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ORIGINAL PAPER

Bats benefit from beavers: a facilitative link between aquatic and terrestrial food webs

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Abstract Bat populations are declining in many areas, partly because up to two-thirds of their wetland habitats have been lost. One natural agent creating wetlands is the beaver, which is recolonizing its former range. Beaver flowages are known for their high production of aquatic invertebrates. We tested the hypothesis that the high numbers of insects emerging from beaver flowages influences their use by foraging bats. We compared bat use and bat numbers above flowages of introduced Canadian beavers *Castor canadensis* and in nearby control ponds where beavers were absent. The two bat species detected, *Eptesicus nilssoni* and *Myotis daubentoni*, used beaver flowages more than non-beaver ponds. This is especially the case for *Eptesicus nilssoni*. Bats also seemed to forage in larger groups while above beaver ponds compared to the control ponds. Beaver flowages appeared to improve bat habitats. A plausible reason for this could be the high number of insects emerging from beaver ponds. Favouring the beaver in habitat management is a tool for creating suitable conditions for many other species, such as bats. In areas not suited for the beaver, insect production can be achieved by imitating the beaver with man-made impoundments. This is especially important in areas which have lost most of their wetlands.

Keywords Bat conservation · Beaver · Emerging insects · *Eptesicus nilssoni* · Facilitation · Foraging habitat · *Myotis daubentoni* · Wetland management

Introduction

Bat populations are facing serious declines in many countries. This decline is largely due to human-caused habitat loss and modifications, affecting both the roosting places and feeding habitats of bats (Daan 1980; Walsh and Harris 1996; Hutson et al. 2001).

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Most microchiropteran bats are dependent on insects for food (Vaughan 1997; Wickramasinghe et al. 2004) and require suitable, low-risk foraging habitats (Fukui et al. 2006). Riparian areas have been found to be especially favourable feeding habitats for many insectivorous bats (Grindal et al. 1999; Fukui et al. 2006; Scott et al. 2009), but these habitats have declined dramatically during the past 100 years. Worldwide, more than half of the wetlands are estimated to have been destroyed, and in Europe up to two-thirds of all wetlands have been lost (Amezaga et al. 2002). In 1997, Vaughan et al. emphasized that one "needs to know which types of rivers, lakes and ponds are preferred by bats, and how freshwater habitats can be managed to attract more foraging bats".

In some areas, such as boreal forests, numerous wetlands still exist (Mack and Morrison 2006). However, most of them are not very productive (McNicol et al. 1987; Henriksen et al. 1998) and have been shown to be inferior habitats for duck broods, for instance, which depend on aquatic invertebrates (Sjöberg et al. 2000; Gunnarsson et al. 2004). Ducklings especially seem to be lacking above-surface foods, such as emerging insects (Nummi et al. 2000). Thus, average boreal wetlands potentially are also not particularly good habitats for insect-dependent bats.

However, one natural disturbance agent that increases the productivity of boreal ponds exists: the beaver (Nummi and Hahtola 2008). As ecosystem engineers (Jones et al. 1994) or keystone modifiers (Mills et al. 1993), beavers *Castor* spp. strongly influence the structure and dynamics of their habitats. By building dams, beavers modify pond and stream morphology and hydrology. These activities result in changes in the function of the riparian zone, ultimately influencing plant and animal community composition and diversity (Naiman et al. 1988). Beavers were decimated from most of their range 100–200 years ago by overhunting, but have now either returned or are returning to many areas (Nolet and Rosell 1998).

Beavers especially affect habitats at the aquatic-terrestrial interface. Where these two habitats meet, organic matter can be transported either from the aquatic to the terrestrial system or vice versa (Nakano and Murakami 2001; Paetzold et al. 2005). The role of allochthonous inputs as an resource for aquatic biota is generally recognized (Fisher and Likens 1973; Wallace et al. 1999), but less is known about the energy flow from aquatic to terrestrial systems (Paetzold et al. 2005). This input can be especially important for consumers living in less productive habitats (Bustamante et al. 1995; Stapp and Polis 2003).

The key elements of beaver flowages include a wide area of shallow water, breakdown of inundated vegetation and increased input of falling tree leaves. Vegetation decomposition results in a release of nutrients that form the base for a food web consisting of detritivores, such as chironomids and isopods (McDowell and Naiman 1986; Nummi 1989). Their increase is mediated further up in the trophic chain, and vertebrates including birds and mammals benefit from this increase (Grover and Baldassarre 1995; Collen and Gibson 2001; Rosell et al. 2005).

To our knowledge, the relationship between bats and beavers has not previously been investigated, apart from observations of bats at tree roosts at beaver ponds (Menzel et al. 2001) and of bat occurrence in beaver meadows (Brooks and Ford 2005). Because many bats intensively use emerging aquatic insects, and because these insects are produced in high numbers in beaver ponds, we assume that bat occurrence in beaver flowages could be affected. In this study we reveal how flooding of forest ponds and streams with beavers affects bats' use of these habitats.

Methods

Study area

The study area was situated in a 39 km^2 boreal watershed in southern Finland (61°10′N, 25°05′E) consisting of circa 100 ponds and small lakes. The shore types of the lakes range from oligotrophic bog and forest without emergent plants to more eutrophic types with lush vegetation. Apart from beaver disturbance, the water conditions have only minor year-to-year variation (Nummi and Pöysä 1995a). The beaver species in the area is introduced *Castor canadensis*, which plays a similar ecological role as *C. fiber*, although it may be a slightly more active builder of lodges (Danilov and Kan'shiev 1983). Beaver flowages were typically formed by building a dam at the outlet of a natural pond; one study pond was formed by damming a creek.

During 2002–2004, bat use and numbers in 11 beaver ponds (size range 0.3–12.3 ha) and 11 nearby control ponds (0.2–14.3 ha) were studied (eight pairs in 2002, two in 2003 and one in 2004). In addition, one pond, originally a control pond that was flooded after the first year, was followed throughout the study period. The beaver population has been followed for 30 years, so we know that of the control ponds, seven had been inhabited by beavers earlier (see Hyvönen and Nummi 2008). This means that the undisturbed state of beaver ponds did not differ from that of the control ponds. The beavers had left the seven control ponds at least six, but most often 10–20 years prior to the study. The beaver effect on insects emergence will dilute within a few years after abandonment (Dessborn et al. 2009), so presumably not much beaver effect was left in the controls.

Bat detection

Bats were detected during two visits, during mid-June and late July in 2002–2004.

A lake pair was normally investigated on the same night; in a randomized order in the first round and then in reversed order in the second. The investigation of the latter pond of each pond pair started 15–30 min after finishing the first one. In case the weather became unsuitable, the lake pair was investigated on consecutive nights, and then during the same time.

Detections were only made on clear, calm nights, and they started ca. 23.30–00.30. We used a D 100 heterodyne ultrasound detector (Pettersson Elektronik, Sweden). The detections were made at two random spots on each lake. Every detection lasted circa 1 h and included 10 one-min bouts. During this minute every echolocation call was counted, and bat species and activity were recorded. Altogether 20 bouts were made on each lake on each visit, except for two lake pairs, where only 10 bouts were made during the first visit. Average bat use is therefore expressed as observations per 30 bouts, and it sums the activity of all 1-min bouts; in Fig. 1 original numbers are shown. A second index expresses the maximum number of simultaneous bat calls, e.g. different individuals, during one round in each pond; observations of the two visits are pooled. The number of different individuals could be detected with the simple heterodyne detector because usually only groups of 2–3 individuals were detected and even the maximum number of individuals was low (4). The species identification was relatively easy, because only five regular bat species exist in Finland (*Eptesicus nilssoni*, *Myotis daubentoni*, *M. mystacinus*, *M. brandtii*, *Plecotus auritus*), and usually only four of them are found in boreal forest areas (Lappalainen 2003; Eeva-Maria Kyheröinen, pers. comm.).

We also compared group foraging in beaver and non-beaver ponds. Continuous group foraging was defined as more than one group observation during the 10 observation bouts. In doing this the two observation visits for each pond were held separately.

The differences in bat activity and numbers between beaver flowages and control ponds were tested pairwise with Wilcoxon's matched-pairs signed-ranks test. The difference in the amount of group foraging in beaver flowages versus control ponds was tested with sign test. All tests were two-tailed.

Results

Two bat species, northern bat *Eptesicus nilssoni* and *Myotis daubentoni*, were detected. Overall, they clearly used beaver ponds more than undisturbed ponds (Fig. 1, Wilcoxon's matched-pairs signed-ranks test, $T = -2.940$, $P = 0.003$). This was particularly the case for *Eptesicus nilssoni* (beaver ponds 11.8, non-beaver ponds 1.3; $T = -2.845$, $P = 0.004$), less clearly for *Myotis daubentoni* (9.4 vs. 2.1; $T = -1.660$, $P = 0.097$). Similarly, when the number of different individuals was considered, the number of all bats was higher in beaver ponds than in non-beaver ponds (3.0 vs. 1.0; $T = -1.994$, $P = 0.046$); again particularly the case for *Eptesicus nilssoni*, too (1.7 vs. 0.4; $T = -2.297$, $P = 0.022$). More (but not significantly) *Myotis daubentoni* were detected in beaver ponds than in non-beaver ponds (1.2 vs. 0.6; $T = -1.057$, $P = 0.291$). In average, the bat use of beaver ponds was eight times higher than that of non-beaver ponds.

Bats foraged more often in groups of 2–4 in beaver ponds than in non-beaver ponds: all bats (7 vs. 0, sign test $P < 0.05$), *Eptesicus nilssoni* (4 vs. 0), *Myotis daubentoni* (5 vs. 0, $P < 0.10$).

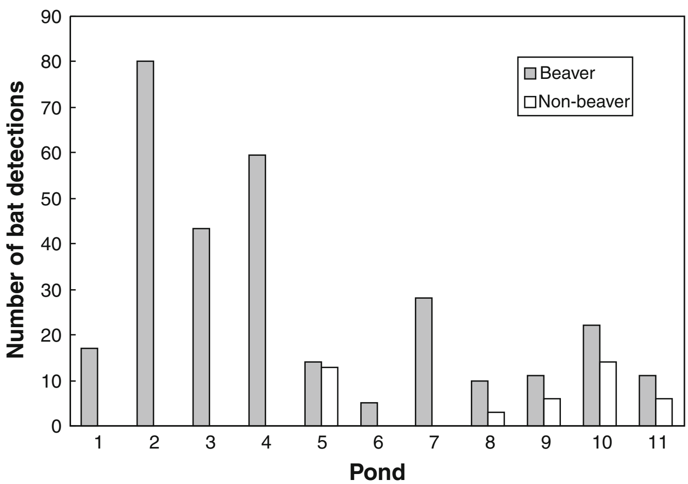


Fig. 1 Bat use of beaver ponds and nearby controls. *Bars* represent the total number of observations during altogether 40 one min detection bouts. Only 30 bouts were used in pond pairs 9 and 10

Discussion

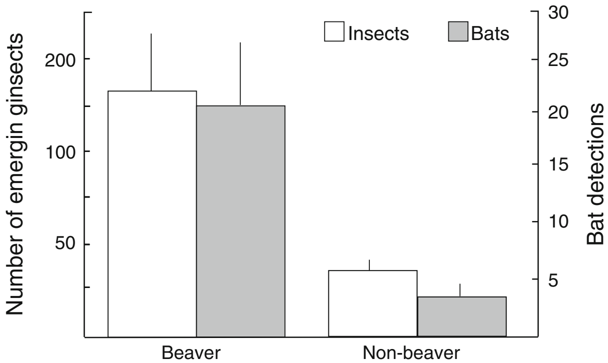
Bats, beaver, and the importance of emerging insects

Bats, especially *Eptesicus nilssoni*, clearly used beaver flowages more than other ponds, a relationship that has not been shown previously. Riparian habitats in general are good for bat foraging; in England and Sweden, they are especially used by *Eptesicus nilssoni* and *Myotis daubentoni* (Rydell 1986; Vaughan et al. 1997). Our study revealed that bats also clearly distinguished between different wetland patches. A likely candidate for the factor behind the pattern is emerging insects, which have been shown to be numerous in both beaver flowages and newly man-made lakes (Danell and Sjöberg 1982; Sjöberg and Danell 1983; Nummi 1992). Both bats of this study feed intensively on aquatic Diptera, Trichoptera and to some extent Ephemeroptera (Rydell 1986; Sullivan et al. 1993). Food resources are critically important for bats since bat populations are assumed to be close to the carrying capacity, and thus, resource limited (Findley 1993; Wickramasinghe et al. 2004).

In an earlier investigation (Nummi and Pöysä 1995b), we have found that in the study area in general, the number of emerging insects was 5 times higher in beaver flowages than in other water bodies (Fig. 2). Our data on emerging insects are only indirect coming from different ponds than the bat observations, but the relationship between insects and bat foraging activity has been revealed empirically in both agricultural (Wickramasinghe et al. 2004) and riverine (Abbot et al. 2009) systems. This relationship has also been shown experimentally in aquatic habitats: Fukui et al. (2006) controlled aquatic insect emergence from a section of stream with an insect-proof cover and compared bat foraging activity within this section with an uncovered part. Clearly more bat foraging was detected in the uncovered part of the stream. The idea behind the experiment was to be able to distinguish between the effects of habitat structure and prey availability on bat foraging.

The main focus of our study was on beaver effects, via any route, and we only suggest the insect emergence as the most plausible explanation of the pattern. In one earlier study of beaver facilitation on teal *Anas crecca* broods, both the food resource situation and the foraging habitat structure improved (Nummi and Hahtola 2008). However, for ducklings depending on shallow shores, the pond shore configuration is of great importance, which should not be the case for bats foraging in the air. In riverine habitats, though, beaver ponds can be structurally beneficial since they provide smooth water surface with trees on both sides, a habitat preferred by Daubenton's bat in that context (Warren et al. 2000).

Fig. 2 Average bat use in beaver flowages and control ponds according to this study, and average insects emergence (per 100 trap days) during June–July from beaver flowages and non-beaver ponds in the study area (data modified from Nummi and Pöysä 1995b)



We also had to rely on the comparison between existing beaver ponds and nearby control ponds because we had no before-during data for bats. However, in one case, one of our original control ponds was colonized by beavers during the study. The effects were clear: bat use increased from zero before beaver colonization to 11 in the first and to 37 bat detections in the 2nd year of flooding. It is typical that in flooded areas chironomids do not become numerous instantly, but only gradually, with the earliest peak during the second year of flooding (Sjöberg and Danell 1983; Nummi 1992).

With limited data, bats also appeared to forage more often in groups of 2–4 in beaver ponds than in non-beaver ponds. Especially for the *Eptesicus nilssoni*, group foraging indicates exceptionally good feeding opportunities. This species normally defends individual feeding territories, but the spacing pattern may change to group foraging when large concentrations of, for instance, water insects are present (Rydell 1986). Female *Myotis daubentoni* more typically forage in groups in good habitats (Wallin 1961).

Inputs from one ecosystem to another have usually been found when marine-derived resources have been subsidizing coastal organisms living in relatively low production habitats (Polis and Hurd 1996; Naiman et al. 2002). Recently, across-habitat linkage based on aquatic insects was described in relation to insectivorous forest birds. Birds used allochtonous aquatic prey especially when the quantity of in situ foods in the forest was low (Nakano and Murakami 2001). Moreover, it is indicated that resource subsidy from aquatic habitats strongly influences the activity of riparian-foraging bat species (Fukui et al. 2006). The presence of beaver enhances this linkage between boreal forest, which has a relatively low production, and the waters to which the beaver builds its dam.

Management of water bodies for bats

Our findings are interesting in light of beaver distribution and bat conservation. After near extinction from Eurasia during the 19th century, European beavers are now coming back via reintroductions. The most recent returns have been in the Netherlands (1988–1995), Czech Republic (1991) and Denmark (1999) (Nolet and Rosell 1998; Bau 2001), and reintroduction to England has long been debated (Macdonald et al. 1995). The beaver of our study was the Canadian beaver but the ecological effects of the two species are very similar (Danilov and Kan'shiev 1983). Beavers can provide good foraging habitats for bats, especially in areas with limited wetlands. And bats, at the same time, act as bioindicators of general ecosystem health reflecting the quality of riparian habitats (Jones et al. 2009).

In some areas, such as intensively farmed agricultural land, it may be impossible to manage beavers. In these cases, measures of active management of habitats should be undertaken. In human-dominated landscapes, sedimentation ponds or other flooded ponds that imitate the effects of the beaver can be constructed. The main use of sedimentation ponds and associated wetlands is in water conservation (Koskiaho et al. 2003), but they also offer an excellent means for promotion of biodiversity and bat conservation. This can be especially important since in many landscapes, e.g. in England, water bodies suitable for bats represent less than 1% of all available habitats (Walsh and Harris 1996). In habitats studied in an agriculture-related bat investigation, organic waters had the highest numbers of insects (Wickramasinghe et al. 2004).

Man-made ponds produce an insect emergence pattern similar to that of beaver ponds (Danell and Sjöberg 1982; Sjöberg and Danell 1983; Nummi 1989). Because good insect production usually lasts 5–7 years, and because sedimentation ponds eventually fill up, the ponds must be dried and dredged regularly. Thus, at the landscape level, it is good to have many small ponds so that when one is under reparation the others are functioning and may be used by bats and other species as well. In Finland, the forest and park service Metsähallitus has been creating wildlife ponds in a special programme (REAH). Bats have also been monitored within this program, and even the locally very rare *Nyctalus noctula* has been detected (S. Kattainen, pers. obs.).

Of the endangered bats of Europe, *Myotis dasycneme* and *Rhinolophus hipposideros* are very dependent on prey of aquatic origin, such as Chironomidae and Trichoptera (Vaughan 1997; Wickramasinghe et al. 2004). Of these two, *Myotis* also concentrates its foraging to riparian habitats (Mickeviciene and Mickevicius 2001; Van De Sijpe et al. 2004). Forested beaver ponds apparently are too closed for *Myotis dasycneme*, but more open beaver or man-made flowages with good insect production are much needed by the species, especially in areas lacking wetlands (Hutson et al. 2008).

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