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Beneficial impacts of Eurasian Beaver (*Castor fiber*) reintroduction on bat communities and aquatic macroinvertebrate prey: a case study from lowland Britain

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Abstract: Riparian ecosystems are valuable habitats for bats, due to high densities of emergent aquatic invertebrates that provide high-quality feeding areas. Throughout Europe, decline and extirpation of European beaver (*Castor fiber*) has been a key driver in the decline of the extent and quality of riparian habitat, and thus recolonisation has considerable potential to restore degraded areas. Previous research has shown that beaver-modified ecosystems can support more bats, but the assumed causal link (an increase in invertebrate prey) has not been tested. Here, we study bat activity and richness/abundance of aquatic macroinvertebrates at a site where free-roaming beavers have colonised naturally from a nearby (unofficial) release location versus a nearby control site with very similar hydrology and habitat matrix. Bat activity was recorded using walked activity transects and fixed-point acoustic detectors. Although bat species richness was similar, bat activity was substantially and significantly higher at the Beaver site versus the Control site overall (42.7%) and for four specific taxa: soprano pipistrelle (*Pipistrellus pygmaeus;* 8.4%), Daubenton's (*Myotis daubentonii*; 46.5%), common pipistrelle (*Pipistrellus pipistrellus;* 110.4%), and noctule (*Nyctalus noctula*; 170.9%). Richness of the larvae/nymphs of emergent aquatic macroinvertebrate species known to form an important part of bat diet was 205.5% higher at the Beaver site compared to the Control site, while abundance was 817.4% higher. Overall bat activity was also linked to habitat (lotic > lentic), survey method (transect > fixed-point), and season (May-July peak). This is the first evidence of a likely causal link between beaver recolonisation and bat activity via an increase in abundance of key aquatic invertebrate prey and we recommended that benefits of beaver reintroduction on bats be considered in future feasibility studies.

Keywords: bat activity; foraging sites; aquatic invertebrates; prey; riparian restoration ecology; rewilding

Introduction

Freshwater habitats support 6-10% of species worldwide yet cover less than 1% of the earth's surface (Dudgeon et al., 2006; De Conno et al., 2018). Over 80% of wetlands and riparian zones throughout Europe have become degraded by human activity (Verhoeven, 2014), including through drainage or hydrological realignment, often for urbanisation or agricultural purposes (Gumiero et al., 2013). Reduction in the extent and quality of wetland habitats is exacerbated given the pressing threats of hydrological systems change under climate change, leading to the potential for increased flooding and lengthy droughts. This has ecological cascade impacts throughout the ecosystem (Vaughan *et al.*, 1996; Walsh and Harris, 1996; Blakey *et al.*, 2017; de Conno *et al.*, 2018; Browning *et al.*, 2021).

Riparian ecosystems are invaluable for aquatic macroinvertebrates and the species at higher trophic levels that use them as their primary food source. One of these functionally-linked taxonomic groups is bats (Chiroptera). Indeed, over 70% of bats globally, including all species found in Europe, are insectivorous with aerial hawking being the most common feeding strategy (Norberg and Rayner, 1987; Fenton, 1990; Jones and Rydell, 1994; Russ, 2012). Macroinvertebrates with an aquatic larval life-stage are important prey for many bat species. For example, Trichoptera feature in the diet of all British bats, while aquatic Diptera are a major dietary component for Daubenton's (*Myotis daubentonii*), pipistrelles (*Pipistrellus* spp.) and Leisler's (*Nyctalus leisleri*) (Vaughan, 1997). Because emergent aquatic macroinvertebrates often remain close to water during their adult life-stage, aquatic sites often constitute high-quality foraging areas (Walsh and Harris, 1996; Fukui *et al.*, 2006; de Conno *et al.*, 2018). Some species, including Daubenton's bat, are particularly water-associated. As these bats feed on emerging Trichoptera and Chironomidae directly from the water's surface, riparian zones with a mosaic of lentic and slow-moving lotic areas provide optimal habitat (Swift and Racey, 1983; Rydell *et al.*, 1994; Flavin *et al.*, 2001). Pipistrelles also forage extensively in such habitats, with soprano pipistrelles (*Pipistrellus pygmaeus*) especially benefiting from high densities of emergent aquatic macroinvertebrates (Harris *et al.*, 1995, Davidson-Watts *et al.*, 1996). Loss, degradation or fragmentation of the riparian ecosystems that constitute high-quality foraging areas is a key threat for many bat species (Stebbings and Griffith, 1986; Frey-Ehrenbold *et al.*, 2013; Blakey *et al.*, 2017; de Conno *et al.*, 2018), especially given widespread insect declines (Shortall *et al.*, 2009; Sorg *et al.*, 2013). The magnitude of decline is exemplified by a study from Germany, which found a 75% decline of in flying insect biomass over 27 years (Hallmann *et al.*, 2017).

The Eurasian beaver (*Castor fiber*) is a keystone species through its role as an ecosystem engineer (Wright *et al.*, 2002; Janiszewski *et al.*, 2014; Brazier *et al.*, 2021). Beaver activity transforms uniform fast-flowing lotic waterbodies to a mosaic of standing water (lentic pools) and low-speed lotic channels. This increases habitat heterogeneity and lateral connectivity (Puttock *et al.*, 2017; Willby *et al.*, 2018). Most of this change is due to dam building, which significantly reduces water velocity (Puttock *et al.*, 2017), attenuates peak flows during flood events (Puttock *et al.*, 2020), and retains water during drought. This not only has socioeconomic benefits for surrounding landscapes, especially with intensifying climate change, but also acts to prevent seasonal desiccation that is catastrophic for aquatic macroinvertebrates (Hood and Bayley, 2008). Water quality downstream is often improved due to filtering, retention of sediment, and capture of nutrients in beaver pools (Brazier *et al.*, 2016). Thus, whilst human-induced extirpation of beavers from large parts of Europe has reduced the extent and quality of wetland and riparian ecosystems, the corollary is that reintroduction and/or recolonisation has considerable potential to restore degraded riparian areas (Rosell *et al.*, 2005; Pollock *et al.*, 2014; Law *et al.*, 2017; Gorczyca *et al.*, 2018; Grudzinski *et al.*, 2022). Indeed, over the last 100 years a combination of species protection, formal reintroductions, and recolonisation has resulted increases in beaver population size and range (Halley and Rosell, 2002). Recent estimates suggest that the European population has increased from ~1,200 individuals in the 19th century to around 1.5 million currently (Halley *et al.*, 2012; Wróbel, 2020 Halley *et al.*, 2021). In the UK, where beavers were extirpated, the population is now estimated to be appropriately 1,000 (Conroy and Kitchener, 1996; Halley *et al*, 2021). Although all UK animals are due to formal or informal releases and subsequent breeding, new populations are increasingly self-establishing due to natural range expansion throughout and between catchments mirroring the situation in mainland Europe (Smeraldo *et al.*, 2017)

There has been some research suggesting that beaver reintroduction/recolonisation can change aquatic macroinvertebrate community composition (Hood and Larson, 2014; Stringer and Gaywood, 2016) and macroinvertebrate biomass has also been found to be higher in the lentic pools above beaver dams than in original lotic habitat (Janiszewski *et al.*, 2014). More specifically, Pliūraitė and Kesminas (2012) found a greater abundance of Chironomidae in beaver pools compared to upstream and downstream locations. In contrast, comparatively little research has investigated the impact of beaver-modified riparian habitats on bats. One study, from Finland, showed that northern and Daubenton's bats (*Eptesicus nilssoni* and *Myotis daubentoni*) occurred at higher levels at a beaver site versus a non-beaver site. However, the focal beaver species was Canadian beaver (*Castor canadensis*), an introduced non-native species (Nummi *et al.*, 2011). A second study, from Poland, found higher activity levels by pipistrelle bats (*Pipistrellus nathusii, P. pipistrellus, P. pygmaeus*) and noctule (*Nyctalus noctula*) in riparian areas with reintroduced

European beavers versus unmodified areas, which the authors hypothesised might be due to greater emergent insect biomass and/or clearer flight lines near water due to tree feeling by beavers (Ciechanowski *et al.*, 2011). However, there has seemingly been little research that specifically links all three interrelated taxa (beavers, aquatic macroinvertebrates, bats) to investigate possible trophic links simultaneously, rather than hypothesising in the absence of direct evidence (e.g. Nummi *et al.*, 2011). Seemingly the only attempt at addressing this gap is from the Enclosed Beaver Project in west Devon from 2011 to 2015 (Symes, 2012), which identified an increase in aquatic macroinvertebrate richness and an increase in bat activity – including by rare Barbastelle (*Barbastella barbastellus*) and Natterer's (*Myotis nattereri*) bats. However, this was this based on an artificial fenced enclosure with invertebrate and bat surveys being conducted in different years.

In this study, we assess aquatic macroinvertebrate richness and abundance (collected via kick sampling), and bat activity (collected via walked activity transects and automated fixed-point acoustic detectors) simultaneously at a site with free-roaming beavers that have self-established via range expansion from a reintroduction zone and a nearby control site with very similar baseline hydrology and habitat. We predict that invertebrate richness and abundance, and bat richness and activity, will be higher at the beaver site than the control site.

Materials and Methods

Study setup and focal sites

The River Otter Beaver Trial (ROBT) run by Devon Wildlife Trust (DWT) was established in 2015 in Southwest England. Beaver sightings had been reported since 2008 involving two individuals presumably resulting informal, unlicenced reintroduction. Breeding was confirmed in 2014. The animals were scheduled to be removed as non-native species, however, widespread public outcry resulted in DWT applying to monitor the population under government licence and a five-year study was sanctioned in 2015 (Natural England, 2015; Crowley *et al.* 2017). By 2019, 13 territories had established and the population was allowed to remain (Brazier *et al.*, 2020; Auster *et al.*, 2022). Population growth and range expansion created 20 family groups by 2022.

The current study took place between April and October 2022 at two field sites ~10 km apart. As specified below, the sites were similar in terms of topography, hydrology and river morphology, surrounding habitat, upstream environment, and wider River Otter catchment. The headwaters were co-located in the same hill range with the confluence downstream of the two study sites (Figure 1a).

- The first site – henceforth the Beaver site – was Clyst William Cross County Wildlife Site. This was privately-owned land centered on a 0.7 km section of the River Tale, an incised tributary of the River Otter, with a ~900 m ditch network and two ponds. These aquatic features were located within 19 ha of semi-natural floodplain comprising lowland fen and marshy grassland dominated by meadow foxtail (*Alopecurus pratensis*), meadowsweet (*Filipendula ulmaria*), rushes (*Juncus*) and sedges (*Carex*) and wet woodland dominated by willow (*Salix*). Beaver signs were observed first in March 2016, due to natural range expansion, and a breeding territory became established in 2017. Since then, beaver activity has modified the site's hydrology by widening and damming the river and merging two ponds into a broader wetland area. Tree felling by beavers has had a significant impact on canopy cover, with drone surveys showing a significant reduction in mean canopy height with greater variability (Brazier *et al*, 2020).

- The second site – henceforth the Control site – was on Killerton Estate managed by the National Trust. It was bisected by the River Culm, an incised tributary of the River Exe, and rising adjacent to the headwaters of the River Tale that bisected the Beaver site. Within the wider 46 ha Estate, a 11 ha section of poor and semi-improved wet and seasonally-inundated grassland within the floodplain – dominated by meadow foxtail (*Alopecurus pratensis*), rushes (*Juncus*) and sedges (*Carex*) with small areas of scrub and priority wet woodland dominated by willow (*Salix*) – was selected. This area incorporated a 1.4 km length of the River Culm and seasonal ponds, with permanent ponds within 200 m of the study area. At the time of the study, Beavers were not present at this site.

This study is a comparison between just two sites (albeit in close proximity and similar in hydrology and habitat matrix, as well as in size). It is recognised that this framework is not as robust as a longitudinal study of the same site before and after beaver reintroduction, however, such a study design was not possible given that beavers colonised via natural range expansion to this site, and thus there being no pre-beaver baseline. Findings and conclusions are appropriately caveated.

Aquatic macroinvertebrate data

Targeted sampling of aquatic macroinvertebrate taxa was undertaken each month (April-October 2022) to coincide with bat monitoring described below. A standardised kick-netting method of 3x one-minute samples was used (Drake *et al.*, 2007), followed by invertebrate extraction based on Murray-Bligh (1999). Identification was conducted *in-situ* using a 15x hand lens with particular focus on larvae/nymphs of species that would ultimately emerge to give a flying adult life-stage, as well as surface-living taxa known to be preyed upon by bats. When necessary, specimens placed in carbonated water for no more than five minutes to temporarily suppress movement to aid identification. As per Balmford *et al.* (1996) and Wickramasinghe *et al.* (2004), specimens were identified to Family level in most cases, although dragonflies and demoiselles were identified to Sub-order (Anisoptera, Zygoptera) and stoneflies and caddisflies were identified to Order (Plecoptera, Tricoptera). Abundance was recorded for all groups.

Bat data

Bat data were collected using walked activity surveys following best practice as outlined by Collins (2016, 2023). Exact transect routes were based on local landscape features but standardised between the sites by following the main watercourse (the River Tale at the Beaver site; the River Culm at the Control site) for approximately half of the transect with the remaining part of the route covering fen and marshy grassland alongside tributaries, ditches, ponds, hedges and edges of wet woodland and scrub. The transect at each site was 3 km in total with 9 locations at which walking was paused to collect point-count data for 5 minutes each on two occasions per point. At the Beaver site, the 3 km transect took the form of a pre-defined circular route that was walked twice per survey (Figure 1b); at the Control site the 3km transect took the form of a linear route was walked twice, once in each direction (Figure 1c). All transects started at sunset and covered a 3-hr period to ensure that any later emerging species, such as Daubenton's and lesser horseshoe (*Rhinolophus hipposideros*), were detected (Russ, 2012; Goodenough *et al.*, 2015; Perks and Goodenough 2021). Two walked activity surveys were undertaken at each site in spring (April and May 2022), two during the summer (July and August 2022) and two during autumn (September and October 2022). The overall sample size for walked transects was 36 hours of bat data across 12 nights in total (6 transects * 2 sites * 3 hours per transect), which is double the minimum sample size recommended in the bat surveying good practice guidelines of one activity survey per season per site (Collins, 2023). In all cases, the Beaver and Control sites were surveyed on consecutive nights. Bat activity was recorded using an Echo Meter Touch 2 Pro bat detector. No precipitation was recorded during any of the transect surveys and wind speed was never higher than two on the Beaufort scale.

Passive acoustic monitoring was undertaken using automated fixed-point detectors. Two AudioMoth detectors were deployed at each site (i.e. four in total), one being sited in lentic habitat surrounded by wet woodland, the other in open lotic habitat at the confluence of a tributary and the main incised channel. The four AudioMoths were deployed for three consecutive nights per month, always during a suitable weather window and overlapping the macroinvertebrate sampling (described above) as much as possible. This gave 84 survey nights in total (3 nights per month * 7 months * 2 habitats per site * 2 sites); which exceeded the upper level of monitoring suggested by Collins (2023) for sites assessed as having high-quality habitat (6 nights per site per month for 7 months rather than the recommended 5 nights per site per month for 7 months). All detectors were mounted on trees at the edge of the water at a height of 1.5-2 m and oriented towards the water; no vegetation or other obstructions were present. Recommended settings for AudioMoths for bat surveys differ but here a sample rate of 384khz, high pass filter, no amplitude threshold and a medium microphone gain was used as per Lopez-Bosch *et al.* (2021), Michez *et al.* (2021) and Orr (2021), which gave the best balance between memory usage and data recording. The most recent firmware 1.7.1 was installed prior to the trial survey. At the time of the study, there was no bat trigger option on the detectors to activate them in response to bat calls. Instead, systematic sampling was undertaken, with AudioMoths programmed to record a 10-second clip every 30 seconds. This provided 1,080 recordings (3 hr recording time) per detector per night, the same as recorded on walked transects but intermittent throughout the night rather than being continuous for a single 3 hr block. Overall, there were 90,720 ten-second files equating to 252 hours of data across 84 nights (3 nights per month * 7 months * 2 habitats (lotic and lentic) * 2 sites).

All bat data were firstly processed in Kaleidoscope (version 5.3.8) to remove any files identified as noise. This reduced 90,720 files to 6,276 files for the Beaver site and 4,696 files for the Control site. Files were then analysed to identify the species (singular or plural) in each recording and add labels. The ‘Count Labels’ function was used to calculate the number of bat passes per species/genus for static locations (AudioMoth data) and transects (EchoMeter data). Any unclear calls were identified to genus level as is common practice due to difficulty in conclusive species identification from call structure alone (Russ, 2012; Collins, 2016).

Data analysis

To explore basic patterns in invertebrate and bat biodiversity between the Beaver and Control sites, chi square goodness of fit tests were used. Then, to examine spatiotemporal patterns in more detail, a series of Generalised Linear Models (GLMs) were run. For macroinvertebrate data, two models were created, firstly for the richness of emergent invertebrate taxa and secondly for abundance of emergent taxa. Each model involved a dependent variable comprising count data, such that Poisson distributions and a log link function were used. The independent variables were categorical and thus entered as fixed factors: (1) site (Beaver vs Control site; binary); (2) seasonality (time of year; numbered months from April to October); and (3) habitat (lotic vs lentic). Both invertebrate models had 84 cases (3 kick samples * 7 months * 2 habitats per site * 2 sites). For bat data, seven models were created. The first model was for the summary metric of overall bat activity (total passes per night regardless of species). The remaining six models were taxon-specific considering either an individual species (common pipistrelle, soprano pipistrelle, noctule, serotine) or an individual species + unidentified congeners (Daubenton’s + *Myotis* congeners; Leisler’s + *Nyctalus* congeners). The predictor framework was more complex for the bat models, with four fixed factors in a partially nested design: (1) site (Beaver vs Control site; binary); (2) seasonality (time of year; numbered months from April to October); (3) survey method (automated fixed-point vs transect data); and (4) habitat (lotic vs lentic). Habitat was entered as a nested term within survey method because habitat data were only collected during fixed-point acoustic surveys (transects were conducted at site level). All the bat models had 96 nights of data (1 transect survey * 6 months * 2 sites = 12) + (3 nights of automated fixed-point data * 7 months * 2 habitats * 2 sites = 84). Finally, the direct link between emergent aquatic macroinvertebrate abundance and bat activity was tested using a Pearson correlation. All statistical analysis was undertaken in IBM SPSS (Version 29).

Results

Aquatic macroinvertebrates

In total, 21 Order/Family macroinvertebrate taxa were recorded at the Beaver site and Control site combined. Of these, 10 taxa were larvae or nymphs of emergent taxa known to be preyed upon by British bat species while aerial hawking, while a further two were taxa known to be taken by Daubenton's bats gleaning from the surface of waterbodies (Table 1). Taxonomic richness of all aquatic macroinvertebrates was higher at the Beaver site (mean 3.000 ± 0.266 SEM per kick sample) than at the Control site (mean 1.619 ± 0.854 SEM per kick sample): this difference was statistically significant (Chi square goodness of fit: $\chi^2 = 4.481$, d.f. = 1, p = 0.034).

When considering emergent aquatic macroinvertebrates alone, taxonomic richness per kick sample was again higher at the Beaver site (1.381 ± 0.460) compared to the Control site (0.452 ± 0.208). The most abundant emergent invertebrate families at the Beaver site were Chironomidae, Ceratopogonidae and Chaoboridae (n = 176, 35 and 28, respectively). Chironomidae were the most abundant at the non-beaver site (n = 17) followed by Baetidae, Tricoptera and Ephemeridae, albeit in much smaller numbers (n = 5, 2 and 2, respectively). Abundance of emergent aquatic invertebrates was also higher at the Beaver site compared to the Control site (6.119 ± 2.151 versus 0.667 ± 0.147).

Generalised linear modelling, undertaken to analyse the complex patterns in the emergent aquatic macroinvertebrates between Beaver and Control sites statistically (also allowing for differences between lotic and lentic habitats and seasonal patterns) showed richness of larvae/nymphs of aquatic macroinvertebrates was significantly different between Beaver and Control sites and at different times of year; there was no significant difference between lotic and lentic habitats (Table 2; Figure 2a-b). When considering abundance of emergent aquatic macroinvertebrates, this was significantly different between site, time of year and lotic vs lentic habitats (Table 2; Figure 2c-d).

Bats

In total, 10 bat species/genera were recorded at the Beaver site compared with 9 bat species/genera recorded at the Control site (Table 3). This was not statistically significant ($\chi^2 = 0.048$, d.f. = 1, p = 0.827). Lesser horseshoe was the only species found at one site (Beaver) and not at the other (Control). Using fixed-point data, average richness per night was very similar across the sites: on average 4.167 ± 0.387 SEM taxa were recorded per night at the Beaver site compared to 4.381 ± 0.254 SEM at the Control site. The number of taxa recorded using transect surveys was considerably lower but the magnitude of the difference between sites was similar: 1.983 ± 0.313 species per night at the Beaver site compared to 2.883 ± 0.094 at the Control site. The most active species across all sites and survey methods were soprano pipistrelle (n = 5,351 passes), common pipistrelle (n = 3,821 passes), and *Myotis* spp. (predominantly Daubenton's + unidentified congeners) (n = 1,987 passes) (Table 3). In total, these taxa accounted for 95% of all activity. Three other taxa comprised most of the remaining 5%: noctule (n = 347 passes), Leisler's + unidentified congeners (n = 120 passes), and serotine (n = 96 passes) (Table 3). Calculation of Shannon's Diversity Index (H) and Shannon's Evenness (EH) for the bat communities at both sites indicated strong similarities (Beaver site: H = 1.236, EH = 0.344; Control site: H = 1.173; EH = 0.359). This indicated that while the activity levels differed between sites, the community structure (relative abundance within the community) was similar.

Overall bat activity measured as total bat passes throughout the study was 11,749 (6,908 at the Beaver site versus 4,841 at the Control site). However, there were notable differences in bat passes per night depending on site and survey method: Beaver site = 183.833 ± 22.609 bat passes per night using transect data and 205.472 ± 29.903 bat passes per night using fixed-point data; Control site = 144.167 ± 38.203 bat passes per night using transect data and 42.306 ± 4.942 bat passes per night using fixed-point data. Generalised linear modelling, undertaken to analyse the complex patterns in the bat activity between Beaver and Control sites statistically (while also allowing for differences between survey methods, lotic and lentic habitats and seasonal patterns), confirmed there were significant differences in bat activity between sites and survey methods, and further showed that time of year and habitat were also significant (trend direction, significance, and magnitude of all findings shown in Table 4 and Figure 3).

Similar GLMs were performed for the six most prevalent taxa (Table 5); the remaining four taxa listed in Table 3 were not recorded frequently enough for specific analysis to be meaningful. There were significant differences between site for common and soprano pipistrelle, Daubenton's + congeners, and noctule (Beaver site higher than Control site in all cases; Table 5). For all taxa except serotine, there was a seasonal pattern in activity, typically either a peak in the summer months or relative temporal stability until a decline at the end of the season (Table 5). Transects recorded significantly more bat passes per night than automated fixed-point detectors for most taxa (Table 5). Within the automated fixed-point data, significantly more activity was recorded in lotic habitats for common and soprano pipistrelle, whilst more activity was recorded in lentic habitats for Daubenton's + congeners (Table 5).

Direct correlation between invertebrate abundance and bat activity

There was a significant positive correlation between abundance of emergent aquatic macroinvertebrates (kick net samples) and overall bat activity (bat passes per night detected via fixed-point detections): Pearson correlation $r = 0.631$; $n = 14$; $p = 0.016$; $r^2 = 0.398$). This analysis used monthly averages per site, since this the only way in which data collected from multiple spatial kick sampling replicates per month could be compared with bat activity on different nights per month could be compared.

Discussion

Our results, from what appears to be the first study to simultaneously consider bats and potential invertebrate prey at sites with and without reintroduced beaver, show that emergent aquatic invertebrate and bat biodiversity are both higher at the Beaver site compared to the Control site. It is important to explicitly mention that this is initial outline research (two sites; one year) and should be thought of effectively as a case study or "proof of concept". We hope this this will act as a springboard for much more detailed follow-up work with a larger number of sites, ideally using a before/after framework, and bringing in more advanced measures such as invertebrate biomass (rather than just abundance) and ideally flying insect emergence surveys.

Aquatic Invertebrates

Beaver-modified environments can be beneficial for macroinvertebrates (Hering *et al.*, 2001). Studies from Finland and the USA show that habitat heterogeneity occurs through successional changes to physical and biological elements, which increase a site's potential to support a greater range of invertebrates with varied habitat requirements (Nummi *et al.*, 2011; Bush *et al.*, 2019). Differences in aquatic macroinvertebrate densities have been identified up and downstream of beaver dams (Smith *et al.*, 1991; Redin & Sjöberg, 2013), while areas directly downstream of beaver dams have also been found to be more biodiverse than similar areas upstream (Wojton & Kukuła, 2021). There can be more subtle effects too, for example, presence of dams affects the size and fecundity of Ephemeroptera (Fuller and Peckarsky, 2011). Here, the richness and abundance of emergent aquatic invertebrates known to form an important part of bat diets (Sologor, 1980, Flavin, 2001, Krüger *et al.*, 2014) was substantially higher at the Beaver site compared to the Control site. The most notable difference in the larval or nymph forms of emergent aquatic invertebrates between the Beaver and Control sites was the abundance of midges (Chironomidae, Ceratopogonidae and Chaoboridae). These are present in the diets of most British bat species (Flavin *et al.*, 2001). This accords with previous work by Nummi and Pöysä (1995), who found that the abundance of emerging insects in beaver-modified riparian systems was five times higher than in waterbodies where beavers were absent, and Pliūraitė and Kesminas (2012), who found a higher abundance of Chironomidae in beaver-created ponds compared to upstream and downstream locations. Although emergent aquatic macroinvertebrates often remain close to water during their adult life-stage, (Walsh and Harris, 1996; Fukui *et al.*, 2006; de Conno *et al.*, 2018), it is important to explicitly caveat that we quantified larvae or nymphs of macroinvertebrates known to be preyed upon by bats, rather than quantifying airborne prey availability. Interestingly, however, two non-emergent taxa recorded only at the Beaver site: lesser water boatmen (Corixidae) and whirligig beetle (Gyrinidae) have been identified in faecal analysis of water-gleaning Daubenton's bat (Flavin, 2001). Both taxa are adapted to lentic environments, so beaver-modified riparian systems would provide more suitable habitat compared to non-modified areas.

Bats

Bats need to consume a high number of invertebrates to maintain energy. For example, a Daubenton's bat, weighing ~10g, requires at least 500 insects per hour (i.e. a successful capture every 7 seconds) to break even on its energy budget (Kalko and Braun, 1991). It seems likely that the higher bat activity at the Beaver site was driven by especially good feeding opportunities. While bat species richness was similar between the sites, bat activity was substantially and significantly higher at the Beaver site. Using comprehensive data from both automated fixed-point acoustic and walked transect surveys, showed that overall activity (mean bat passes per night) was higher at the Beaver site. Greater activity was also recorded at the Beaver site relative to the Control for the four most common taxa: soprano pipistrelle, Daubenton's, common pipistrelle, and noctule. These higher activity levels are despite data from Devon Biological Records Centre (2022a, 2022b) showing substantially more confirmed bat records and roost sites within 5 km of the Control site (n =144 records in preceding 10 years; nearest roost <500 m) than within 5 km of the Beaver site (n = 64 records; nearest roost > 2km). This suggests that although bat activity at a site might be influenced by the abundance and proximity of roosts in the surrounding area, the higher activity levels at the Beaver site found here are actually despite an opposing underlying trend in favour of the Control site. This highlights the importance of areas of high prey density and the attraction of high-quality feeding grounds within the bat landscape (Warren *et al.*, 2000; Fukui *et al.*, 2006; Nummi *et al.*, 2011; de Conno *et al.*, 2018).

Soprano pipistrelle and Daubenton's are known to prefer riparian habitats (Vaughan, 1997) as much of their diet is aquatic Diptera; Daubenton's also favour Tricoptera and Ephemeroptera (Flavin, 2001; Sullivan *et al.*, 1993). Both species preferentially forage of water with a smooth surface (Warren *et al.*, 2000), so the increase in lentic and slow-moving lotic stretches of water due to beaver activity axiomatically increased preferred feeding habitat and might be a partial driver of the higher activity of these two species at the Beaver site. For Daubenton's, this conclusion is also supported by greater bat activity being recorded in lentic habitats compared to lotic habitats. Common pipistrelles and noctule are not riparian specialists but are attracted to any area where insect biomass is high and emergent aquatic macroinvertebrates are often included in their diet (Flavin, 2001).

Recorded bat activity (passes per night) was higher for walked transects than automated fixed-point acoustic surveys for all species combined and also for all taxa except Leisler's. This accords with previous research by Perks and Goodenough (2022) that found transects recorded higher levels of activity than fixed-point surveys using Anabat detectors both overall and specifically for common pipistrelle, soprano pipistrelle and Daubenton's. However, Stahlschmidt and Bruhl (2012) found automated fixed-point surveys to be more effective than walked transects, likely because fixed-point detectors provide a record of bat activity throughout the full nocturnal period and can, as here, detect late-emerging species such as lesser horseshoe that are often missed in walked transects conducted in the early part of the night.

Bat activity and larvae/nymphs of emergent aquatic invertebrates also showed seasonal patterns. Overall bat activity, and emergent aquatic invertebrate richness and abundance, all showed a seasonal peak from May to July in comparison with lower levels early in the season (April) and late in the season (August-October). Patterns for individual bat species varied, with the seasonal peak for soprano pipistrelle being earlier (June-August) than common pipistrelle (July-September). The general decline in activity for noctule through the season is consistent with a summer and autumnal increase in terrestrial insect biomass. This reduces the importance of aquatic invertebrates for non-riparian specialist bats (Fukui *et al.*, 2006), especially as their preferred Ephemeroptera emerge early in the season (Flavin, 2001).

Conclusion: Conservation implications and recommendations

Our findings indicate greater bat activity, and more larvae/nymphs of emergent aquatic invertebrates, at a site that has undergone substantial ecosystem engineering by beavers compared to a similar site nearby. It is important to caveat that while previous longitudinal habitat research has shown the Beaver site has changed over time (Brazier *et al*, 2020), beavers as the causal mechanism of change in bat communities via increased prey density is inference rather than empirical. This is because our study is fundamentally based on site comparison over space rather than the same site over time, notwithstanding that beaver activity is the only substantive difference between the sites that are geographically close and share similar habitat and hydrology. It is also important to reiterate this work is, in essence, a case study based on just two sites.

Despite these caveats, the likely role of beavers revealed here does add to a growing weight of evidence: Nummi *et al.* (2011) showed bat activity in Finland was higher at sites with non-native Canadian beaver (albeit without a link to likely invertebrate prey), Ciechanowski *et al.* (2011)

found higher activity of pipistrelle in Polish riparian areas with reintroduced European beavers versus unmodified areas (again without a link to prey), and Symes (2012) demonstrated an increase in both bat activity and macroinvertebrate abundance in different years in an enclosed beaver population. It is therefore recommended that likely benefits of beavers to bats be considered in future reintroduction feasibility studies.

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References

Auster, R.E., Barr, S.W. & Brazier, R.E. (2022). Renewed coexistence: learning from steering group stakeholders on a beaver reintroduction project in England. *European Journal of Wildlife Research*, 68, 1-22.

Balmford, A., Green, M.J.B. & Murray, M.G. (1996). Using higher-taxon richness as a surrogate for species richness: Regional tests. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 263, 1267-1274.

Blakey, R.V., Kingsford, R.T., Law, B.S. & Stoklosa, J. (2017). Floodplain habitat is disproportionately important for bats in a large river basin. *Biological Conservation*, 215, 1-10.

Brazier, R.E., Puttock, A., Graham, H., Anderson, K., Cunliffe, A. & Elliott, M. (2016). Quantifying the multiple, environmental benefits of reintroducing the Eurasian Beaver. *EGU General Assembly Conference Abstracts,* EPSC 2016-7243.

Brazier, R.E., Puttock, A., Graham, H.A., Auster, R.E., Davies, K.H. & Brown, C.M. (2021). Beaver: Natures ecosystem engineers. *Water*, 8, p.e1494.

Brazier, R.E., Elliott, M., Andison, E., Auster, R.E., Bridgewater, S., Burgess, P., Chant, J., Graham, H., Knott, E., Puttock, A.K., Sansum, P. & Vowles, A. (2020). River Otter Beaver Trial: Science and Evidence Report, *Devon Wildlife Trust.*

Browning, E., Barlow, K.E., Burns, F., Hawkins, C. & Boughey, K., (2021). Drivers of European bat population change: a review reveals evidence gaps. *Mammal Review*, 51, 353-368.

Bush, B.M., Stenert, C., Maltchik, L. & Batzer, D.P. (2019). Beaver-created successional gradients increase β-diversity of invertebrates by turnover in stream-wetland complexes. *Freshwater Biology*, 64, 1265-1274.

Ciechanowski, M., Kubic, W., Rynkiewicz, A. & Zwolicki, A. (2011). Reintroduction of beavers *Castor fiber* may improve habitat quality for vespertilionid bats foraging in small river valleys. *European Journal of Wildlife Research*, 57, 737-747.

Collins, J. (Ed.) (2016). *Bat Surveys for Professional Ecologists: Good Practice Guidelines* (3rd edn). The Bat Conservation Trust: London.

Collins, J. (Ed.) (2023). *Bat Surveys for Professional Ecologists: Good Practice Guidelines* (4th edn). The Bat Conservation Trust: London.

Conroy, J.W.H. & Kitchener, A. (1996). *The Eurasian beaver (Castor fiber) in Scotland: a review of the literature and historical evidence*. Scottish Natural Heritage.

Crowley, S.L., Hinchliffe, S. & McDonald, R.A. (2017). Nonhuman citizens on trial: the ecological politics of a beaver reintroduction. *Environment and Planning A: Economy and Space*, 49, 1846-1866.

Davidson-Watts, I., Walls, S. & Jones, G. (2006). Differential habitat selection by *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* identifies distinct conservation needs for cryptic species of echolocating bats. *Biological Conservation*, 133, 118-127.

de Conno, C., Nardone, V., Ancillotto, L., De Bonis, S., Guida, M., Jorge, I., Scarpa, U. & Russo, D. (2018). Testing the performance of bats as indicators of riverine ecosystem quality. *Ecological Indicators*, 95, 741-750.

Devon Biological Records Centre (2022a) *Results of data search within 5 km of ST0757803108 Enq no. 10-2339. Obtained 4 October 2022.*

Devon Biological Records Centre (2022b) *Results of data search within 5 km of SS9700801315 Enq no. 10-2340. Obtained 4 October 2022.*

Drake, C.M., Lott, D.A., Alexander, K.N.A. & Webb, J. (2007). *Surveying terrestrial and freshwater invertebrates for conservation evaluation*, Natural England Research Report 5, pp.1-123.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L. and Sullivan, C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges, *Biological Reviews*, 81,163-182.

Fenton, M.B. (1990). The foraging behaviour and ecology of animal-eating bats. *Canadian Journal of Zoology*, 68, 411-422.

Flavin D. A., Biggane S. S., Shiel C. B., Smiddy P. & Fairley J. S. (2001). Analysis of the diet of Daubentons bat *Myotis daubentonii* in Ireland. *Acta Theriologica* 46, 43–52.

Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R. & Obrist, M.K. (2013). Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *Journal of Applied Ecology*, 50,252-261.

Frick, W.F., Kingston, T. & Flanders, J. (2020). A review of the major threats and challenges to global bat conservation. *Annals of the New York Academy of Sciences,* 1469, 5-25.

Fukui, D.A.I., Murakami, M., Nakano, S. & Aoi, T. (2006). Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology*, 75, 1252-1258.

Fuller, M.R. & Peckarsky, B.L. (2011). Ecosystem engineering by beavers affects mayfly life histories. *Freshwater Biology*, 56, 969-979.

Goodenough, A.E., Deans, L., Whiteley, L. & Pickering, S. (2015). Later is better: optimal timing for walked activity surveys for a European bat guild. *Wildlife Biology*, 21, 323-328.

Gorczyca, E., Krzemień, K., Sobucki, M. & Jarzyna, K. (2018). Can beaver impact promote river renaturalization? The example of the Raba River, southern Poland. *Science of the Total Environment.* 615, 1048-1060.

Grudzinski, B.P., Fritz, K., Golden, H.E., Newcomer-Johnson, T.A., Rech, J.A., Levy, J., Fain, J., McCarty, J.L., Johnson, B., Vang, T.K. & Maurer, K. (2022). A global review of beaver dam impacts: Stream conservation implications across biomes. *Global Ecology and Conservation*, 37, p.e02163.

Gumiero, B., Mant, J., Hein, T., Elso, J. and Boz, B. (2013). Linking the restoration of rivers and riparian zones/wetlands in Europe: sharing knowledge through case studies. *Ecological Engineering*, 56, 36-50.

Halley D.J. & Rosell, F. (2002). The beavers reconquest of Eurasia: status, population development and management of a conservation success. *Mammal Review*, 32, 153-178.

Halley, D., Rosell, F. & Saveljev, A.P. (2012). Population and distribution of Eurasian beaver (*Castor fiber). Baltic Forestry*, 18, 168-175.

Halley, D.J., Saveljev, A.P. & Rosell, F. (2021). Population and distribution of beavers *Castor fiber* and *Castor canadensis* in Eurasia. *Mammal Review*, 51, 1-24.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, h., Hörren, Goulson, D. & de Kronn, H. (2017). More Than 75 Percent Decline Over 27 Years in Total Flying Insect Biomass in Protected Areas, *PLOS ONE*, 12, e0185809

Harris, S., Morris, P., Wray, S. & Yalden, D. (1995). *A Review of British Mammals: Population Estimates and Conservation Status of British Mammals Other Than Cetaceans*. Peterborough: JNCC.

Hering, D., Gerhard, M., Kiel, E., Ehlert, T. & Pottgiesser, T. (2001). Review study on near-natural conditions of Central European mountain streams, with particular reference to debris and beaver dams. *Limnologica*, 31, 81-92.

Hood, G. A. & Bayley, S. E. (2008). Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biological Conservation*, 141, 556–567.

Hood, G.A. & Larson, D.G. (2014). Beaver-created habitat heterogeneity influences aquatic invertebrate assemblages in boreal Canada. *Wetlands*, 34, 19-29.

Janiszewski, P., Hanzal, V. & Misiukiewicz, W. (2014). The Eurasian beaver (*Castor fiber*) as a keystone species–a literature review. *Baltic Forestry*, 20, 277-286.

Jones, G. & Rydell, J. (1994). Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 346, 445-455.

Kalko, E. & Braun, M. (1991). Foraging areas as an important factor in bat conservation: estimated capture attempts and success rate of *Myotis daubentonii* (Kuhl, 1819). *Myotis*, 29, 55-60.

Krüger, F., Clare, E.L., Symondson, W.O., Keišs, O. & Pētersons, G. (2014). Diet of the insectivorous bat *Pipistrellus nathusii* during autumn migration and summer residence. *Molecular Ecology*, 23, 3672-3683.

Law, A., Gaywood, M. J., Jones, K. C., Ramsay, P., & Willby, N. J. (2017). Using ecosystem engineers as tools in habitat restoration and rewilding: Beaver and wetlands. *Science of the Total Environment*, 605,1021–1030

López-Bosch, D., Huang, J.C.C., Wang, Y., Palmeirim, A.F., Gibson, L. & López-Baucells, A. (2021). Bat echolocation in continental China: a systematic review and first acoustic identification key for the country. *Mammal Research*, 66, 405-416.

Michez, A., Broset S. & Lejeune, P. (2021). Ears in the Sky: Potential of Drones for the Bioacoustic Monitoring of Birds and Bats, *Drones*, 5, 9–9.

Murray-Bligh, J. (1999). *Procedures for Collecting and Analysing Macroinvertebrate Samples*. Environment Agency.

Natural England (2015). Natural England approves trial release of beavers", 28 January 2015 (updated 15 February 2015), https://www.gov.uk/government/news/natural-england-approves-trial-release-of-beavers (accessed 03 June 2023).

Norberg, U.M. & Rayner, J.M. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 316, 335-427.

Nummi, P., Kattainen, S., Ulander, P. & Hahtola, A. (2011). Bats benefit from beavers: a facilitative link between aquatic and terrestrial food webs. *Biodiversity and Conservation*, 20, 851-859.

Nummi, P. & Pöysä, H. (1995). Habitat use by different-aged duck broods and juvenile ducks. *Wildlife Biology*, 1, 181-187.

Orr, A. (2021) *A comparative study of the accuracy of surveying methods for European bats: is real- time data collected from activity transect using heterodyne detectors more or less accurate than data collected from the implementation of Audiomoths via passive fixed-point surveys*. MSc Dissertation, University of Gloucestershire

Perks, S.J. & Goodenough, A.E. (2021). Comparing acoustic survey data for European bats: do walked transects or automated fixed-point surveys provide more robust data? *Wildlife Research*, 49, 314-323.

Pollock M.M., Beechie T.J., Wheaton J.M., Jordan C.E., Bouwes N., Weber N. & Volk C. (2014). Using beaver dams to restore incised stream ecosystems. *Bioscience,* 64, 279–290.

Puttock, A., Graham, H.A., Cunliffe, A.M., Elliott, M. & Brazier, R.E. (2017). Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands. *Science of the Total Environment, 576,* 430-443.

Puttock, A., Graham, H. & Brazier, R. (2020). Does changing connectivity due to beaver engineering result in changing hydrological function? Understanding the impacts of the return of the Eurasian beaver to Great Britain. *EGU General Assembly Conference Abstracts,* 2158.

Pliūraitė, V. & Kesminas, V. (2012). Ecological impact of Eurasian beaver (*Castor fiber*) activity on macroinvertebrate communities in Lithuanian trout streams. *Open Life Sciences*, 7, 101-114.

Redin, A. & Sjöberg, G. (2013). Effects of beaver dams on invertebrate drift in forest streams, *Šumarski list*, 137, 597-607.

Rosell, F., Bozser, O., Collen, P. & Parker, H. (2005). Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review*, 35, 248-276.

Russ, J. (2012). *British Bat Calls: A Guide to Species Identification*. Exeter, United Kingdom: Pelagic Publishing.

Rydell, J., Bushby, A., Cosgrove, C.C. & Racey, P.A. (1994). Habitat use by bats along rivers in northeast Scotland, *Folia Zoólogica-Praha,* 43, 417-417.

Shortall, C.R., Moore, A., Smith, E., Hall, M.J., Woiwod, I.P. & Harrington, R. (2009). Long-term changes the in abundance of flying insects. *Insect Conservation and Diversity*, 2, 251-260.

Smeraldo, S., Di Febbraro, M., Ćirović, D., Bosso, L., Trbojević, I. & Russo, D. (2017). Species distribution models as a tool to predict range expansion after reintroduction: A case study on Eurasian beavers (*Castor fiber*). *Journal for Nature Conservation*, 37, pp.12-20.

Smith, M.E., Driscoll, C.T., Wyskowski, B.J., Brooks, C.M. & Cosentini, C.C. (1991). Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. *Canadian Journal of Zoology*, 69, 55-61.

Sologor E. A. (1980). Kizučeniû pytaniâ *Vespertilio serotinus* [To the knowledge of feeding in *Vespertilio serotinus*]. In: *Kuzâkin A. P. & Panûtin K. K. (eds.), Voprosy teriologii*. 188–190.

Sorg M., Schwan H., Stenmans W. & Müller A. (2013). Ermittlung der Biomassen flugaktiver Insekten im Naturschutzgebiet Orbroicher Bruch mit Malaise Fallen in den Jahren 1989 und 2013, *Mitteilungen gus dem Entomologischen Verein Krefeld*, 1–5.

Stahlschmidt, P. & Brühl, C.A. (2012). Bats as bioindicators–the need of a standardized method for acoustic bat activity surveys. *Methods in Ecology and Evolution*, 3, 503-508.

Stebbings, R.E. & Griffith, F. (1986). *Distribution and Status of Bats in Europe*. Institute of Terrestrial Ecology.

Stringer, A.P. & Gaywood, M.J. (2016). The impacts of beavers *Castor* spp. on biodiversity and the ecological basis for their reintroduction to Scotland, UK. *Mammal Review*, 46, 270-283.

Sullivan, C.M., Shiel, C.B., McAney, C.M. & Fairley, J.S. (1993). Analysis of the diets of Leislers *Nyctalus leisleri*, Daubentons *Myotis daubentoni* and pipistrelle *Pipistrellus pipistrellus* bats in Ireland. *Journal of Zoology*, 231, 656-663.

Swift, S.M. & Racey, P.A. (1983). Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *Journal of Zoology*, 200, 249-259.

Symes, M. (2012). Bat Activity Survey of the Devon Beaver Project Site, Devon Wildlife Trust

Vaughan, N. (1997). The diets of British bats (Chiroptera). *Mammal Review*, 27, 77-94.

Vaughan, N., Jones, G. & Harris, S. (1996). Effects of sewage effluent on the activity of bats (Chiroptera: Vespertilionidae) foraging along rivers. *Biological Conservation,* 78, 337-343.

Verhoeven, J.T. (2014). Wetlands in Europe: perspectives for restoration of a lost paradise. *Ecological Engineering*, 66, 6-9.

Walsh, A.L. & Harris, S. (1996). Foraging habitat preferences of vespertilionid bats in Britain. *Journal of Applied Ecology*, 33, 508-518.

Warren, R.D., Waters, D.A., Altringham, J.D. & Bullock, D.J. (2000). The distribution of Daubentons bats (*Myotis daubentonii*) and pipistrelle bats (*Pipistrellus pipistrellus*)(Vespertilionidae) in relation to small-scale variation in riverine habitat. *Biological Conservation*, 92, 85-91.

Wickramasinghe, L.P., Harris, S., Jones, G. & Vaughan Jennings, N. (2004). Abundance and species richness of nocturnal insects on organic and conventional farms: effects of agricultural intensification on bat foraging, *Conservation Biology*, 18, 1283-1292.

Willby, N.J., Law, A., Levanoni, O., Foster, G. & Ecke, F. (2018). Rewilding wetlands: beaver as agents of within-habitat heterogeneity and the responses of contrasting biota. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373, p.20170444.

Wojton, A. & Kukuła, K. (2021). Transformation of benthic communities in forest lowland streams colonised by Eurasian beaver *Castor fiber* (L.). *International Review of Hydrobiology*, 106, 131- 143.

Wright, J.P., Jones, C.G. & Flecker, A.S. (2002). An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, 132, pp.96-101.

Wróbel, M. (2020). Population of Eurasian beaver (*Castor fiber*) in Europe. *Global Ecology and Conservation*, 23, p.e0104.

Table 1: Aquatic macroinvertebrates identified during kick samples at the Beaver site versus the Control. The taxa that, according to Sologor (1980), Flavin (2001) and Krüger et al. (2014), are included in the diet of one or more UK bat species are highlighted, with species marked by an asterisk being taken from the surface of water by Daubenton's (*Myotis daubentonii*) only.

					Abundance	
Taxonomic Group	**Common Name**	**Life stage**	**Emergent?**	**Bat prey?**	**Beaver site**	**Control site**
Anisoptera	Dragonfly	Larvae	Yes	Yes	2	
Argulidae	Fish louse	Adult			2	
Asellidae	Hoglouse	Adult			22	3
Baetidae	Swimming mayfly	Nymph	Yes	Yes	4	5
Ceratopogonidae	Biting midge	Larvae	Yes	Yes	35	1
Chaoboridae	Phantom midge	Larvae	Yes	Yes	28	
Chironomidae	Non-biting midge	Larvae	Yes	Yes	176	17
Corixidae	Lesser water boatman	Adult		Yes*	20	
Dytiscidae	Diving beetle	Adult			2	
Ephemeridae	Burrowing mayfly	Nymph	Yes	Yes	2	2
Gammaridae	Fresh water shrimp	Adult			143	2,446
Gerridae	Pond skater	Adult			1	
Gordiodea	Hairworms	Adult				3
Gyrinidae	Whirligig beetle	Adult		Yes*	4	
Hydrometridae	Water measurer	Adult			1	
Nepidae	Water scorpion	Adult			2	
Notonectidae	Greater water boatman	Adult			17	
Plecoptera	Stonefly	Nymph	Yes	Yes	1	
Sialidae	Alderfly	Larvae	Yes	Yes	1	1
Tricoptera	Cased caddisfly	Larvae	Yes	Yes	4	2
Zygoptera	Demoiselle	Larvae	Yes	Yes	2	

Table 2: Generalised Linear Models examining the influence of beaver presence (site), seasonality (time of year) and habitat (lotic or lentic) on richness/abundance of emergent aquatic macroinvertebrates. A Poisson probability distribution with a log link function was used. The chi square values are likelihood ratio for overall model and Wald for specific factors. Means are per-kick sample averages.

Factor and degrees of freedom		Richness of emergent taxa (# of taxa)			Abundance of emergent taxa (# of individuals)		
		χ^2	P	Details	χ^2	P	Details
Overall model	8	53.672	<0.001	-	501.903	<0.001	-
Site	1	17.825	<0.001	Higher at Beaver site than Control (mean = 1.381 vs 0.452); Figure 2a-b	124.087	<0.001	Higher at Beaver site than Control (mean = 6.119 vs 0.667); Figure 2c-d
Time of year	6	25.191	<0.001	Seasonal peak May-July; Figure 2a-b	147.111	<0.001	Seasonal peak May-July; Figure 2 c-d
Lotic/ Lentic	1	1.561	0.212	-	46.538	<0.001	Higher at lentic vs lotic (mean = 4.809 vs 1.976); Figure 2 c-d

Table 3: Presence of bat taxa at the Beaver site and the Control site based on data from automated fixed-point surveys and transect surveys, together with activity recorded as the total number of bat passes as a proxy for abundance.

Species		**Beaver site**		**Control site**	
		Automated fixed-point	**Transects**	**Automated fixed-point**	**Transects**
Common pipistrelle	*Pipistrellus pipistrellus*	2,116	474	937	294
Soprano pipistrelle	*Pipistrellus pygmaeus*	2,525	259	1,968	599
Daubenton's + congeners	*Myotis* spp. (inc. *M. daubentonii)*	1,118	63	691	115
Noctule	*Nyctalus noctule*	191	50	59	47
Leisler's + congeners	*Nyctalus* spp. (inc. *N. leisleri*)	45	6	48	21
Serotine	*Eptesicus serotinus*	41	11	28	16
Brown/grey long-eared	*Plecotus* spp.	4	1	5	8
Barbastelle	*Barbastella barbastellus*	-	1	1	3
Greater horseshoe	*Rhinolophus ferrumequinum*	1	-	-	1
Lesser horseshoe	*Rhinolophus hipposideros*	2	-	-	-

Table 4: Generalised Linear Model examining the influence of beaver presence (site), seasonality (time of year), survey method (automated fixed-point or transect data) and habitat (lotic or lentic) on bat activity (passes per night). A Poisson probability distribution with a log link function was used. Chi square values are likelihood ratio for overall model and Wald for specific factors. Means are per-night averages. Note that the variable lotic/lentic is nested within survey method because habitat data were only collected during fixed-point acoustic surveys (transects were conducted at site level).

Factor	d.f.	χ^2	P	Details
Overall model	9	3527.960	<0.001	-
Site	1	360.215	<0.001	Higher at Beaver than Control (Fig 3a-b)
Time of year	6	1649.185	<0.001	Seasonal peak May-Aug (Fig 3 c-d)
Survey method	1	265.900	<0.001	Higher for transects than fixed-point on average (mean = 164.000 vs 116.430 SEM) but some differences between sites and habitats (Fig 3 a-b)
Lotic/Lentic (Survey method)	1	1164.658	<0.001	Higher at lotic vs lentic based on sampling via habitat-specific fixed-point detectors (Fig 3a-b)

Table 5: Generalised Linear Models examining the influence of beaver presence (site), seasonality (time of year), survey method (automated fixed-point or transect data) and habitat (lotic or lentic) on bat activity (passes per night) as a proxy for abundance for specific taxa. Note that the variable lotic/lentic is nested within survey method because habitat data were only collected during fixed-point acoustic surveys (transects were conducted at site level). Model settings were as per Table 4.

	Factor	**d.f.**	χ^2	**P**	**Details**
Common pipistrelle	Overall model	9	3378.968	<0.001	-
	Site	1	461.668	0.003	Higher at Beaver than Control (mean = 53.966 vs 25.650)
	Time of year	6	1529.571	<0.001	Seasonal peak July-September
	Survey method	1	130.765	<0.001	Higher for transects than fixed-point (mean = 64.000 vs 36.355)
	Lotic/Lentic (Survey method)	1	801.125	<0.001	Higher at lotic vs lentic (mean = 56.140 vs 16.550)
Soprano pipistrelle	Overall model	9	1055.512	<0.001	-
	Site	1	8.795	0.003	Higher at Beaver than Control (mean = 58.000 vs 53.488)
	Time of year	6	775.729	<0.001	Seasonal peak June-August
	Survey method	1	89.439	<0.001	Higher for transects than fixed-point (mean = 71.500 vs 53.494)
	Lotic/Lentic (Survey method)	1	114.695	<0.001	Higher at lotic vs lentic (mean = 60.070 vs 44.900)
Daubentons + congeners	Overall model	9	2087.638	<0.001	-
	Site	1	69.918	<0.001	Higher at Beaver than Control (mean = 24.606 vs 16.792)
	Time of year	6	1394.801	<0.001	Seasonal peak in June
	Survey method	1	2.525	0.112	-
	Lotic/Lentic (Survey method)	1	531.541	<0.001	Higher at lentic vs lotic (mean = 34.100 vs 8.980)
Noctule	Overall model	9	263.975	<0.001	-
	Site	1	49.666	<0.001	Higher at Beaver than Control (mean = 8.088 vs 2.986)
	Time of year	6	123.887	<0.001	General decline throughout season but notable fluctuation
	Survey method	1	53.323	0.005	Higher for transects than fixed-point (mean = 164.000 vs 116.430)
	Lotic/Lentic (Survey method)	1	0.400	0.527	-
Leislers + congeners	Overall model	9	55.771	<0.001	-
	Site	1	2.680	0.102	-
	Time of year	6	25.372	<0.001	End of season drop-off
	Survey method	1	7.964	<0.001	Higher for transects than fixed-point (mean = 164.000 vs 116.430)
	Lotic/Lentic (Survey method)	1	2.398	0.121	-
Serotine	Overall model	9	33.437	<0.001	-
	Site	1	0.665	0.415	-
	Time of year	6	12.155	0.059	-
	Survey method	1	18.898	<0.001	Higher for transects than fixed-point (mean = 164.000 vs 116.430)
	Lotic/Lentic (Survey method)	1	2.420	0.120	-

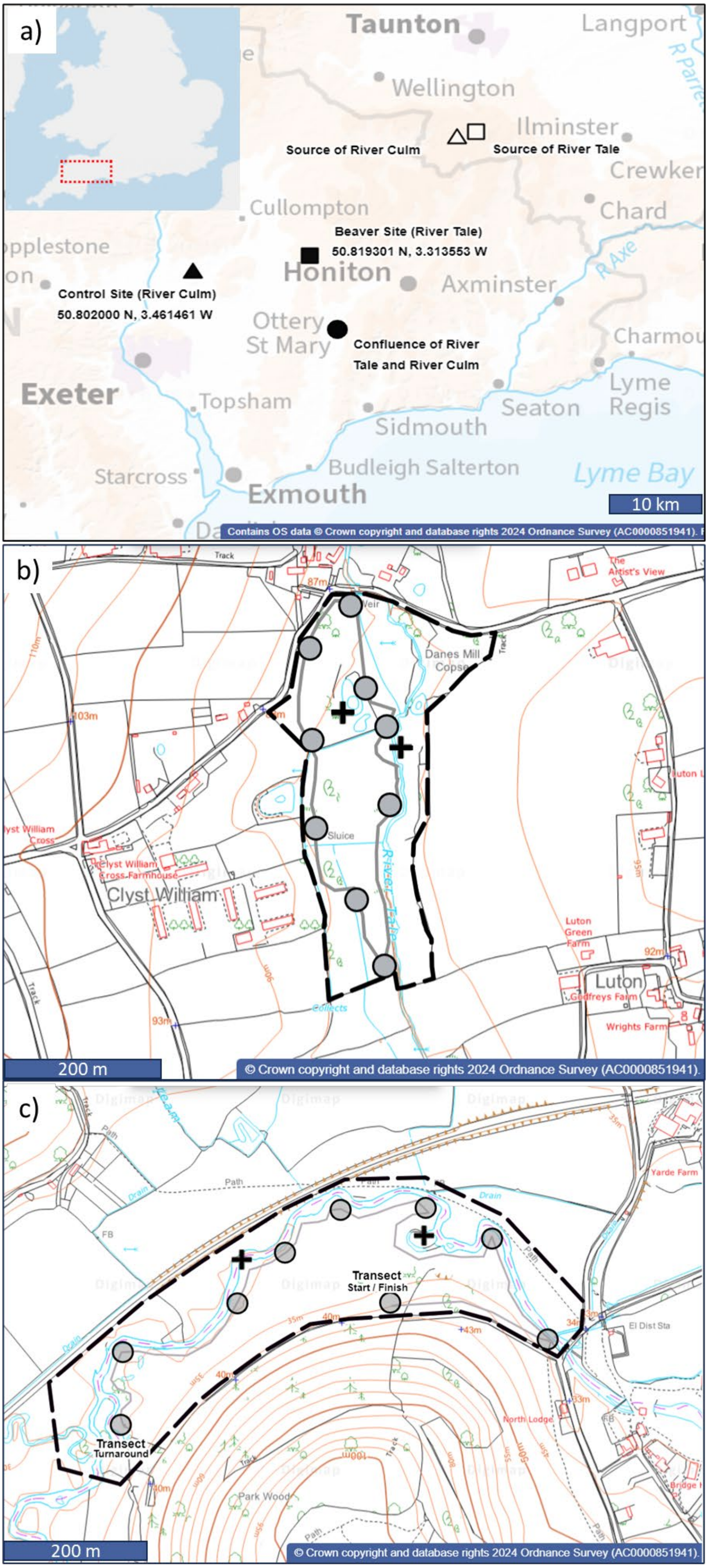

Figure 1: Study sites and bat data sampling setup showing: (a) the study sites in geographical context; (b) the Beaver site; and (c) the Control site. For (b) and (c) the site boundary is shown by the black dashed line, the transect route is shown via a grey line with the 5-minute stop locations shown by grey dots. The locations for the passive acoustic monitoring via Audiomoths are shown by black crosses. The circular route at the Beaver site was walked twice as a loop to create a 3 km route surveyed over 3 hr for one transect; the linear route at the Control site was walked as an out-and-back (also 3km over 3 hr).

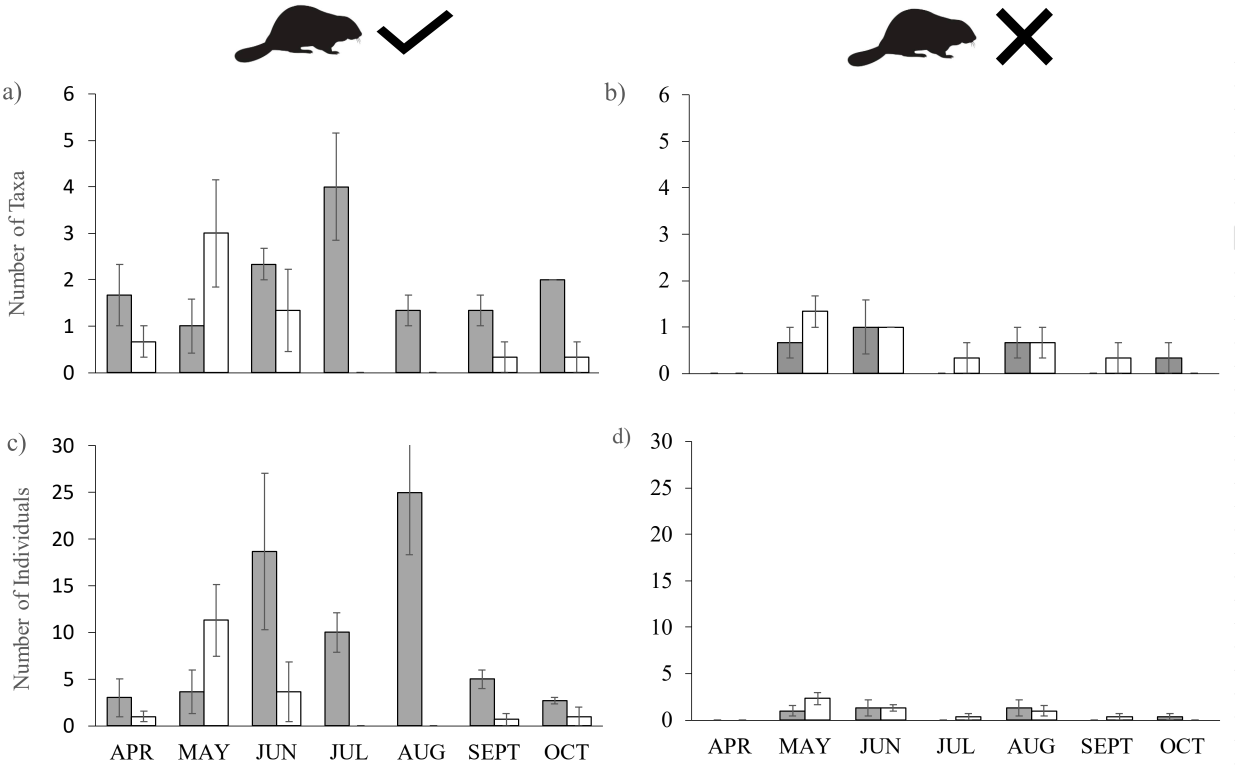

Figure 2: Spatiotemporal pattens in emergent aquatic invertebrates known to be taken by bats (see Table 1) at sites with reintroduced European beaver and where beaver remain absent showing: (a) richness (number of taxa) at the Beaver site; (b) abundance (number of individuals) at the Beaver site; (c) richness at the Control site; and (d) abundance at the Control site. In all cases, grey bars represent lentic habitats and white bars represent lotic habitats. Error bars show SEM.

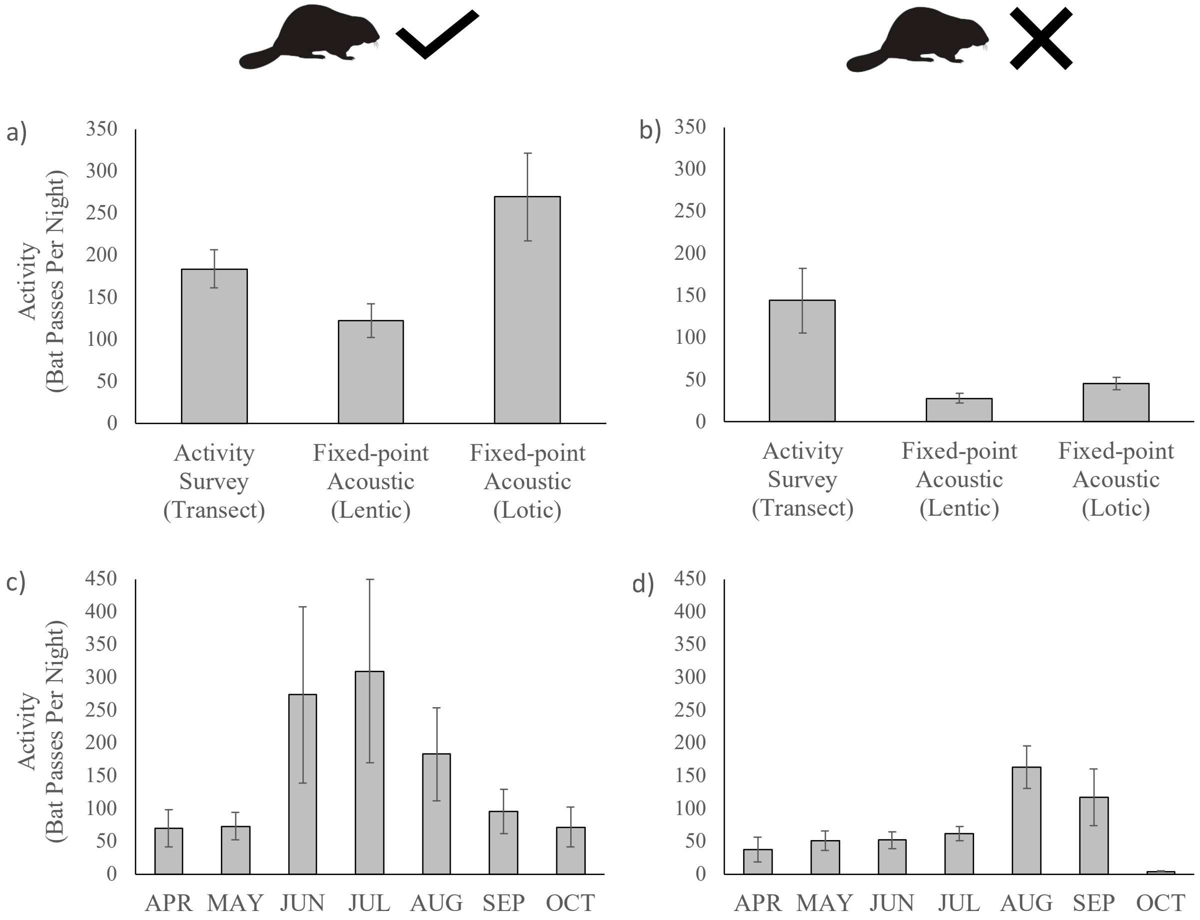

Figure 3: Spatiotemporal patterns in bat activity at sites with reintroduced European beaver and where beaver remain absent. Top: Bat activity, recorded as passes per night, on walked activity surveys (transects) and fixed-point acoustic detectors (Audiomoths) placed in lentic and lotic habitats for (a) Beaver site and (b) Control site. Bottom: Seasonal patterns in bat activity using fixed-point detectors averaged across lentic and lotic habitats for (c) Beaver site and (d) Control site. Error bars show SEM.