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Foraging habitats preferences of bats: new question in interpretation of bat detector data

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Abstract. Studies of foraging habitat use by bats are nowadays common in many surveys and nature conservation projects. The use of ultrasound detectors has revolutionized the field studies of bats, but fast spreading methods are often not properly used in the beginning. We discuss the pitfalls of comparing bat detector data from habitats with different availability. Our examples show that in many situations smaller habitats may be assessed as preferred habitats and extensive habitats are regarded as "avoided", in spite of the fact that the animal spends most of the time there. We conclude that it is important to consider also habitat availability, habitat function and prey availability to correctly evaluate habitat preference. We find that in habitat use studies in bats, the time spent in a habitat is probably a more objective measure for habitat preference than relative flight activity. Improper interpretation of the data from acoustic studies may lead to serious mistakes in conservation management of bat populations.

Chiroptera, habitat use, selection, acoustic methods, activity

Studies of foraging habitat use and preference by bats (Chiroptera) are nowadays common in many ecological surveys and nature conservation projects (Hayes 2000, Gannon et al. 2003, Miller et al. 2003). There is an increasing need to consider habitat requirements of bats in landscape management activities (Miller et al. 2003). The use of ultrasound detectors has revolutionized the field studies of bats, offering great possibilities and advantages (Ahlén & Baagøe 1999). Past research has increased our knowledge and understanding of the ecology of bats and significant information has been obtained (Hayes 2000, Gannon et al. 2003). However, new methods are often not properly used in the beginning and there is still an ongoing dispute about the correct use and interpretation of the data, as well as the limitations of these methods (Hayes 2000, Sherwin et al. 2000, Fenton 2003, Miller et al. 2003). There are more known problems of acoustic studies – bat species produce echolocation calls of different intensity (Griffin 1958, Fenton 1999, 2003) and the variability of bat echolocation calls is great (Kapteyn 1993, Obrist 1995, 2004). Additionally many studies lack of clearly stated limitations of acoustic instrumentation (Hayes 2000, Gannon et al. 2003). Compared to other methods, such as radio tracking, bat detector surveys often lead to different results. Forests, for example, are found to be one of the most intensively used habitats in many radio tracking studies. In particular, older broad-leaved forests are regarded in Europe as a key foraging habitat for many bat species (Arlettaz 1996, Walsh & Harris 1996, Sierro 1999, Meschede & Heller 2000, Bontadina et al. 2002, Russo et al. 2002). However, acoustic sampling with ultrasound detectors often shows lower importance of the forest interior, based on the observed low flight activity. Especially when researchers compared bat activity in the forest interior and at forest edges or ponds with the help of bat detectors, they recorded comparatively few sounds in the forest interior. They concluded that this habitat is less intensively used by bats than the other habitats (e.g. Crampton & Barclay 1996, Grindal 1996, Krusic & Neefus 1996, Grindal & Brigham 1999). Such studies may have dramatic consequences for forest management strategies: It could be argued that forest harvesting may create suitable foraging habitat for bats along edges and in the openings of cutblocks (cf. Crampton & Barclay 1996, Grindal 1996).

We argue that in many studies it is not clear whether the observed high activity in the smaller habitats as ponds or forest edges is caused by preference for these habitats or if it is just an effect of concentration. The aim of the paper is to discuss the interpretation of bat detector data in respect of foraging habitat preferences by bats in situations where the studied habitats have different availability.

Determining habitat preferences

Generally, the purpose for determining habitat preferences of a species is to evaluate habitat quality – its contribution to the sustenance of the population. Importance of a habitat is its quality relative to other habitats. Use of habitat is generally considered to be selective if the animal makes choices rather than wandering haphazardly through its environment. Habitat preference can be a result of habitat selection and means disproportionate use of one habitat relative to others. Assessment of habitat quality is thus based on the presumption that preference, and hence selection, are linked to fitness and that preference can be inferred from patterns of observed use. Three general study designs have been used to infer habitat quality (Garshelis 2000). For habitat use studies on bats, use-availability design (disproportionate use of a habitat compared to its availability is taken as evidence of selection) and site attribute design (comparison of habitat characteristics of sites used by an animal to unused or random sites) are used to infer habitat quality usually based on radiotelemetry. Also the "density" (e.g. bat activity/time recorded by bat detector), as in demographic response design (Garshelis 2000), is indirectly used for assessing the habitat preference in acoustic studies: Based on relative flight activity, authors often made conclusions about the importance of the habitat (e.g. Grindal 1996, Krusic & Neefus 1996, Walsh & Harris 1996). Typically, a higher flight activity of bats in a habitat, compared to other habitats, is taken as an evidence of habitat preference.

Selectivity, preference and habitat size

How difficult it is to decide between habitat selectivity and habitat preference can be shown in simplified model situations (Fig. 1). We have two model habitats and only one individual bat (flying all the night) present in each case. Every point represents a location of the bat during the night (in fixed time intervals). There are six different model situations of habitat use. We want to show possible interpretation of the results based on flight activity (recorded bat passes/night) and habitat use (time spent in each habitat calculated from proportion of locations in each habitat – as in radio-telemetry studies). We count bat passes during the night in each habitat at one point within the range of the ultrasound detector. The detection range is smaller than habitat size, as is usual in field studies. The detection rate is estimated from the probability of bat detection in the habitat (assuming an equal study effort – 10× bigger habitat = 10× lower chance to detect the bat). We can see that the results are comparable, if the area of the habitats is the same (Fig. 1 – situations A, B).

(A) The bat spends half of the night in the first habitat and the same time in the second habitat. The detector will record the same flight activity (an equal chance to detect the bat in both habitats). Due to similar habitat use and habitat availability it is not possible to say if the bat is flying haphazardly through the study area or if it selects between habitats and decides to use them equally (1:1). There is clearly no preference, but the selection is questionable.

(B) In the second situation we see a 1:3 ratio of time spent in each habitat and we will probably record corresponding results with the bat detector (3× higher chance to detect the bat in one habitat versus the other). We can say that the bat selects its foraging habitat and clearly prefers one of them.

If the habitats have a different size, the habitat use (based on time spent in habitat) and results from the detector are very different (Fig. 1 – situations C–F):

(C) The observed habitat use is 9:1 (time spent in habitats) and corresponds approximately to habitat size (10:1). The number of bat passes is similar to situation A. The detector will record the same level of flight activity – which looks like there is no selection or preference. But an understanding of this situation is more complicated. We cannot distinguish in this situation if the bat is flying haphazardly through habitats and does not prefer one of them, or if the bat selects between habitats and prefers the larger one, because it spent 10× more time there.

(D) In this situation we can see clear selection and preference for the smaller habitat. The bat spent 3× more time in the smaller habitat. The detector will record, in this situation, 30× higher activity in this habitat due to concentration in a smaller area. However, the difference (3 vs. 30) shows, that "quantifying" of preference is not straightforward.

(E) This is the most complicated situation. The bat spent three-quarters of the night in the bigger habitat and the rest in the smaller habitat (3:1). We will record higher flight activity in the smaller habitat (3:10). This situation is very common and most researchers would conclude that this habitat is preferred, because there is a higher activity. But there are more possible explanations:

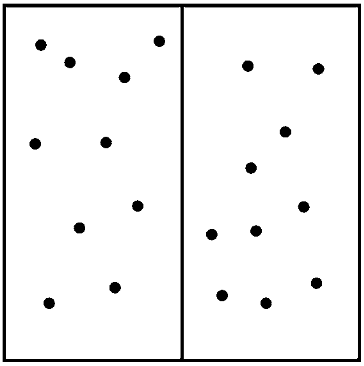
(1) The bat prefers the bigger habitat, but also uses the smaller habitat to a lesser extent (3:1). The result based on bat detector is confusing and is caused by effect of concentration in the smaller area.

(2) There is a concentration of available prey for one-quarter of the night in the smaller habitat and the bat forages there. Then the availability decreases due to prey activity schedules or temperature. For the next three-quarters of the night the prey is more abundant in the bigger habitat and the bat forages there. The bigger habitat is more important (more profitable) if the whole night is considered. The detected higher activity in the smaller habitat is again an effect of concentration in the smaller area.

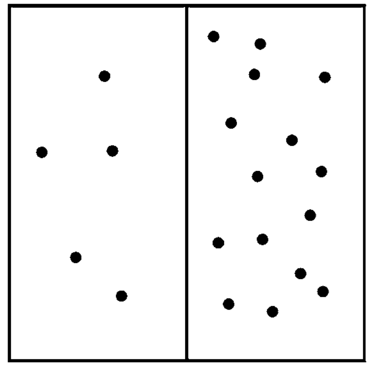
(3) The bat exploits first the more profitable smaller habitat until the prey availability decreases (limited resource) due to foraging. Then the individual moves to forage in the less profitable (bigger) habitat. We can assume that in this case by increasing the size of the smaller habitat, food resources would increase too, and it would make sense for the bat to forage longer in this habitat than before. We can assume that the smaller habitat is more attractive and really preferred.

We can only conclude in situation E that the smaller habitat is preferred if we know that foraging in the bigger habitat is caused by decreasing prey availability in the smaller one as a result of the bats foraging activity (explanation 3).

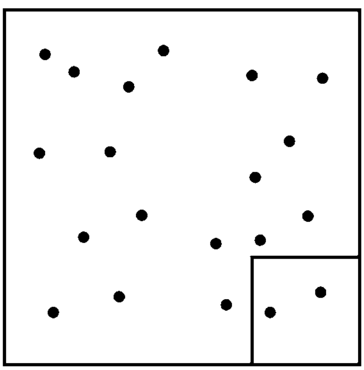
(F) In the last situation the bat uses both habitats the same time. But we will detect 10× higher activity in the smaller habitat. Again, most authors would conclude in the light of higher flight activity and a "use-availability" design that there is a clear preference for the smaller habitat because there is a higher activity than expected from availability. However, the bat uses both habitats equally. Based on habitat use, we can only suppose that the bat selects between habitats, but we do not know whether it does prefer either of them. The situation is again a question of



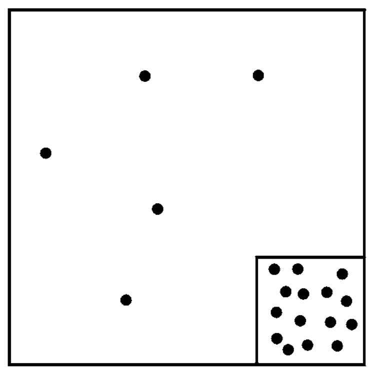
A) Selectivity?; no preference;
use 1:1; detection 1:1.



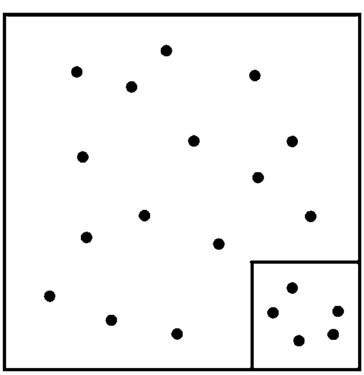
B) Selectivity and preference;
use 1:3; detection 1:3.



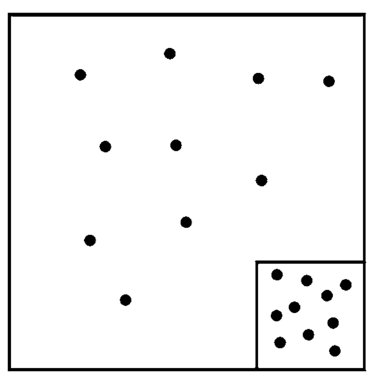
C) Selectivity?; preference?;
use 10:1; detection 1:1.



D) Selectivity and preference;
use 1:3; detection 1:30.



E) Selectivity and preference;
use 3:1; detection 3:10.



F) Selectivity; preference?;
use 1:1; detection 1:10.

←
Fig. 1. Habitat selectivity and preference of an individual bat in a model situation based on habitat use (time spent in a habitat) and acoustic method (detection of bat passes). Black spots represent location of the animal in the studied habitats in fixed time intervals during the night. In situations A and B, both habitats have the same size and in situations C−F, one habitat is 10× bigger.
Obr. 1. Selekcia a preferencia habitatu jednotlivého netopiera v modelovej situácii na základe využívania habitatu (čas strávený v habitate) a akustických metód (detekcia preletov netopiera). Čierne body zobrazujú pozíciu jedinca v študovanom habitate vo fixných časových intervaloch počas noci. V situácii A a B sú oba habitaty rovnako veľké, v situáciách C–F je jeden habitat 10× väčší.

limiting factors, as prey availability. If there are no limiting factors, there is no preference in this situation. Irrespective of varying habitat sizes, bats would use both habitats to the same extent. In a situation where resources such as food are limited, and the availability of the resource is better in the smaller habitat, we could assume preference. With increasing size of the habitat, the time the bat spends there would increase.

Consequences

Our example shows that in many situations smaller habitats may be assessed as preferred foraging habitats and extensive habitats are regarded as "avoided", in spite of the fact that the animal spends most of the time there.

McLellan (1986) argued that habitat use (based on time) is a better indicator of selection (but not automatically preference!) than use relative to availability (in our case; flight activity or use-availability). He reasoned that an animal familiar with its home range knows the availability and location of resources, and therefore the animal's location at any given moment represents selection. A similar conclusion for habitat use in general was made by Garshelis (2000), who reviewed delusions in habitat use studies.

To evaluate foraging habitat preference, we conclude that it is important to consider habitat selection as well as habitat availability and prey abundance. We suggest that, if resources are not limited, the observed use (time spent in a habitat) is also the best parameter for assessment of habitat preference. If there are limitations (see case F), comparative studies in areas of different habitat compositions may help to answer, whether a given habitat typed is preferred.

Finally we must agree with Miller et al. (2003), Gannon et al. (2003) and Fenton (2003), that bat detectors are not Silver Bullet (magical tool for solving problems). There are hazards if the crucial questions are not asked and answered in the study design.

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Súhrn

Preferencia lovných habitatov u netopierov: nová otázka v interpretácii údajov z detektorov. V súčasnosti sú štúdie lovných habitatov bežné v mnohých výskumoch a ochranárskych projektoch. Používanie detektorov prinieslo revolúciu do terénneho výskumu netopierov, ale nové metódy sú v začiatkoch často nesprávne využívané. V práci diskutujeme o možných rizikách pri porovnávaní údajov z habitatov o rozdielnej ploche. Na príkladoch je ukázané, že malé habitaty sa v mnohých prípadoch hodnotia ako preferované

a rozsiahle habitaty ako nepreferované, aj napriek tomu, že tu živočíchy trávia najviac času. Považujeme za potrebné zohľadňovať aj dostupnosť habitatu (v zmysle jeho plochy), funkciu habitatu a potravnú ponuku pre správne hodnotenie habitatovej preferencie. Dospeli sme k tomu, že v štúdiách využívania habitatov netopiermi je čas strávený v habitate pravdepodobne objektívnejším meradlom pre habitatovu preferenciu ako relatívna letová aktivita netopierov. Nesprávna interpretácia údajov z akustických štúdií môže viesť k vážnym chybám v starostlivosti o populácie netopierov.

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