive sur une de ces voies. Nous établissons en outre un lien entre le nombre d'animaux dans une voie et la taille de leurs dortoirs respectifs. Les résultats portent à croire que les murins des marais n'ont pas recours qu'aux plans d'eau pour rejoindre leur habitat d'alimentation; ils utilisent la dispersion directionnelle le long de voies de déplacement au-dessus de plans d'eau, combinée à des raccourcis au-dessus de la terre ferme. Ces résultats fournissent des renseignements pouvant être utilisés pour mieux comprendre l'utilisation des voies de déplacement par les chauves-souris. Ces connaissances peuvent également être appliquées aux enquêtes. [Traduit par la Rédaction]

Mots-clés : déplacement, mécanisme de dispersion, comptages de sorties, chiroptères, murin des marais, *Myotis dasycneme*, taille de la population, méthode d'enquête.

Introduction

Movements of mammals are widely studied. Knowledge of distances, directions, and route used by mammals play a major role in determining the structure and dynamics of populations, communities, and ecosystems. Knowledge of movement patterns of mammals living in an anthropogenic habitat are of special interest, as they provide information on how mammals cope with habitat fragmentation and changes in land use. A more cohesive understanding of animals' movement is crucial for conservation biologists wishing to restore degraded landscapes or mitigate negative effects of habitat fragmentation.

Mammals like lemurs, wolves, bats, seals, and sea lions live in large aggregations in a single location. Some of these colonial mammals do not share their food. The concentration of numerous nonsharing individuals has a dramatic effect on their daily spatial distribution. Colonial foragers need to move large distances away from their roost to find enough food without interference from competitors (Robson et al. 2004; Wolf et al. 2007). As travel cost increase with distance, it is essential for individuals to make de-

isions based on both expected and observed density of prey and competitors. Little is known regarding how most colonial mammals optimize the trade-off between foraging and commuting (e.g., Dukas and Edelstein-Keshet 1998; Daniel et al. 2008).

Bats form a unique group among nonsharing colonial mammals. A remarkable aspect of their dispersal behaviour is the use of flyways (paths with one dominant flying direction; also termed commuting routes in this paper) (e.g., Verboom 1998). A large percentage of the colony uses the same route from the roost to their foraging areas (in the morning the direction reverses) following clearly defined linear landscape features such as waterways, hedgerows, and tree lines (Downs and Racey 2006). Flyways of bats branch in several directions, each branch takes them farther away from the centre (the roost). The main aim of this study was to analyze the commuting and dispersal behaviours of the pond bat (*Myotis dasycneme* (Boie, 1825)).

The pond bat lives in large maternity roosts more or less in the centre of their foraging habitat. The entire group uses a communal home range of >100 km² (Voûte and Sluiter 1974). After emerg-

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ing from the roost, these bats fly to their nearby hunting habitat. The habitat close to the roost rarely holds enough resources (e.g., food) for the entire group. Like most animals, bats avoid interference between competitors (Mackey and Barclay 1989; Stillman et al. 1997; Baum and Kraft 1998). Therefore, some bats from the group start to commute away from the centre, with individuals often flying distances up to 25 km (Haarsma and Tuijter 2009).

Pond bats are specialized in trawling insects from the water surface with their large hind feet (Boonman and Limpens 1995). Several authors (e.g., Verboom et al. 1999; Van de Sijpe et al. 2004; Ciechanowski and Zapart 2012) claim pond bats prefer to use waterways for long-distance commuting within their home range. Although pond bats can combine commuting with foraging, most movements during the first part of the night are away from the roost. Bats are quite flexible in terms of foraging habitat; most bat species can hunt in several habitats (Kalko and Schnitzler 1993; Obrist 1995). During periods of extreme weather conditions, such as precipitation and high wind speeds (Beaufort scale >4), bats are known to change their hunting tactic; for example, they may hunt in more sheltered habitats or use a smaller home range. Also the presence of moonlight and structural clutter (e.g., duckweed) can alter their hunting tactic (Boonman et al. 1998; Ciechanowski et al. 2007).

In this study, we analyze the commuting behaviour of the pond bat on waterways based on group size and dispersal ploys. We described the commuting tactic, with several parameters such as the “time of the first bat passing along the commuting route”, “duration of commuting activity”, and “relative number of bats passing on their commuting route”. We hypothesized that (i) the commuting intensity of bats in a particular time and place would depend on the distance of this place to the roost and the group size of the respective roost; (ii) external conditions, e.g., weather conditions and habitat structure, influence the number of bats on the route, but do not influence commuting tactic parameters (e.g., time of arrival of first bat); and (iii) pond bats are not completely reliant on waterways for reaching their foraging habitat.

Materials and methods

Study area and identification of bats on the commuting route

In this study, we focus on commuting routes over water. The study area covered the provinces of Zuid-Holland, Overijssel, Friesland, Noord-Holland, and Utrecht. Slight differences in habitat structure exists between each province. In the Netherlands, almost all the waterways used by pond bats are man-made or, at least, improved by widening or straightening. The waterways were constructed or improved for various reasons, including peat exploitation, transport, and recreation. This has resulted in a pattern of long, straight, and broad waterways, alternated with large water bodies. It is relatively easy to identify pond bats on these waterways with a bat detector, as a characteristic rhythm of fm-QCF pulses can be detected around 35 kHz (Boonman and Limpens 1995).

The pond bat predominantly uses houses and churches as summer roosts. Pond bats tend to switch roosts within a village (Fig. 1). These switches are frequently induced by human disturbance (Stebbins 1988; Lewis 1995). During switches, their broad geographical location tend to remain unchanged. When pond bats do switch roosts, they often do so within a limited area, such as a village. Because of this behaviour, the commuting routes used by bats remain largely unchanged, which is of key importance for the research described here.

Observations on commuting routes

During 6 years of study between 2002 and 2009, researchers and bat volunteers studied pond bats along several waterways (all waterways wider than 10 m) between known roosts and their

hunting areas. The observations were always made from, or in the proximity of, a bridge, as these form effective observation sites (with the waterway generally being narrower). For each route, the distance (d) over water between roost and observation location was measured from a topographical map and expressed in kilometres.

On some waterways, observations were made on several occasions, whereas on other waterways, observations were made only once or twice during the entire research period. All the observations were made between April and September, starting 20 min before sunset. During the entire observation effort, the time (in hours and minutes) and direction of each bat was recorded. The time that each bat passed the observation location was later transformed to minutes after sunset. Here, the “time of the first bat passing along the commuting route” is used as a dependent variable. “Duration of commuting activity” describes the time interval between arrival of the first and last bat on the route. The interval ends if no more pond bats pass in the general commuting direction 15 min after the last bat sighting. The “total number of bats present on the route” is the sum of all the observed bats passing in one direction within the period of commuting activity. Although it is possible that bats turned around and returned to the commuting route without our knowledge, we minimized this factor by also counting bats flying in the opposite direction and then subtracting them from the total number of bats on the route (to avoid overestimation of foraging individuals). Species were identified using a Pettersson D100 bat detector combined with visual observations. The “mean number of bats on a route per minute” is calculated by dividing the total number of bats on a route by the duration of the commuting period (again at least two bats are needed to calculate this value).

Instead of correcting the data on bats on commuting routes for the influences of weather and the effect of structural clutter, we decided to only use data collected during standard conditions: low wind speeds (Beaufort scale <4) and no precipitation. Furthermore, we excluded all observations with no pond bat sightings and observations made in locations with inconvenient environmental conditions for the pond bats (e.g., extreme densities of duckweed or organic waste on the water surface). We did, however, want to correct our data for moonlight and cloud cover.

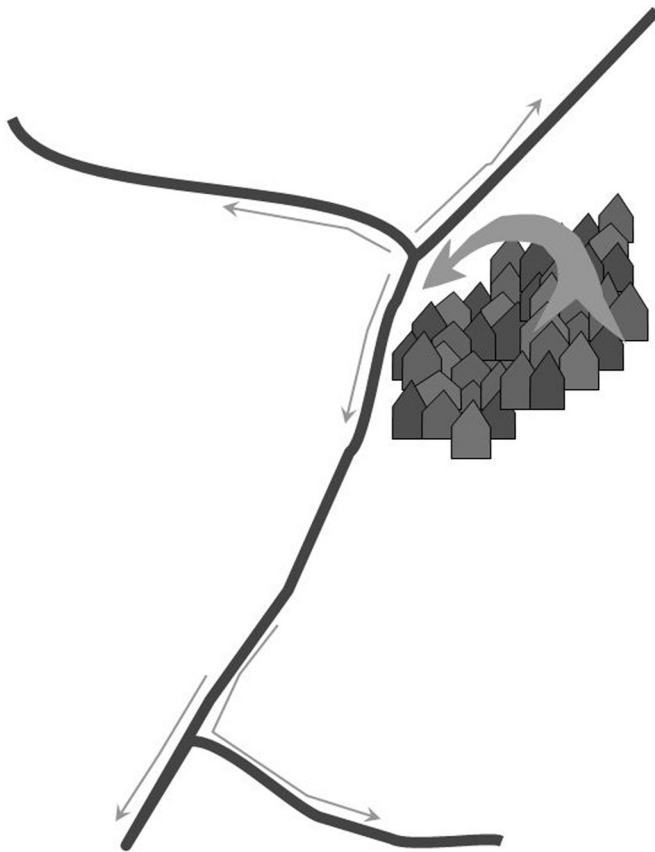
Potential intensity of moonlight, associated with moon phases, was defined using a 1–5 scale, where 1 is the new moon, 3 is the first quarter, and 5 is the full moon. Cloud cover was estimated using the following three categories: 0%–25% cover (clear night sky or some isolated clouds), 25%–75% cover (several scattered clouds but not covering more than 75% of the night sky), and 75%–100% cover (scattered clouds covering more than 75% of the night sky to a completely overcast night sky). Potential intensity of moonlight is influenced by cloud cover; to account for this effect, we used the following formula to calculate a “corrected moon phase”: if the sky was covered by more than 75% clouds, the presence of the moon was halved (results were rounded towards the nearest integer value).

Roost size and emerging bats

The number of animals on a commuting route is likely to be related to the number of animals present in their respective summer roost (i.e., roost size). These numbers will probably vary seasonally. To link seasonal variations in roost size with seasonal variations in the number of commuting bats, we selected one roost and regularly counted both the number of animals on the flyway (using the approach described here) and the number of animals emerging from the roost.

The (maternity) roost selected for this purpose is located in an old factory building in the village of Waddinxveen (52°1'N, 4°39'W). From 2002 to 2009, the number of emerging pond bats from this maternity roost were counted by a group of volunteers. These exit counts were mostly performed on a schedule of once

Fig. 1. An example of possible commuting routes used by a group of pond bats (*Myotis dasycneme*) from a village. Although the roost used might change, the routes used by this group remain fixed. Even when the bats use several roosts simultaneously, they will use the same routes.



every 2 or 3 weeks from April to September. In 2006 and 2008, the exit counts were done less regularly, but always at least three times per year. The bats could emerge from two sides of the building (north and south side); therefore, each exit count was done by at least two bat workers simultaneously. They used tally counters (clickers) and bat detectors during each count. The ambient light made it easy to discern all the emerging bats. The observers also sighted the silhouettes of the bats against the night sky. All emerging bats were counted until there was a gap of 15 min in emergence, at which point the emergence was considered complete. Incidentally, one or two entering bats were observed during the exit count. These were subtracted from the total number of emerging bats. As with the number of bats on the commuting route, the number of emerging bats is also influenced by weather conditions. For comparability, we used only observations gathered during standard weather conditions as listed above. The other 29 summer roosts in the research area were studied less intensively. Fourteen roosts were counted only once between 2002 and 2009. We used the maximum number of bats observed emerging from these roosts to compare with the number of bats on their respective routes.

Statistical analyses

Statistical analyses were carried out using SPSS version 17 (SPSS Inc., Chicago, Illinois, USA). The Spearman rank correlation coefficient (r_s) was used to test the relation between “number of passing bats on the route” and “number of bats emerging from the roost”. An ANCOVA was used to look for the relation between the three possible response variables, i.e., “time of the first bat pass-

Table 1. Results of the ANCOVA test with “time of the first pond bat (*Myotis dasycneme*) passing along the commuting route” as the dependent variable.

Independent variable	F	df	p
Distance (<i>d</i>)	105.756	1	0.000*
Corrected moon phase	0.633	4	0.639
Habitat structure	0.509	4	0.729
Habitat structure × corrected moon phase	0.455	10	0.917

Note: An asterisk indicates a significant relation ($p < 0.05$).

ing along the commuting route”, “duration of commuting activity”, and the log-transformed “relative number of bats passing on their commuting route”, and the categorical factors “corrected moon phase” and “habitat structure” (Zuid-Holland, Overijssel, Friesland, Noord-Holland, and Utrecht), as well as the covariates “distance (*d*)” and “total number of bats on the route”. The homogeneity of variance assumption was tested using a Levene’s test. The variances were not significantly different and homogeneity of variance assumption was accepted.

Results

Total data set

Between 2002 and 2009, a total of 199 counts were made along commuting routes during standard weather and environmental conditions. On 185 counts, more than two pond bats were observed (at least two bats are needed to calculate the “commuting duration”). The commuting counts were performed at 56 different locations. The total observation time was 27 841 min (464 h). In the same period, 44 exit counts from the maternity roost in Waddinxveen were performed, for a mean of 5.6 times per year. Each emergence count lasted, on average, 1 h and 20 min.

Time of the first bat passing along the commuting route

We found a significant relation between time of the first bat passing along the commuting route (min after sunset) and distance (*d*) from the observation point to the roost. The relation with other (possible) causal factors such as habitat structure, corrected moon phase, and their interaction was not significant (Table 1). The farther the distance, the later the first bat arrived at the observation point (Fig. 2). The first bats passing along the routes arrived between 11 and 124 min after sunset (mean 52 min). The last bat passing on route arrived between 46 and 149 min after sunset (mean 82 min). The total period for which bats could be observed commuting on the routes was between 11 and 149 min after sunset. Seventy-five percent of all passing bats on the flyways were observed between 42 and 100 min after sunset; 50% were observed between 53 and 84 min.

Duration of commuting activity

The total duration of the passing of commuting bats (i.e., time between first and last arrival) increased significantly with the total number of individuals commuting on the flyway ($r_s = 0.636$, $n = 193$, $p < 0.001$). This relation was not influenced by the distance (*d*), corrected moon phase, habitat structure, or the interaction between corrected moon phase and habitat structure (Table 2). Small numbers of bats (between 2 and 3 individuals) passed, on average, within 11 min of each other; mean size groups (13–17 individuals) took, on average, 38 min to pass; large groups of bats (29 individuals or more) took, on average, 47 min to pass (Fig. 3). The shortest duration of passing of commuting bats observed was 1 min (2 passing bats), whereas the longest duration was 85 min (74 passing bats).

Mean number of bats per minute

The results show that the number of passing bats per minute was related to the distance (*d*) between roost and observation location ($r_s = -0.380$, $n = 193$, $p < 0.001$; Fig. 4). On locations close to

Fig. 2. Relation between “time of the first pond bat (*Myotis dasycneme*) passing along the commuting route” (min after sunset) and “distance between roost and observation location” (five categories: 0 to 1, 1 to 2, 2 to 4, 4 to 6, and 6 to 8 km). Box plots show the 25th and 75th percentiles (boxes), the 10th and 90th percentiles (whiskers), and outliers (solid circles). The horizontal lines within the boxes are means.

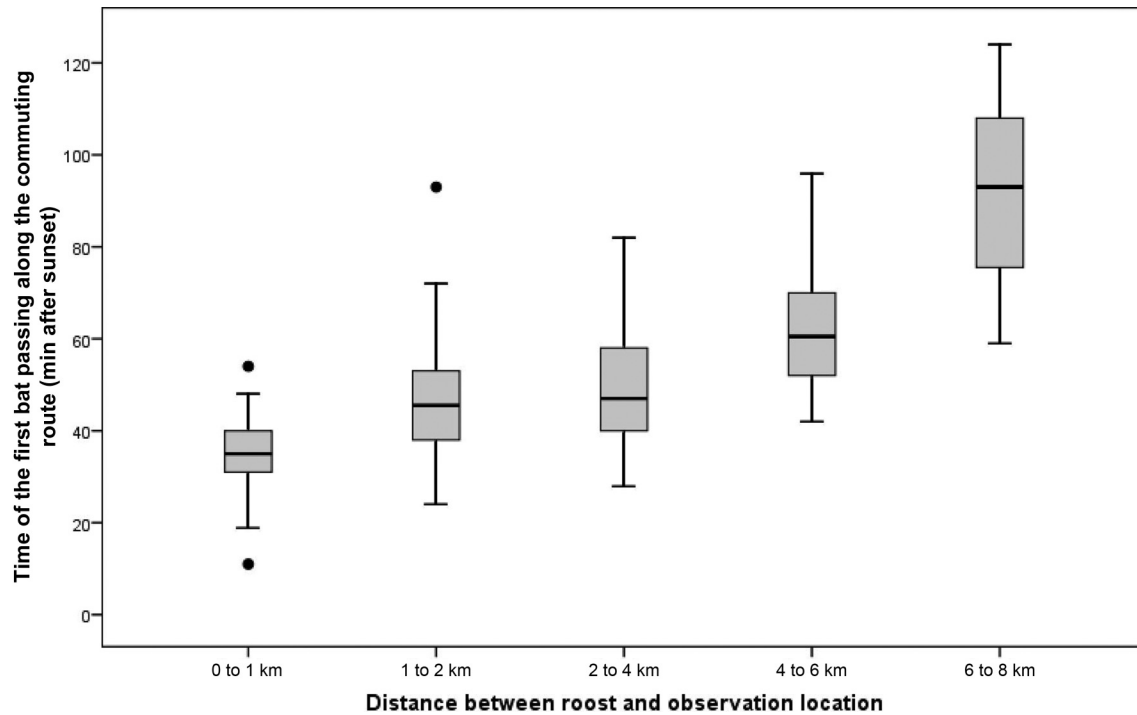


Table 2. Results of the ANCOVA test with “duration of commuting activity” of pond bat (*Myotis dasycneme*) as the dependent variable.

Independent variable	F	df	p
Total number of bats on route	77.226	1	0.000*
Distance (<i>d</i>)	0.734	1	0.393
Corrected moon phase	0.536	4	0.709
Habitat structure × province	0.693	4	0.598
Habitat structure × corrected moon phase	0.435	10	0.928

Note: An asterisk indicates a significant relation ($p < 0.05$).

the roost (between 0 and 1 km), high numbers of bats per minute were observed (mean 0.89 bats per min). The number of passing bats declined in relation to distance (*d*). The lowest densities were observed between 6 and 8 km from the roost (0.28 bats per min, which approximately equals 1 bat every 3–4 min).

Bats on the commuting route did not pass at regular intervals, but followed a skewed normal distribution: at the beginning of the night, many passing bats were observed and these numbers gradually decreased. Only infrequent observations of passing bats were made after 100 min after sunset (Fig. 5). The farther the observation location was located from the respective roost, the less obvious this pattern became: on routes located between 6 and 8 km from the roost, no clear peak in numbers was observed.

Relationship between total number of bats passing along the commuting route and number of bats emerging from the roost

During this research, the bat population in Waddinxveen was studied in detail. The number of bats emerging from this roost was correlated significantly with the number of bats passing along the respective commuting route ($r_s = 0.458$, $n = 26$, $p = 0.019$); during the year, a mean 13% of bats emerging from the roost passed along this commuting route (range between 9% and 18%). The lowest numbers of bats were observed in weeks 16 and 32, whereas the highest numbers of bats were observed between weeks 23 and 29 (Fig. 6). To compare the data from this site with

data from less intensively studied roost sites, we choose to select data gathered between week 23 and week 29 (the period when the largest number of bats was observed in both the flyway and the roost in Waddinxveen). Again, we found a significant relation between number of bats emerging from a roost and number of bats passing on the respective commuting route ($r_s = 0.567$, $n = 85$, $p < 0.001$). The relative number of bats passing on the commuting route decreased with distance (*d*) (Fig. 7)—between 0 and 1 km, a mean of 24.0% of the roosting population was observed; between 1 and 2 km, a mean of 13.4% of the roosting population was observed; between 2 and 4 km, a mean of 14.4% of the roosting population was observed; between 4 and 6 km, a mean of 10.9% of the roosting population was observed; between 6 and 8 km, a mean of 2.7% of the roosting population was observed. This relationship was not significantly influenced by the corrected moon phase, habitat structure, or their interaction (Table 3).

Dispersal along waterways

The number of bats on a given point along the studied commuting routes (i.e., waterway) is much higher than one would expect if pond bats would disperse at random over their habitat. If we assume the waterways are, on average, 40 m wide (which also equals the mean echolocation range of the pond bat; Boonman and Limpens 1995), then at 1 km distance from the roost one should, assuming bats disperse at random, observe approximately 1.57% of the animals from the roost (40 m is 1.57% of the circumference of a circle with a radius of 1 km). In fact, we observed a mean of 18% (with a minimum of 3% and a maximum of 36%; Fig. 7) of the roosting population, indicating that pond bats cluster on flyways.

Pond bats can disperse themselves over their communal home range strictly by relying on flyways over waterways or using a combination of flyways over water and routes over land. If pond bats use shortcuts over land, then instead of continued flight along waterways, they would bifurcate from the linear transect according to Fig. 8a and distribute themselves over a quadratic

Fig. 3. Relation between duration of commuting pond bats (*Myotis dasycneme*) (min) and number of bats passing along the flyway (six categories: 1 to 3, 4 to 7, 8 to 12, 13 to 17, 18 to 28, and >29 individuals). Box plots show the 25th and 75th percentiles (boxes), the 10th and 90th percentiles (whiskers), and outliers (solid circles). The horizontal lines within the boxes are means.

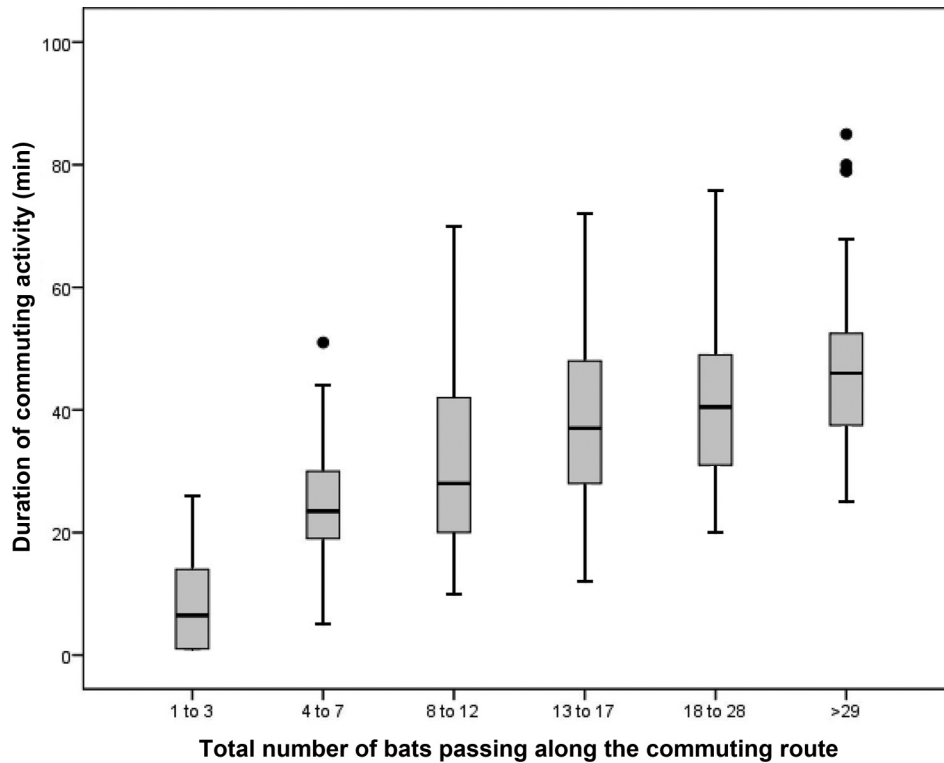


Fig. 4. Relation between number of passing pond bats (*Myotis dasycneme*) per minute and distance between roost and observation location (five categories: 0 to 1, 1 to 2, 2 to 4, 4 to 6, and 6 to 8 km). Box plots show the 25th and 75th percentiles (boxes), the 10th and 90th percentiles (whiskers), and outliers (solid circles). The horizontal lines within the boxes are means.

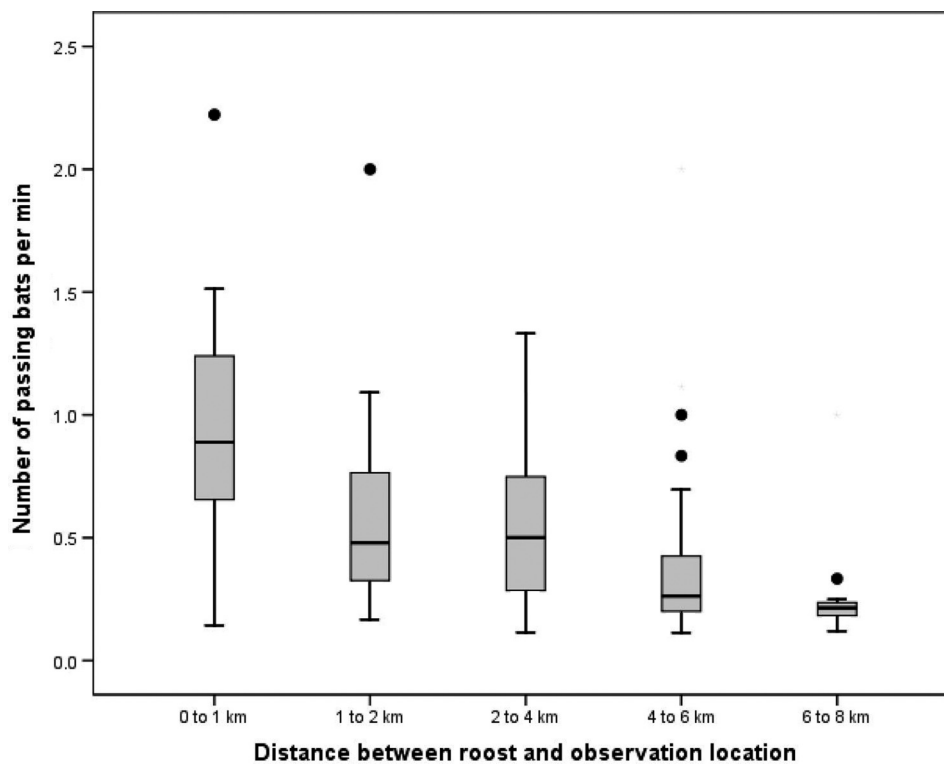


Fig. 5. Relation between mean number of passing pond bats (*Myotis dasycneme*) along the commuting route and time of arrival of bats after sunset (five categories: 0 to 1, 1 to 2, 2 to 4, 4 to 6, and 6 to 8 km). On average, the peak number of bats per minute was observed at the following distances from the roost—0 to 1 km: 52 min after sunset; 1 to 2 km: 61 min after sunset; 2 to 4 km: 62 min after sunset; 4 to 6 km: 83 min after sunset; 6 to 8 km: 109 min after sunset.

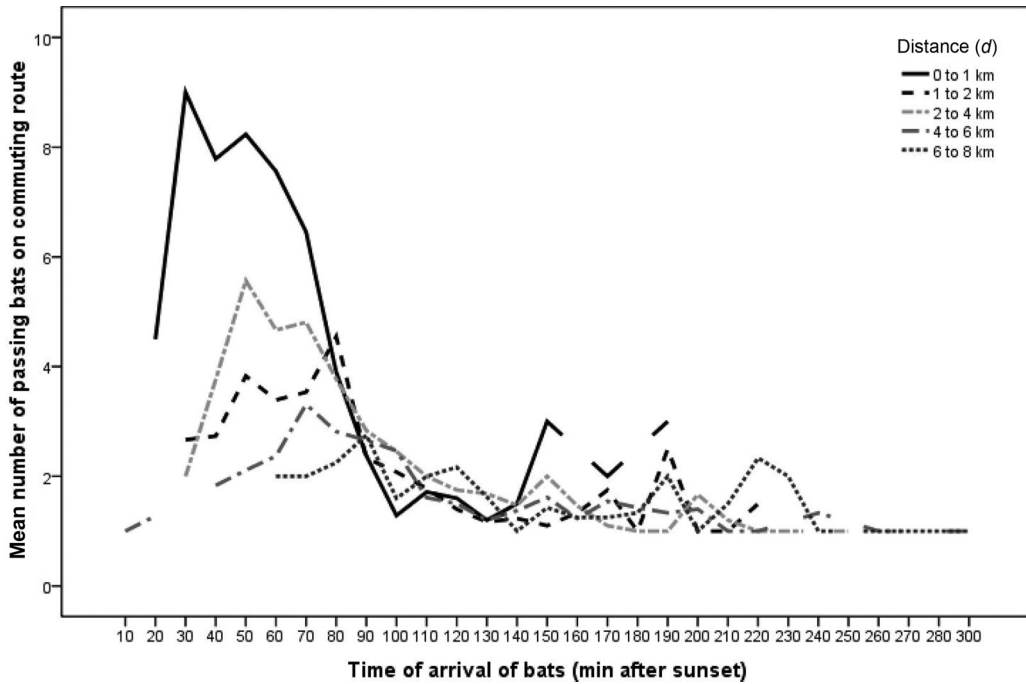
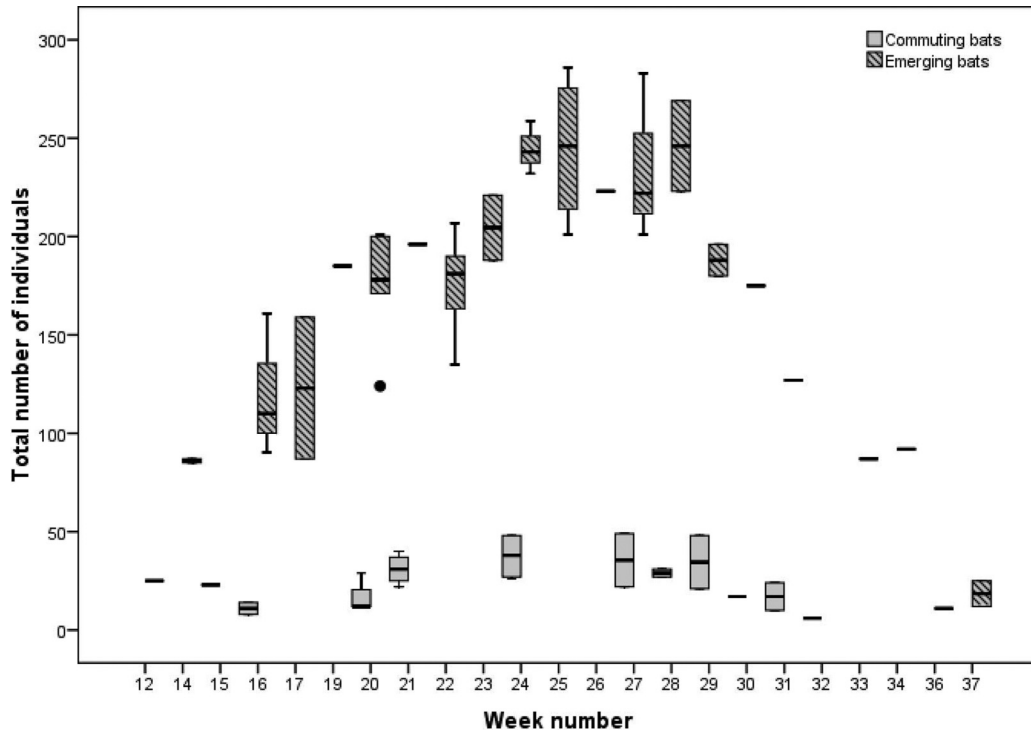


Fig. 6. Relation between seasonal variation (weeks) of “number of emerging pond bats (*Myotis dasycneme*) from maternity roosts in Waddinxveen” and “number of bats passing on the respective commuting roost”. Box plots show the 25th and 75th percentiles (boxes), the 10th and 90th percentiles (whiskers), and outliers (solid circles). The horizontal lines within the boxes are means.



increasing surface. Their numbers on a given distance from their roost would be comparable with other such points at the same distance. Furthermore, their numbers along a transect away from the roost would decline gradually. However, if their distribution

would strictly depend on the presence of flyways (Fig. 8b), their numbers on a given distance would be more variable because some flyways will lead to hunting sites without branching into other directions, while others will branch more frequently. Con-

Fig. 7. Relation between percentage of the population of the roost observed on the pond bats' (*Myotis dasycneme*) commuting route and distance between roost and observation location (five categories: 0 to 1, 1 to 2, 2 to 4, 4 to 6, and 6 to 8 km). Box plots show the 25th and 75th percentiles (boxes), the 10th and 90th percentiles (whiskers), and outliers (solid circles). The horizontal lines within the boxes are means.

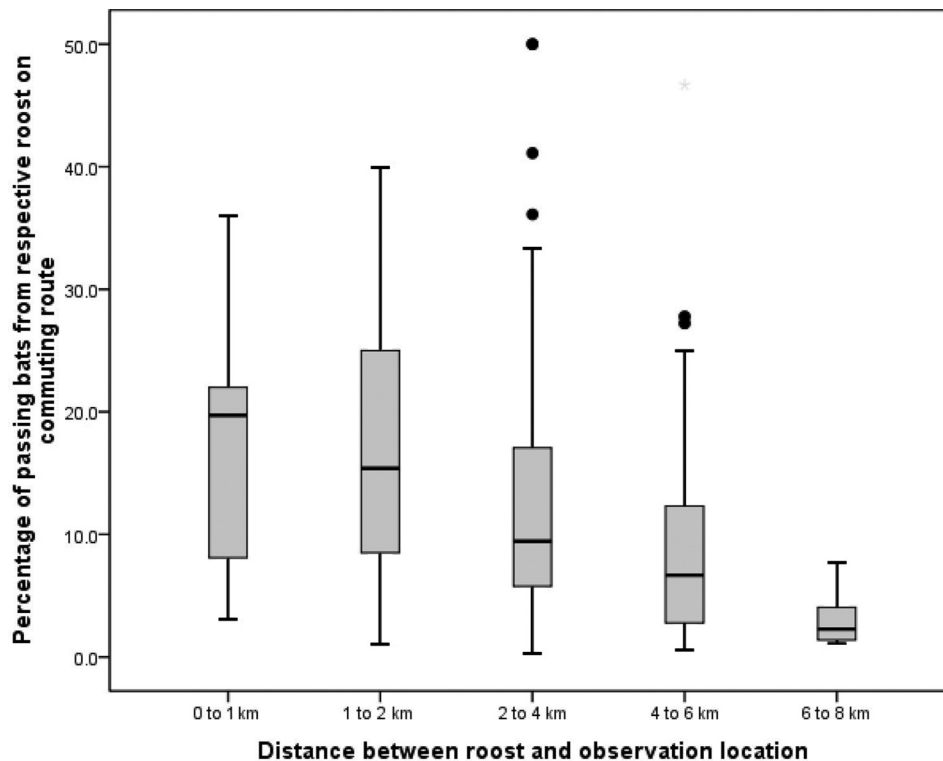


Table 3. Results of the ANCOVA test with log-transformed “relative number of pond bats (*Myotis dasycneme*) passing on their commuting route” as the dependent variable.

Independent variable	F	df	p
Distance (<i>d</i>)	37.603	1	0.000*
Corrected moon phase	1.423	4	0.235
Habitat structure	1.777	4	1.43
Habitat structure × corrected moon phase	1.022	6	0.419

Note: Only data from weeks 23 to 29 were used for this test. An asterisk indicates a significant relation ($p < 0.05$).

sequently, the number of bat along a transect would decline stepwise. Given the small difference between lower and upper quartiles at each distance (*d*) in Fig. 7, we assume pond bats use more shortcuts over land than previously assumed. Facts contributing to this hypotheses are observations made of pond bats hunting above meadows and along the edge of a forest. Other facts are observations on flyways over waterways close to the roost (Fig. 7), where a mean of 18% of the resident population is observed (i.e., 82% of the population uses alternative routes).

Discussion

We studied pond bats because we are most familiar with this species. Many other bat species are considered central-place foragers (e.g., Broders et al. 2006; Daniel et al. 2008) and use commuting routes (e.g., Holderied et al. 2006; Schaub and Schnitzler 2007). Variations in dispersal ploys are caused by differences in social organization (e.g., group size) and in life-history traits (e.g., wing aspect ratio and flight speed). Also, habitat quality, roost choice, and the homogeneity of the habitat will influence commuting behaviour (Kunz 1988; Lewis 1995).

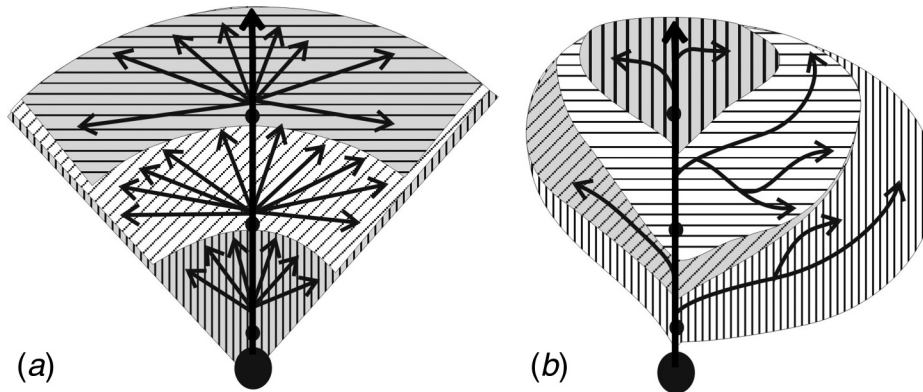
We are aware the man-made Dutch landscape is different than the ancient western Palaearctic landscapes; for example, the Polish and German lakelands (e.g., Schleswig Holstein and the

Masurian region). We believe that the effect of the landscape on the parameters describing the commuting tactic will be small. In each landscape, the bats will face similar constraints: the individuals from one roost will need to distribute themselves over their communal home range and they will use habitats for commuting, foraging, or both. Furthermore, they must choose whether to use shortcuts over land or continue to follow flyways over water to reach the farthest location of their home range.

Among possible internal factors influencing commuting tactics are fitness of the bat itself and the different energy demands during pregnancy, lactation, and after lactation. Lactating bats, for example, have to return during the night to nurse their young, which will decrease the maximum distance from the roost. With a bat detector it is impossible to identify between individual bats, therefore no information was gathered about the internal factors during this study. Fitting the data to match the reproduction period of the pond bats is impossible, as the start and duration of this period are highly unpredictable (Haarsma and van Alphen 2009b). For future studies, more information about internal factors and gender of passing bats would be a welcome addition. To achieve this, other study methods are needed such as capturing bats with mist nets.

We did not study the effect of the availability of prey, although we consider prey an important external condition that influences commuting tactics. Prey abundance has seasonal variation, which is influenced by environment factors such as temperature, wind, and relative humidity and precipitation. Pond bats have a very diverse diet, such as scarab beetles (Scarabidae), moths (Lepidoptera), mayflies (Ephemeroptera) and nonbiting midges (Chironomidae) (Ciechanowski and Zapart 2012). It is very difficult to collect a representative sample of prey items available in a habitat. Most methods used, e.g., trawling with a net or using an insect trap, are biased towards certain prey orders or families, habitats, and weather conditions.

Fig. 8. Schematic representations of the group distribution of central-place foragers across their home range. The roost is represented by the large solid circle at the base of each diagram; the observation transect is represented by the thick vertical arrows radiating from the roost; the observation locations are represented by the smaller solid circles along the observation transect. The number of animals that pass each observation location will distribute themselves across one of the shaded areas. (a) The distribution of these animals depends on flight along waterways in combination with shortcuts over land. (b) The distribution of these animals depends on the presence of flyways.



To understand more about the distribution pattern of pond bats, especially their usage of shortcuts over land, additional studies are needed. We recommend observing several points along a flyway, each located farther from the roost. With this method one is also able to check for the effect of branch presence on the number of bats.

In our study area, confusion between the two West European water trawling species, the Daubenton's bat (*Myotis daubentonii* (Kuhl, 1817)) and the pond bat, was unlikely. In the first place, the Daubenton's bat is very rare in our research area (which is also confirmed by surveys with mist nets; Haarsma and van Alphen 2009a). Furthermore, the identification of the pond bat on broad waterways is relatively easy because they use QCF-type echolocation. In other regions and on narrow waterways (<10 m wide), we recommend using a time-expansion detector. Bat workers should be aware of the silent flight of the pond bat. On frequently used routes, pond bats are known to fly using highly directional and often very short QCF calls (Van de Sijpe 2011). Visual observations are therefore always needed when observing pond bats on their commuting routes.

It can be difficult to count high numbers of emerging bats in the dark, especially without tools such as night-vision goggles. Comparison between videos made with an infrared camera and human observers showed that humans can underestimate the total number of bats, but this only becomes problematic when more than 1000 individuals emerge (Brown et al. 2008). Pond bats in the Netherlands and Europe do not live in these large numbers, therefore underestimation is not an issue.

Conclusion

We were able to describe the commuting and dispersal behaviours of the pond bat with parameters such as the "time of the first bat passing along the commuting route", "duration of commuting activity", and "relative number of bats passing on their commuting route". In the Netherlands, the community intensity of pond bats in a particular time and place depends on both distance of this place to the roost and group size of the respective roost. External conditions such as the intensity of moonlight and habitat structure have no significant influence on the commuting behaviour of the pond bat. Pond bats do not disperse at random, but instead cluster along their commuting route, flyways to their hunting habitat. The results suggest pond bats are not completely reliant on waterways for reaching their foraging habitat; the number of bats decreases gradually with distance, instead of a stepwise decrease. This could mean that pond bats use directional dispersal

following commuting routes over waterways in combination with shortcuts over land.

Implementation of results

The results of this study might be implemented as practical guidelines for survey work on commuting routes and roosts. The method (as described here) can be reversed, with location of roost and population size as unknown variables. The time of the first bat passing along the commuting route can be used as a coarse indication of the distance to a roost location; the later the first bat arrives, the farther away the roost is situated. Figure 2 provides a visual representation of the relation between the two variables. The standard error of the mean is small for small distances and gets larger as the distance between observation location and roost increases. Estimations of distances are therefore more accurate for nearby locations. The distance between roost and observation location can also be roughly deduced from the mean number of bats per minute; the farther the distance between the two, the fewer animals per minute were observed. Because of the irregular passing behaviour of bats on the route, this measurement is only accurate after a complete count of all passing bats. The population size of the bats' roost can be estimated by counting the total number of bats flying along the route in the same direction, taking into account the distance between observation location and roost. On average, between 2.7% and 24.0% of the bats from a roost were observed on the routes.

The results from this study can also be implemented as practical guidelines for the observation effort needed to identify a commuting route during, e.g., planological surveys. Pond bats can be observed passing along their flyway between 11 and 149 min after sunset, although the highest number of bats were observed (depending on distance from the roost) between 52 and 109 min after sunset. The farther the distance between roost and observation location, the later the pond bats arrive. The latest "first bat" was observed 124 min after sunset. For conservation purpose, researchers occasionally need to know whether a waterway is used by bats as a commuting route. We advise either a complete survey or a random sample of at least 30 min. The maximum observation period needed for a complete count of all bats passing along a route is 79 min and average between 20 and 40 min, depending on the number of bats passing. This observation does not include the 15 min break needed to determine the end of the commuting activity.

Lastly, our results can be used for protection purposes. The European Habitats Directive (which is the basis for national legis-

lation in European countries) protects bat roosts and resting places and prohibits damage, destruction, or deterioration of the function of a bat roost. In general terms, the Directive aims to safeguard the ecological functionality of bat roosts. This means the legislation can also be applied to commuting routes and foraging habitats, if these can be considered an essential attribute of the roost. This argument can only be applied if the fragmentation or severance of a route has a major impact on the viability of a roost, e.g., because the bats find it more difficult to reach their hunting grounds and other roosts. The results from this study show that pond bats cluster on their flyways; the percentage of the roosting population observed on flyways exceeds a random distribution. Up to 35% of the population of a nearby roost can be observed on one route. This observation has large consequences for the application of the European legislation, as flyways have an essential ecological function for pond bats. We hope that legislation will be applied accordingly.

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