

The impact of Eurasian beaver communities on emergent insects and their avian predators



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Abstract

Aquatic ecosystems have suffered decades of degradation as a result of anthropogenic activities, and are now facing the threat of global climate change. In order to prevent further loss and deterioration of these habitats, effective restoration measures must be implemented. Of key importance is restoration at the landscape scale in order to maintain and restore habitat connectivity. The reintroduction of the Eurasian beaver (*Castor fiber*) is one such way to achieve this. A rise in the number of beaver reintroduction programmes across the UK has provided research opportunities into the benefits that these large herbivores provide. Studies have shown that beavers, as ecosystem engineers, increase habitat connectivity, heterogeneity and species richness through their routine activities such as tree felling and dam building. Of the research completed however, there is a lack of understanding around the impact beavers have on emergent insects, and the influence this has on their avian predators. This study explores the aquatic-terrestrial links created by beavers on the Bamff Estate in Scotland, and investigates insect emergence and bird feeding activity by comparing beaver modified habitat to unmodified habitat. Insect emergence was quantified at all sites and results show that both abundance and biomass were higher at beaver sites. Furthermore, bird surveys undertaken across the sites reveal increased bird feeding activity at beaver sites. Variations in environmental characteristics between sites suggest that beavers create more favourable habitats for emergent insects, with peak emergence positively linked to increased water temperature at beaver sites. Amongst the multitude of benefits that beavers provide in restoring habitat connectivity, they are an effective way of increasing the availability of aquatic insect prey to bird communities.

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1. Introduction

1.1 Ecological Context

Freshwater habitats provide some of the most biodiverse ecosystems in the world supporting 10% of all known species and half of the world's vertebrate species (Strayer and Dudgeon 2010). Despite accounting for less than 1% of the Earth's total surface area, and only 0.01% of the world's water, freshwater ecosystems contain huge amounts of life whilst also providing a multitude of ecosystem services to humans (Gleick 1996). Annually they are estimated to be worth trillions of dollars (Postel and Carpenter 1997). As a result of human activity, these ecosystems have suffered severe loss and degradation and now represent one of the most threatened habitat types globally (Holland *et al.* 2012). An increase in demand and pressure placed on them through intensified flow regulation, water abstraction, fisheries, invasive species and pollution has all contributed to widespread negative ecological impacts (Strayer and Dudgeon 2010). The Living Planet Index shows the abundance of freshwater species populations declined by 83% between 1970 and 2014, equating to an annual decline of 4% over this period (WWF 2018). Now widely acknowledged as a global crisis, finding solutions to conserve and restore our freshwater systems has become a major part of contemporary freshwater ecology.

1.1.1 Importance of connectivity between habitats

A major consequence from the loss and degradation of freshwater systems is fragmentation. Connectivity between landscapes is crucial in maintaining the structure and function of ecosystems (Crooks and Sanjayan 2006) and can be defined as the “extent to which movements of genes, propagules, individuals and populations are facilitated by the structure and composition of the landscape” (Rudnick *et al.* 2012).

As our global population and human activity increases, less and less of the Earth's surface remains free from modification. Landscapes that were once a mosaic of untouched, natural ecosystems now contain isolated, scattered habitats amongst human dominated landscapes (Hood and Larson 2015). Fragmentation limits the biological, physical and chemical exchanges that are crucial in maintaining biodiversity, impacting ecosystems at multiple scales from individual organisms to

entire ecosystems (Lamberti *et al.* 2010). Freshwater systems play a key role in the transfer of energy within and between landscapes at different dimensions. Ward (1989) defines four dimensions of ecosystem connectivity: longitudinal, lateral, vertical and temporal.

Vertical connectivity includes interactions between surface water and groundwater, and longitudinal connectivity refers to the links between upstream and downstream habitat (Ward 1989). This is particularly important for migratory species in order to fulfil their life cycle and feeding requirements (Nummi *et al.* 2011). Species such as Atlantic and Pacific Salmon and the European eel require freedom of movement between freshwater and ocean habitats in order to reproduce and fulfil their lifecycles (Aas *et al.* 2011, Vowles *et al.* 2015). They suffer from the development of obstructions such as weirs and dams that make passage difficult, and in many cases impossible (Larinier 2000).

Lateral connectivity refers to the transfers of energy from one system to another, and finally the temporal dimension refers to connections over time at varying scales from daily to historical time scales (Amoros and Bornette 2002). Both of these dimensions are important in maintaining links between the main river channel and its floodplain which provides important refugia for juvenile and larval fish during high in-channel flows (Opperman *et al.* 2013). Water on the floodplain is slower, warmer and less turbid than water in the channel which enables higher photosynthesis rates in aquatic plants and algae, resulting in increased rates of productivity. Consequently, floodplains are able to support higher concentrations of zooplankton and aquatic insects than the main river channel making them excellent nursery habitat (Sommer *et al.* 2004, Jeffres *et al.* 2008). Some species of fish are known to time their spawning to coincide with high flows in order to ensure food supplies for their young (Opperman *et al.* 2013). Unfortunately, more and more spawning habitat has been lost due to floodplain development for urban and agricultural expansion. The extinction of the Burbot (*Lota lota*) in the UK is widely believed to be attributed to this loss of floodplain connectivity as it favoured spawning in floodplain backwaters (Fisher 2000).

Transfers of energy not only take place between distinct aquatic systems, but also between aquatic and terrestrial systems. Lateral and temporal connectivity are important in creating and maintaining aquatic-terrestrial linkages with the riparian

zone which is explained by the flood-pulse concept (Junk *et al.* 1989). Intermittent flooding benefits riparian forests by dispersing water, nutrients, minerals and seeds, contributing to their productivity and enhancing species richness (Kozłowski 2002). Sedimentation from deposition creates new substrate for seedling establishment whilst scouring of soil by larger flood events create favourable conditions for pioneer species (Stromberg 1997). Timing of these events is crucial as highlighted by Gosselink *et al.* (1981) who note the positive effect of flooding and nutrient dispersal in spring and winter on plant productivity before the growing season begins. Varying degrees of tolerance to flood depth and duration results in plant distribution along ecological gradients and creates forest communities at various stages of succession (Stromberg 2001). This helps to create habitat heterogeneity providing habitat for numerous species of insects, birds and mammals (Kozłowski 2002).

The integration of riparian zones with aquatic systems is critical to the development of many emergent insects who split their life cycle between both habitats. Developing as larvae within an aquatic system, they then emerge as adult insects and spend the majority of their adult stage in the riparian zone (Kubendran and Ramesh 2016). Timing of their emergence is crucial in maintaining aquatic-terrestrial food web dynamics, and within riparian zones they contribute between 25-100% of the energy and carbon intake of terrestrial consumers such as birds, bats, lizards and spiders (Baxter *et al.* 2005, Sardina *et al.* 2017).

A considerable amount of research has been undertaken to investigate the relationship between aquatic insects and bats, who favour riparian zones for foraging, travel and shelter (Grindal *et al.* 1999). On the Horonai Stream in Hokkaido, Japan, a strong positive correlation was found between bat foraging activity and emergent insect abundance (Fukui *et al.* 2006). Fukui *et al.* (2006) concluded that the flux of aquatic insects emerging from streams is one of the most important factors influencing the distribution of riparian-foraging bats.

There appear to be fewer studies investigating the relationship between emergent insects and birds. However of those completed, evidence shows that emergent insects affect survivorship and feeding patterns in birds. Peak foraging is seen to be correlated with periods of midge, damselfly and mayfly emergence (Graber and Graber 1951, Gray 1993, Murakami and Nakano 2002). Emergent aquatic insects have also been seen as an important contribution to the diet of farmland birds

feeding from farmland ponds (Lewis-Phillips *et al.* 2019). With declines observed in the population of birds, particularly farmland and insectivorous, it is important to consider ways in which we can conserve them (Bowler *et al.* 2019).

With this in mind, and the increased understanding of the importance of maintaining and creating connectivity between landscapes, efforts are now underway to investigate the most effective ways in which to remediate the effects from past ecosystem degradation, and to restore biodiversity and ecological function (Bernhardt and Palmer 2011).

1.1.2 Rewilding as a restoration measure

Ecological restoration can be defined as “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (SER 2004). For surface water systems, the main aim of restoration is to achieve “good ecological quality” as set out by the European Water Framework Directive developed in 2000. This is judged by the degree to which present-day conditions deviate from reference conditions which are those present before anthropogenic influence (European Commission 2000). Efforts to address this have largely involved human intervention through the removal of levees to recover floodplain functionality, scheduling water releases from reservoirs to restore riparian vegetation, removing flow blockages and re-meandering straightened sections of river channel (Law *et al.* 2017). Although these methods can be effective, restoring systems back to pristine conditions is an unrealistic goal due to present day changes in land use, catchment soils and vegetation and consequently many projects fail their expectations (Law *et al.* 2017, Higgs *et al.* 2014, Bennion *et al.* 2011). Projects that are deemed successful are often only focused on one habitat type or ecosystem, for example restoring a reach of a river could bring many localised benefits however it does not consider the wider catchment. Generally, degradation has occurred across the entire catchment and therefore restoration needs to be catchment scale orientated (Bond and Lake 2003).

One approach to achieve catchment restoration is through rewilding which aims to create diverse ecological systems that are dynamic and variable, and independent of human intervention. It is a relatively new concept developed in the 1980s through the Wildlands Project which aimed to connect core wilderness areas across North America through corridors (Soulé and Noss 1998). As an ongoing process it allows

ecosystems to become more natural over time (Pereira and Navarro 2015). In Britain this includes adopting a catchment scale approach which aims to connect ecosystem processes through the landscape from upland to coast (Sandom and Wynne-Jones 2019).

One aspect of rewilding includes the re-introduction of species that were a key component to the system in undisturbed conditions (Law *et al.* 2017). Species who alter landscapes in dynamic ways are particularly effective in restoring connectivity and ecological processes and are referred to as ecosystem engineers (Hood and Larson 2014). These can range from ants who change the structure and composition of local soils to elephants who alter population and food web dynamics through widespread disturbances of trees and shrubs (Naiman 1988, Elmes 1991). Ecosystem engineers exist in aquatic habitats and examples of these include the common hippo (*Hippo amphibious*) and American alligator (*Alligator mississippiensis*). Regular movement of hippos to new feeding islands creates incised channels through wetlands such as the Okavango Delta which act as corridors between aquatic and terrestrial habitats (McCarthy *et al.* 1998). Alligators in the Everglades marshes increase diversity and production through their creation of wallows which retain water during droughts and create a refuge for fish. This provides a food source for fish eating birds whose food resources are limited during drought periods (Mazzotti *et al.* 2008).

In Europe, an important ecosystem engineer is the Eurasian beaver (*Castor fiber*) who is able to transform their environment through building structures, the only mammal species apart from humans to do so. They were first recorded living in Britain 2 million years ago but over exploitation for their pelts, meat and castoreum led to their extinction (Gaywood 2017). It is unclear when the beaver became extinct in Britain, but it may have been as early as the 1500s or into the late 1800s (Coles 2006, Kitchener and Conroy 1996).

The Eurasian beaver suffered over exploitation across Europe, and at the beginning of the 20th century there were only 1200 Eurasian beavers left in eight isolated populations prompting them legal protection. This protection, along with reintroduction programmes and natural dispersal have helped to recover populations, and today there are at least 1.05 million Eurasian beavers populating most of the countries they used to inhabit (Halley *et al.* 2012).

Beavers are large (11-27 kg) semi-aquatic rodents who require two basic elements in their habitat; freshwater and broadleaved woodland. Being herbivores, they feed on a wide range of aquatic and terrestrial plants, felling trees and shrubs to build dams whilst feeding on the bark and leaves (Gaywood *et al.* 2008). These dams, made from wood, stones and mud, allow water levels to rise and create beaver ponds which in turn extend their territory across which they travel using the canals they have constructed in order to stay safe. Through these building activities, they modify riparian and river ecosystems through their restoration of ecosystem function, habitat dynamics and heterogeneity (Halley and Rosell 2002).

The hydrological, geomorphic and ecological benefits provided by beavers have been widely acknowledged. Beaver dams adjust the flow regime of a river by dissipating energy and slowing the flow of water with the effect of attenuating storm event hydrographs (Nyssen *et al.* 2011). They also act as sediment and pollutant traps transforming erosional streams into depositional pond environments and improving water quality downstream (Puttock *et al.* 2018). This is particularly effective in agricultural streams that suffer from the input of nutrient rich surface runoff (Puttock *et al.* 2017). Beaver damming also plays a major role in landscape connectivity by increasing water storage on floodplains and reconnecting floodplains with channels (Macfarlane *et al.* 2017). This in turn affects aquatic-terrestrial linkages particularly in the riparian zone where beavers are known to influence plant and animal community composition and diversity (Naiman *et al.* 1988); aquatic-terrestrial connectivity is especially important in food chain dynamics and studies have shown that beavers enhance habitat for invertebrates and insects having a positive impact on bat and bird populations (Nummi *et al.* 2011, Nummi 1992). That said, the majority of studies investigating the impact beavers have on birds have focused on waterfowl, and less is understood about the impacts beavers bring to farmland and insectivorous birds.

In England, enclosed Eurasian beaver re-introduction programmes are on the rise with the most recent re-introduction located in Finchingfield, Essex. Other ongoing projects in places such as Devon, Kent and Yorkshire are largely focused on the role beavers play in natural flood management (Auster *et al.* 2019).

In Scotland there are currently two wild populations of beaver. On the Tay catchment, a population of around 430 beavers reside. Their origin is unknown

although they are likely the result of accidental or deliberate release (Auster *et al.* 2019). In the Knapdale Forest, beavers were introduced in 2009 as part of the Scottish Beaver Trial in order to study their role in enhancing the Scottish environment (Scottish Natural Heritage 2015). Following the success of this trial and an assessment of the Tayside population, the Scottish Government announced that beavers are allowed to remain, and in May 2019 they were listed as a European Protected Species (Gaywood 2018, Scottish Government 2019).

However, beavers were re-established in Scotland before the discovery in 2006 of the Tayside population. In 2002, beavers were introduced to a large enclosure on the Bamff Estate in Perthshire as part of a private demonstration project. They have been breeding successfully since 2005, and extended their territory beyond their original enclosure and are now living wild (Ramsay, pers. commun.). A considerable amount of research has been undertaken into how beavers have impacted the hydrology, physiochemical processes and biodiversity here (Law *et al.* 2016, Law *et al.* 2017, Willby *et al.* 2014). Before beavers were present the landscape consisted of small, straightened agricultural streams with little variation in depth, substratum, velocity or biodiversity. The re-introduction of beavers has seen changes in vegetation with the cumulative number of plant species recorded increased on average by 148%. Similarly, invertebrate richness has also increased by an estimated 28% (Law *et al.* 2016).

However to date, there have been no specific studies on how the beavers here have influenced aquatic-terrestrial connectivity. With a growing gap in literature on the impact that beavers have on bird populations, and not exclusively waterfowl, this study aims to address this inconsistency by investigating the influence beavers have on emergent insects and the subsequent role this plays in providing feeding resources for birds.

1.2 Study aims and outcomes

The purpose of this study is to investigate whether beavers have an independent effect on aquatic-terrestrial connectivity on the Bamff Estate which historically has suffered from human inflicted degradation. It will build on work by Naiman *et al.* (1984) who studied the effect of beavers on emergent insects in North America, and Nummi (1992) who investigated the relationship between beavers, emergent insects

and waterfowl. It will be the first study that quantifies insect emergence from the beaver ponds on the Bamff Estate, and that relates this to feeding activity in birds.

In order to accomplish this, the following hypotheses are proposed:

H₁ - Beaver sites harbour a higher abundance and biomass of emergent insects

H₂ - Beaver sites harbour a higher diversity of emergent insects

H₃ - There are significant differences in environmental characteristics between beaver sites and non-beaver sites

H₄ - Water chemistry influences abundance and diversity of emergent insects

H₅ - Bird feeding activity is increased at beaver sites

2. Methodology

2.1 Study area

The study was conducted in eastern Scotland on the Bamff Estate ($56^{\circ}37'32.81''\text{N}$, $3^{\circ}13'36.72''\text{W}$) (Figure 1). The nearest town is Alyth which is approximately 20 miles northwest of Dundee. The estate is situated in the foothills of the Grampian mountains covering 525 ha of hills, forest and farmland with the highest point rising to 425 m above mean sea level (Jones *et al.* 2007). In 2018, the area received 1051 mm of rain, with a mean maximum temperature of 11.39°C and a mean minimum temperature of 4.06°C (Meteorological Office 2018).

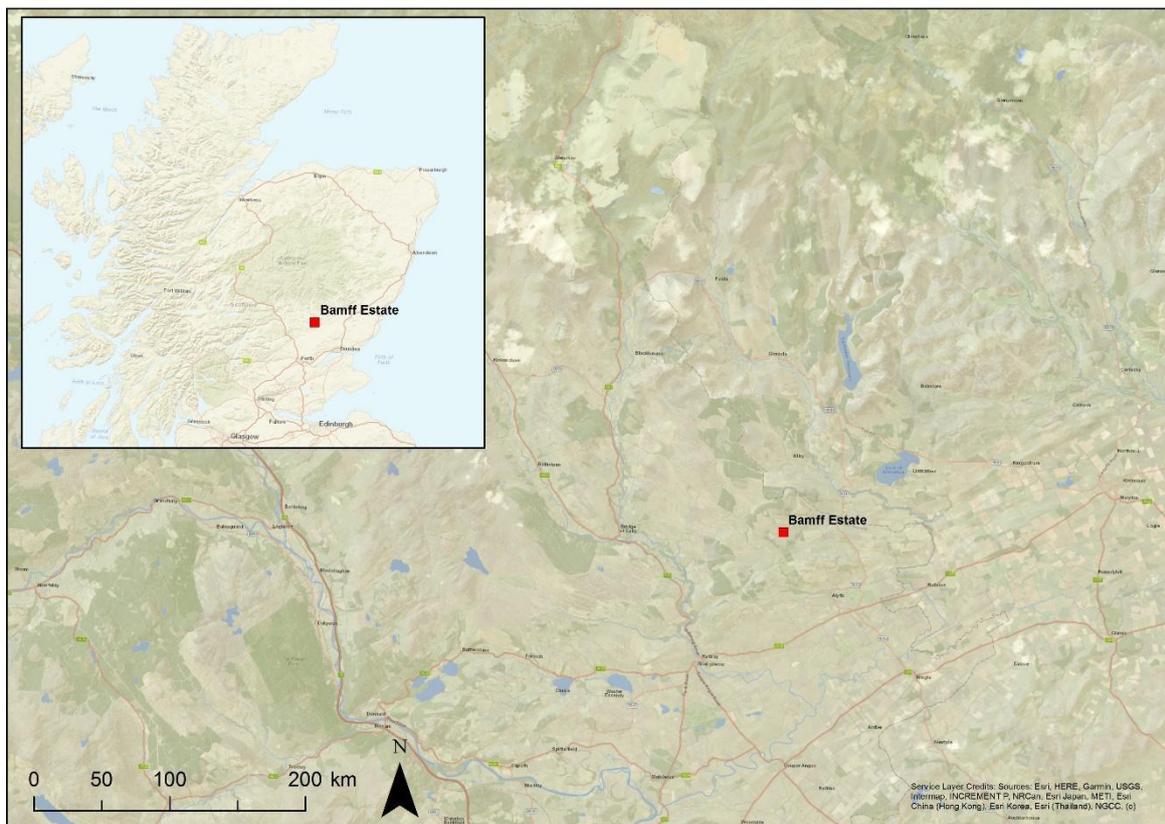


Figure 1: Site location map

Agriculture on the estate is a combination of arable and grazed sheep and cattle. It has been organic since 1995. Forestry is a mixture of native and plantation woodland which is used to fuel a wood-chip district heating scheme (Ramsay, pers. commun).

The estate is drained by a small, spring-fed agricultural stream known as the Burneished Burn. The stream and its tributaries were straightened and realigned

prior to 1860, likely for agricultural drainage purposes which was common throughout Europe at this time (Mant and Janes 2005).

In March 2002, beavers were introduced to a large enclosure on the estate as part of a private demonstration project. The pioneering pair of Norwegian beavers were followed by two Polish beavers and a number of Bavarian beavers. They have been breeding successfully since 2005 and have extended their territory beyond their original enclosure and are now living wild (Ramsay, pers. commun).

2.2 Data collection

2.2.1 Site selection

Six sites within the Bamff Estate were selected for this study including three beaver sites and three non-beaver sites (Figures 1 and 2). These were located at beaver modified and unmodified sections of the Burneished Burn and its tributaries. Beaver sites are defined as being located within a beaver pond along a stream section modified by beavers. Non-beaver sites are defined as being located at a weir impoundment along an unmodified stream section.

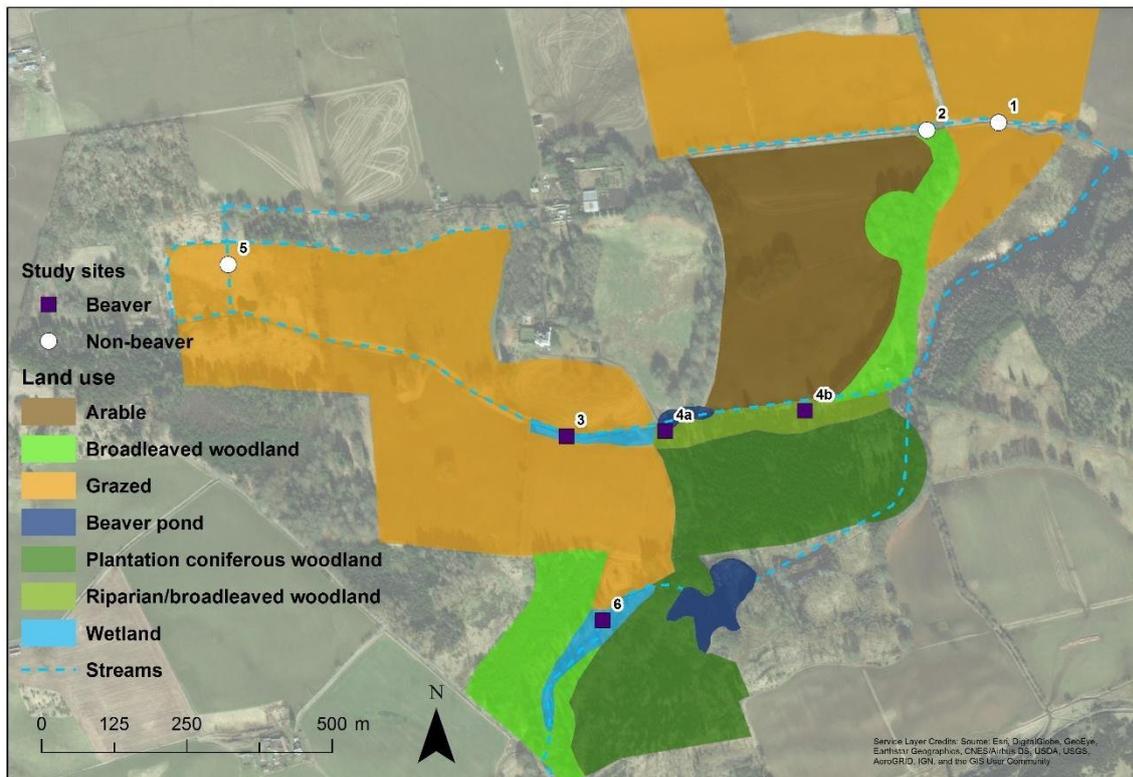


Figure 2: Study sites location map showing proximal land use

Non-beaver sites were chosen first as these were limited in their location to weir impoundments. The main characteristics of these sites were the presence of flow, little in-channel vegetation, and no tree shade. Three beaver sites were then selected to be as representative of the non-beaver sites as possible. This meant choosing sites in beaver ponds away from the littoral zone, next to beaver dams where there was some flow to ensure the sites were comparable. Photographs of all study sites are shown in Figure 3.

Site 4a was initially chosen to be located within one of the larger, more established beaver ponds. However, owing to the excessive vegetation and the distance from a beaver dam, it was deemed unrepresentative of the non-beaver sites and the decision was made to move it closer to the beaver dam. This site became site 4b and ensured that all 3 beaver sites were representative of the non-beaver sites. Data from both sites (4a and 4b) will be included in the study and analysed in the discussion.

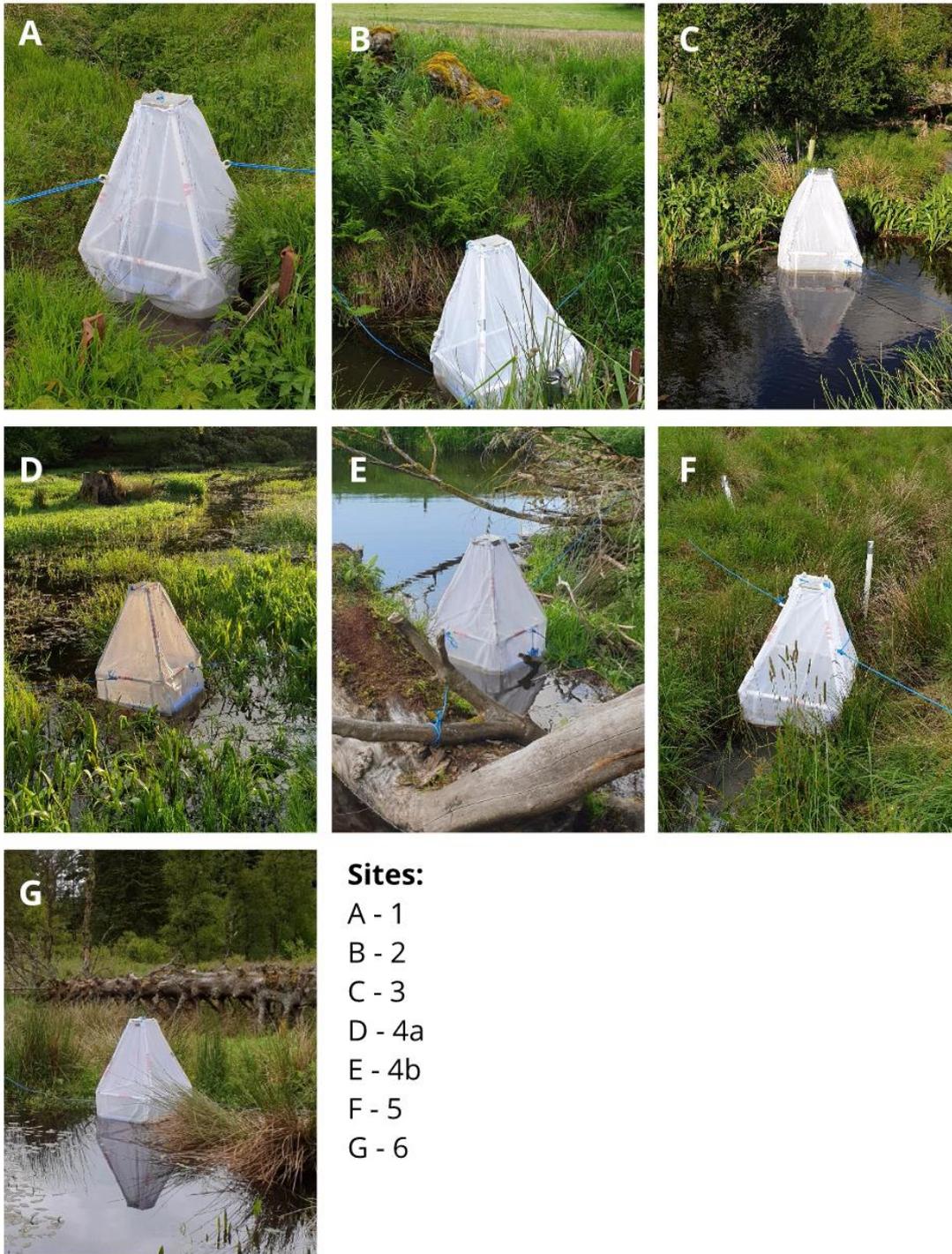


Figure 3: Photographs of each study site

2.2.2 Environmental data

The physical status of each site was recorded to create a dataset of prevailing environmental conditions before sampling began in May 2019. These variables included canopy shade percentage cover, percentage of macrophyte cover including emergent, floating and submergent, water depth, flow velocity and land use surrounding the site. Notes on general observations were also recorded.

Velocity was taken at each site by placing a filled bottle 5 m upstream of the position of the emergent trap. Time was recorded for how long the bottle took to reach the trap and speed (m/s) was calculated using distance and time.

2.2.3 Water chemistry

Water chemistry was measured before sampling began with oxygen levels, temperature, pH and conductivity recorded using the probes listed in Table 1.

Table 1: Probes used for measuring environmental parameters

Parameter recorded	Probe
pH	Hach pHc101 IntelliCAL
Temperature	Hach LDO101 IntelliCAL
Conductivity	Hach CDC401 IntelliCAL
Oxygen	Hach LDO101 IntelliCAL

During sampling, temperature and dissolved oxygen concentration were measured daily at each site in the vicinity of the emergence traps before emergent insects were collected in order to avoid disruption (Figure 4).



Figure 4: Sampling of water temperature and dissolved oxygen using a HachLDO101 Intellical probe at Site 1

2.2.4 Insect monitoring

Emergent insects were collected daily for a 14 day period between 29th May to 12th June 2019 between 12 pm and 4 pm each day. Poor weather on June 12th resulted in the traps being blown over, therefore no data was collected on this day.

Insects were caught in handmade, purpose built floating emergence traps which consisted of a frame constructed from plastic tubing on Styrofoam floats, held together at the top by a transparent plate to allow light through (Figure 5).



Figure 5: Emergent insect trap frame with Styrofoam floats (these were positioned on the outside of the trap when placed on the water)

The frame was covered with a fine mesh net allowing the insects to be caught on emergence. The traps measured 50 cm x 50 cm x 100 cm (w x l x h) and were positioned and secured with ropes at each site. Insects were collected manually using an aspirator and were preserved in sterilin tubes filled with 70% industrial methylated spirit (IMS).

2.2.5 Bird monitoring

Bird surveys were conducted in order to establish feeding activity at each site. Daily bird monitoring had been planned however due to inclement weather a total of 6 surveys were undertaken. Of these, 3 were conducted at dusk and dawn to coincide with maximum bird activity as advised by the British Trust for Ornithology (BTO 2011). The remaining 2 surveys were undertaken at midday to allow the inclusion of all species as foraging activity of swallow peaks around midday (Zielinski and Wojciechowski 1999).

Surveys were conducted as per Lewis-Phillips *et al.* (2019) with a slight modification whereby 3 five minute surveys were conducted with a two minute gap between each one to minimise the chance of duplicating individual recordings (Bibby *et al.* 1998). During each survey birds seen to be feeding or foraging at each site were recorded to species level and their behaviour was noted.

Surveys were conducted using binoculars from a set location that maximised site visibility and were undertaken in good weather in the absence of heavy rain and strong winds to ensure good visibility and to avoid bias from lowered bird activity (BTO 2011). A distance of over 200 m was kept between sites and visit order was randomised in order to reduce replicate records of birds moving between sites which would result in spatial autocorrelation (Ralph *et al.* 1995).

2.2.6 Weather data

Weather data, principally air temperature, wind speed and precipitation, was collected using a Davis Vantage Pro weather station situated on the estate in proximity to the study sites.

2.3 Data analysis

All plots and analyses were created using R software 3.5.3 (R Core Team 2019).

2.3.1 Insect abundance, biomass and diversity

Insect abundance (number of insects sampled/0.25m²) and insect biomass (weight of insects sampled/0.25m²) was calculated daily for each site. Following a similar method to Rolauuff *et al.* (2001), the insects were sorted to order and then counted for each site to calculate abundance. Biomass was determined after drying each sample to a constant weight using a desiccator. Each sample was weighed in grams to four decimal places.

Diversity was assessed using both a diversity index and a diversity estimator; acknowledging that a lower bound for species richness is particularly valuable when studying mobile and diverse communities (Chao and Chiu 2016).

For the index, Shannon was selected on the basis that it accounts for both abundance and evenness of species present. To estimate diversity, Chao1 was used. It relies on the ratio between singletons and doubletons in a given sample (Peterson and Meier 2003). Both metrics were calculated using the vegan package (Oksanen *et al.* 2018).

Independent t-tests were used to compare the measures of abundance, biomass and diversity at beaver and non-beaver sites.

2.3.2 Environmental influences on insect abundance

Generalised Linear Mixed Models (GLMMs) were used to ascertain the relationships between environmental predictor variables and insect emergence (abundance and biomass). The environmental variables included in the models were selected using a Pearson correlation calculation between potential predictors of insect abundance. Variables from pairs with correlation coefficients >0.7 were removed (Booth *et al.* 1994). The remaining input variables were Z-transformed.

The GLMM analysis for abundance used a Poisson distribution with a log link function, while that for biomass used a Gaussian distribution. This was in recognition of the differing structures of both datasets, with abundance being comprised of positive integer count data (Bolker *et al.* 2009). Both models were implemented using the lme4 package and they each included a site ID variable as a random effect to control for potential temporal autocorrelation resulting from repeat surveys throughout the study period (Bates and Maechler 2010).

Akaike's information criterion (AICc <2) was used to select the most parsimonious model in each case, with a lower value indicating a more parsimonious model (Burnham and Anderson 2002, Grueber *et al.* 2011). This preparatory step was undertaken using the `glmulti` package (Appendix 1) (Calcagno and Manzacourt 2010).

On the basis of the AICc values, the analyses were conducted using water temperature, and the presence of beavers as a binary dummy variable. For the abundance model the interaction term between beavers and water temperature was also included.

3. Results

3.1 Emergent insects

3.1.1 Abundance

Across the time series, a total of 2032 insects were recorded with beaver sites accounting for 91% of this total (Table 2).

Table 2: Total and daily mean counts of emergent insect abundance/0.25m²

Site type	Total count	Daily mean count	SE
Non-beaver	192	4.571	0.755
Beaver	1840	43.810	9.960

The mean daily insect emergence count for beaver sites was almost tenfold higher than non-beaver sites at 43.8 and 4.57 respectively. Figure 6 shows clear peaks and troughs in emergence across all sites throughout the study period although site 4b and 6 show the most variation.

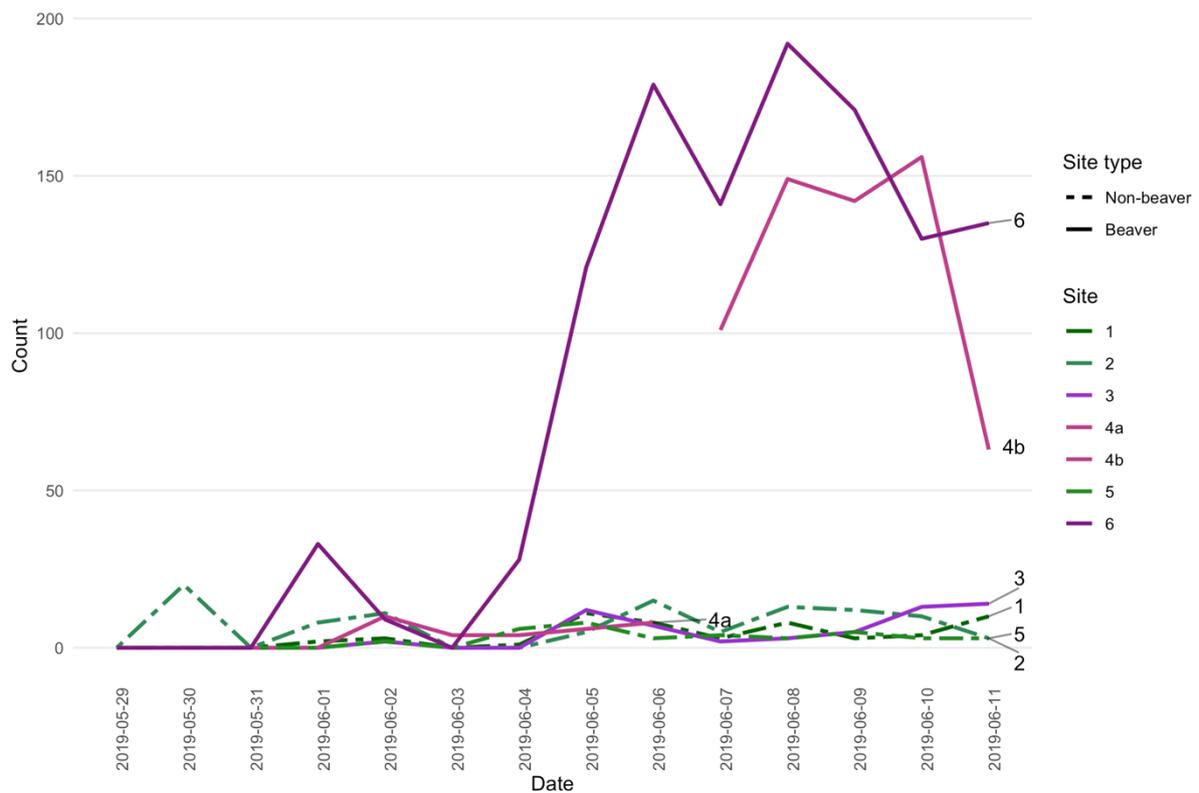


Figure 6: Time series displaying emergent insect counts/0.25m²

Peaks are seen across all sites on June 5th and across most of the sites on June 8th. Zero counts were recorded on May 31st and decreases are seen across all sites on 3rd and 7th June.

The highest insect emergence counts were observed after June 3rd where a step increase in emergence of 0 to 175 is recorded at site 6. June 6th sees the largest peak in insect emergence with a count of 192 at site 6.

A sharp decline in counts is seen at site 4b from June 10th from 156 to 63 insects. This decline is not recorded at the remaining sites. Site 3 saw similar emergence counts to the non-beaver sites with emergence peaking at just 15 bugs on June 10th.

Of the non-beaver sites, site 2 saw the highest emergence counts at 20 on May 30th. Non-beaver sites saw more days with zero counts than beaver sites with all sites showing emergence counts of 0 on June 3rd. Site 6 and site 3 also saw zero counts on this date with only site 4a recording insect emergence (count of 5).

Figure 7 displays a histogram representing the frequency of insect counts at beaver and non-beaver sites.

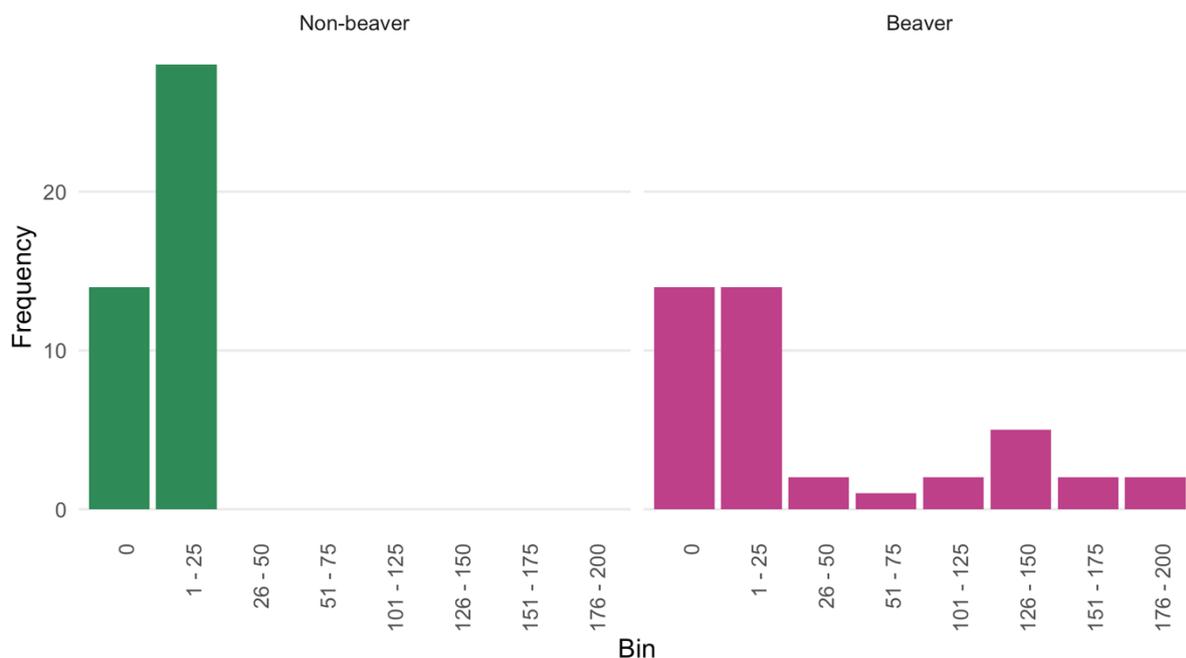


Figure 7: Histogram displaying emergent insect counts/0.25m²

In contrast to non-beaver sites, beaver sites show there are numerous occasions where counts in excess of 100 were recorded. For both site types, zero counts were equal and counts between 1 – 25 were the most prevalent.

The t-test result showed that there was a significant difference in abundance between beaver and non-beaver sites with a p-value <0.001. Results from the GLMM output indicated that beaver, water temperature and the interaction between beavers and water temperature significantly predicted emergent insect abundance/0.25m² (Table 3).

Table 3: GLMM parameter estimates for emergent insect abundance/0.25m² ($p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$)

	Estimate	SE	Z-statistic	Lower CI	Upper CI	p	Significance
(Intercept)	1.150	0.726	1.583	-0.274	2.573	0.113	
Beaver	1.921	0.951	2.020	0.057	3.786	0.043	*
Water temperature	-0.582	0.199	-2.932	-0.972	-0.193	0.003	**
Beaver:Water temperature	0.654	0.202	3.247	0.259	1.049	0.001	**

3.1.2 Diversity

Figure 8 shows total counts of each order from beaver and non-beaver sites. In total there were six orders of emergent insects present in beaver ponds and four orders present in non-beaver ponds.

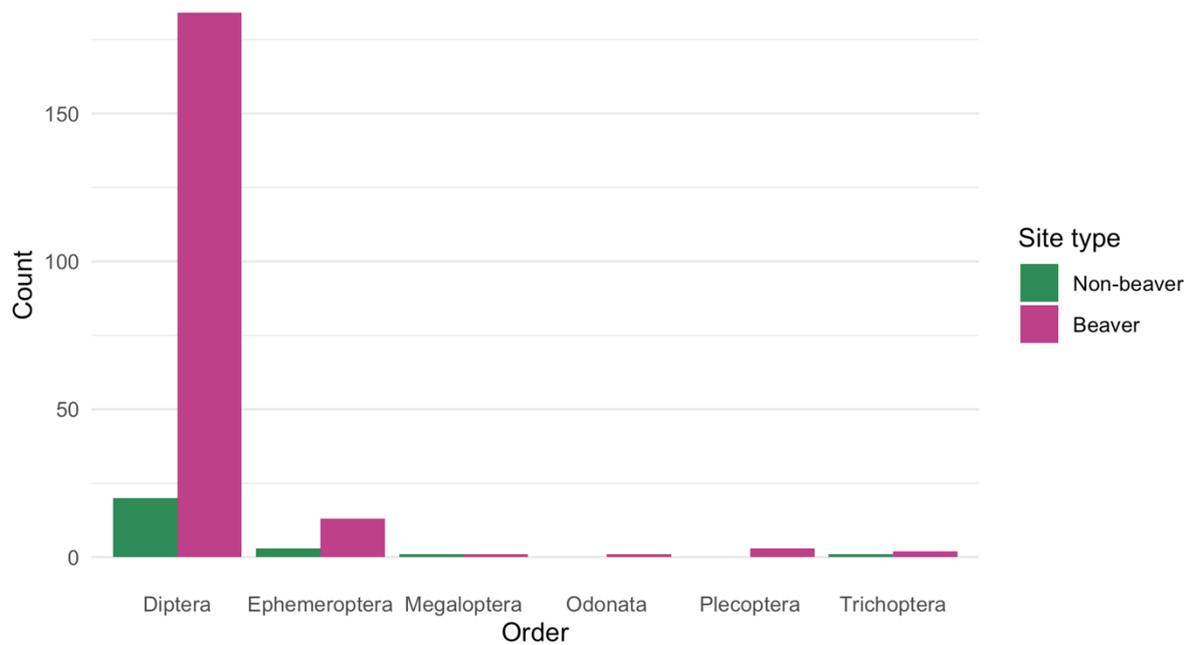


Figure 8: Bar chart displaying total counts of each order from all beaver and non-beaver sites

The most common order at both site types was Diptera, with a total of 1750 at beaver sites and 179 at non-beaver sites. The second most common was Ephemeroptera, totalling 63 at beaver and 7 at non-beaver sites. Megaloptera was more prevalent in beaver sites with a total of 14 counts compared to 1 at non-beaver sites. Plecoptera and Odonata were only present in beaver sites.

Figure 9 shows boxplots of the two most prevalent orders from beaver and non-beaver sites.

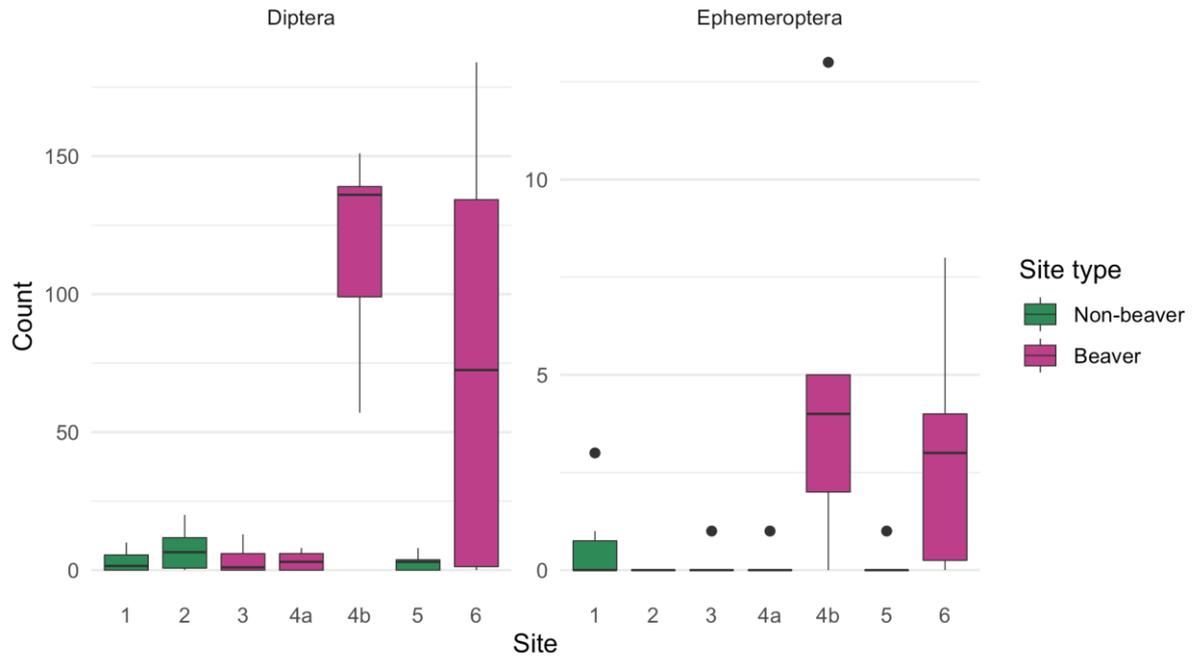


Figure 9: Box plots displaying counts of Diptera and Ephemeroptera from beaver and non-beaver sites

The largest ranges at all sites were seen in counts of Diptera. Beaver sites, where Diptera were found to be most prevalent, saw the greatest variance. Counts at site 6 ranged from 0 to 184, while the largest range at non-beaver sites was 0-20 at Site 2.

Site 4b sees the largest range in Ephemeroptera of 0-13. Ephemeroptera counts hold the largest number of outliers which are seen across all sites likely due to the relative infrequency of observations.

Chao1 estimates species richness to be very similar at all sites apart from sites 2 and 5 (Table 4). These sites see lower Chao1 values of 1 and 2 with the remaining sites estimated to be higher at 4 and 5. The t-test on Chao1 showed species richness was not significantly different between beaver and non-beaver sites as shown by a p value of >0.01 .

The Shannon's H results for each site are relatively low with the highest value seen at Site 1 (0.743) and the lowest at Site 2 (0) (Table 4).

Table 4: Chao1 and Shannon H values for all sites

Site:	1	2	3	4a	4b	5	6
Chao1	4	1	4	5	4	2	5
Shannon	0.743	0.000	0.489	0.582	0.218	0.124	0.212

3.1.3 Biomass

Total and mean daily biomass of insect emergence was higher at beaver sites than non-beaver sites (Table 5).

Table 5: Total emergent insect biomass/0.25m² at beaver and non-beaver sites

Site type	Total (g)	Daily mean (g)	SE
Non-beaver	0.1595	0.004	0.001
Beaver	0.5999	0.014	0.002

Figure 10 shows the variation within these totals.

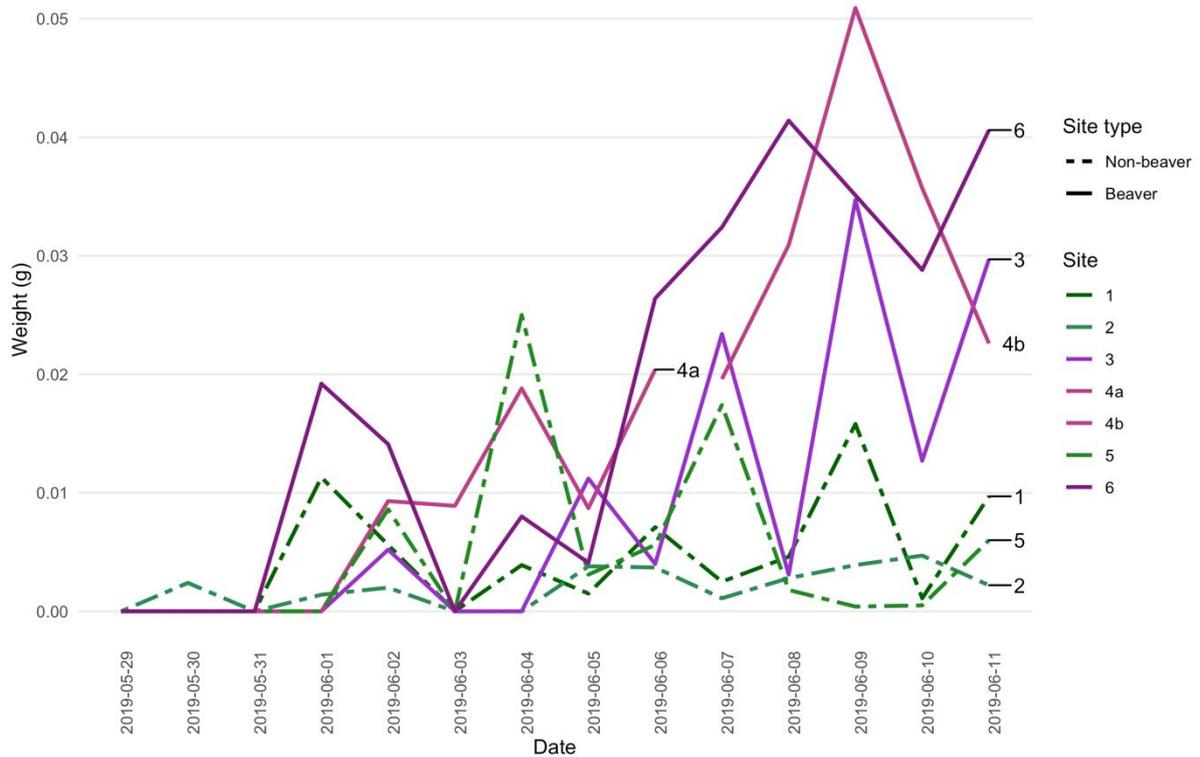


Figure 10: Time series displaying total biomass from each site (g)

There are clear peaks and troughs in biomass at each site. The greatest biomass of 0.051 g is seen at site 4b on 9th June. Sites 2 and 3 also saw large peaks on this day of 0.033 g and 0.015 g respectively. Conversely, site 5 recorded a biomass of zero on this day.

Site 2 showed consistently low biomass which peaked at 0.05 g on June 10th. All sites apart from site 3 saw a low biomass on June 5th with site 1 recording the lowest biomass of 0.002 g.

Biomass at site 6 is seen to decrease from 0.02 g to 0.005 g between May 31st and June 5th where it then sharply increases to 0.027 g on June 6th.

Ranges in biomass are shown in Figure 11 with beaver sites seeing larger ranges than non-beaver sites.

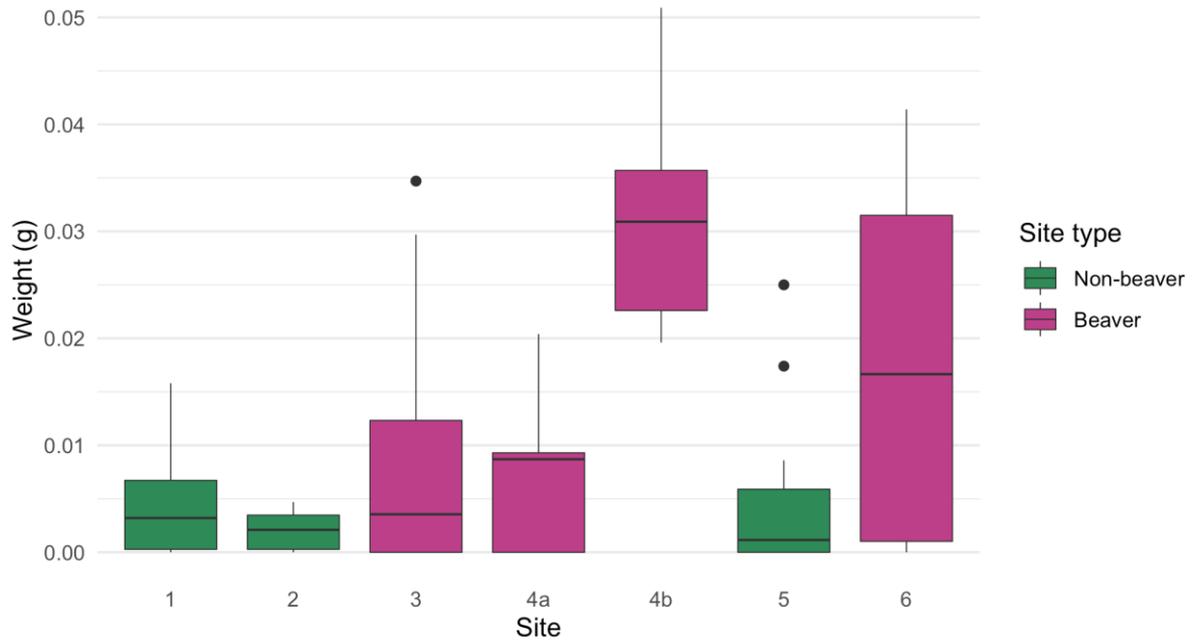


Figure 11: Box plots displaying biomass from each site

The largest range is observed at site 6 of 0 – 0.0414 g, and the smallest range is recorded at site 2 of 0 – 0.0047 g.

Overall median biomass is greater at beaver sites compared to non-beaver sites, however there is overlap when looking at the upper and lower quartiles. For example, the upper quartile at site 5 of 0.018 g significantly overlaps with the range seen at sites 4a and 3. This is also seen at site 1 which overlaps with the lower quartile range of site 3.

The t-test run shows biomass to differ significantly between beaver and non-beaver sites as shown by a p-value <0.001. Of the environmental parameters tested, the GLMM output shows only water temperature is significant in predicting insect emergence (Table 6).

Table 6: GLMM parameter estimates for emergent insect biomass/0.25m² ($p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$)

	Estimate	SE	Z-statistic	Lower CI	Upper CI	p	Significance
(Intercept)	0.007	0.005	1.598	-0.002	0.016	0.178	
Beaver	0.008	0.006	1.271	-0.004	0.020	0.254	
Water temperature	0.004	0.002	2.193	0.000	0.007	0.032	*

3.2 Environmental parameters

3.2.1 Site characteristics

The following tables show the main characteristics of each site. Macrophyte cover and number of species are higher at beaver sites than non-beaver sites with 12 species recorded at site 6. Velocity is higher at non-beaver sites whilst depth varies more across beaver sites.

Table 7: Measured site characteristics

Site	Canopy shade cover (%)	Macrophyte cover (%) (E = emergent, S = submergent, F = floating)	Velocity (m/s)	Water depth (cm)
1	30	-	0.2083	26.4
2	0	E = 20	0.1852	36
3	0	S = 30, E = 20, F = 15	0.0714	22.4
4a	0	S = 80, E = 70, F = 50	0.008	106
4b	20	S = 10, E = 20	0.0178	25.5
5	30	-	0.2	40
6	0	S = 50, E = 40, F = 40	0.0152	13.3

Table 8: Observed site characteristics

Site	Notes on site
1	Narrow stream (50 cm wide), steep sides, overhanging bankside vegetation
2	<i>Caltha palustris</i> , <i>Eleocharis palustris</i> , well vegetated bankside, trees and shrubs within 3-5 m
3	<i>Elodea candensis</i> , <i>Eleocharis palustris</i> , <i>Cyperaceae</i> spp. <i>Poaceae</i> spp. <i>Alisma plantago aquatico</i> , <i>Potamogeton natans</i> , <i>Myosotis scorpioides</i> , trees and shrubs within 3-5 m
4a	<i>Elodea candensis</i> , <i>Eleocharis palustris</i> , <i>Cyperaceae</i> spp. <i>Poaceae</i> spp. <i>Alisma plantago aquatico</i> , <i>Potamogeton natans</i> , <i>Myosotis scorpioides</i> , <i>Lemna minor</i> , <i>Iris pseudacorus</i> , <i>Rumex aquaticus</i> , <i>Hottonia palustris</i> , trees and shrubs within 3-5 m

- 4b** *Alismo plantago aquatico, Elodea candensis*, fallen tree and lots of woody debris
- 5** Narrow stream (50 cm wide), steep sides, overhanging bankside vegetation
- 6** *Elodea candensis, Eleocharis palustris, Cyperaceae spp. Poaceae spp. Alismo plantago aquatico, Potamogeton natans, Myosotis scorpioides, Lemna minor, Iris pseudacorus, Rumex aquaticus, Hottonia palustris*, trees and shrubs within 3-5 m

3.2.2 Water chemistry

Table 9 shows pH and conductivity values that were collected from each site on the 29th May before sampling began.

Table 9: Conductivity and pH values at each site

Site:	1	2	3	4a	4b	5	6
Conductivity (µS/cm)	1247	1050	1078	754	907	750	1524
pH	8.37	7.71	7.05	8.48	7.98	7.55	8.30

pH is relatively consistent across all sites however conductivity shows much more variation, with Site 6 being twice as high as Site 4a.

Figure 12 shows daily water temperature values taken at each site throughout the study.



Figure 12: Time series displaying water temperature at each site (°C)

The t-test result shows that there is a significant difference between water temperature at beaver sites and non-beaver sites with a p-value <0.001 . Mean water temperature at beaver sites (14°C) is higher than that recorded at non-beaver sites (11.4°C), but all sites are seen to fluctuate across the time series. Peaks in temperature are generally well correlated between the sites, but beaver sites are distinguished by having considerably higher peaks in water temperature than non-beaver sites.

Site 6 sees the highest water temperature, peaking at 18.5°C on June 7th and site 4a sees the lowest at 9.4°C on the 29th May. Lower temperatures are observed across all sites on the 29th May and the 12th June.

Figure 13 shows daily dissolved oxygen (DO) concentration levels recorded at each site throughout the study period.

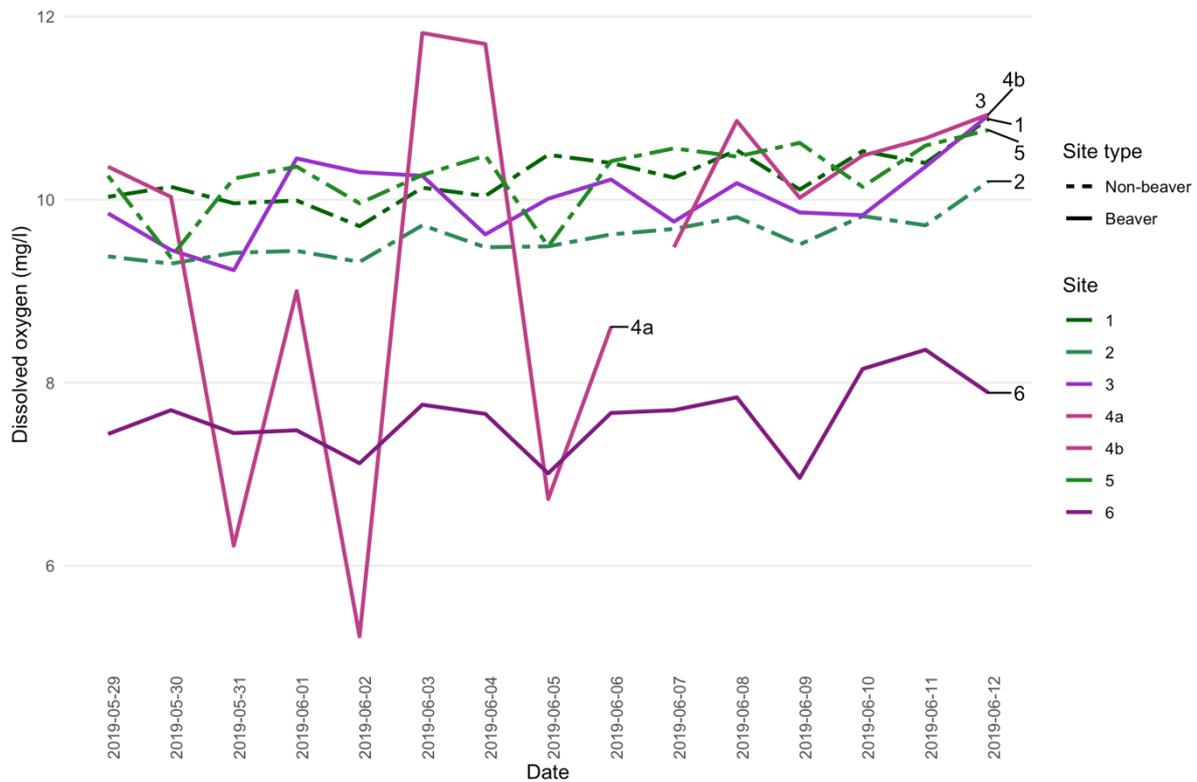


Figure 13: Time series showing dissolved oxygen (DO) concentration at each site mg/l

Again, the t-test result shows that DO is significantly different between beaver and non-beaver sites with a p-value <0.001. Mean DO concentration at non-beaver sites is higher (10.03 mg/l) than beaver sites (9.03 mg/l), however similarly to water temperature, there is more fluctuation at beaver sites across the time series. The lowest DO concentration recorded (5.23 mg/l) was on June 2nd at site 4a which also saw the highest concentration of 11.82 mg/l.

At sites 3, 4 and all non-beaver sites, DO concentration remains relatively consistent fluctuating around 10 mg/l. Site 6 sees consistently lower DO levels than any other site and site 4a sees the greatest fluctuations ranging from 6.22 mg/l to 11.82 mg/l.

3.2.3 Weather data

Figure 14 shows an hourly time series of air temperature daily mean precipitation throughout the study period.

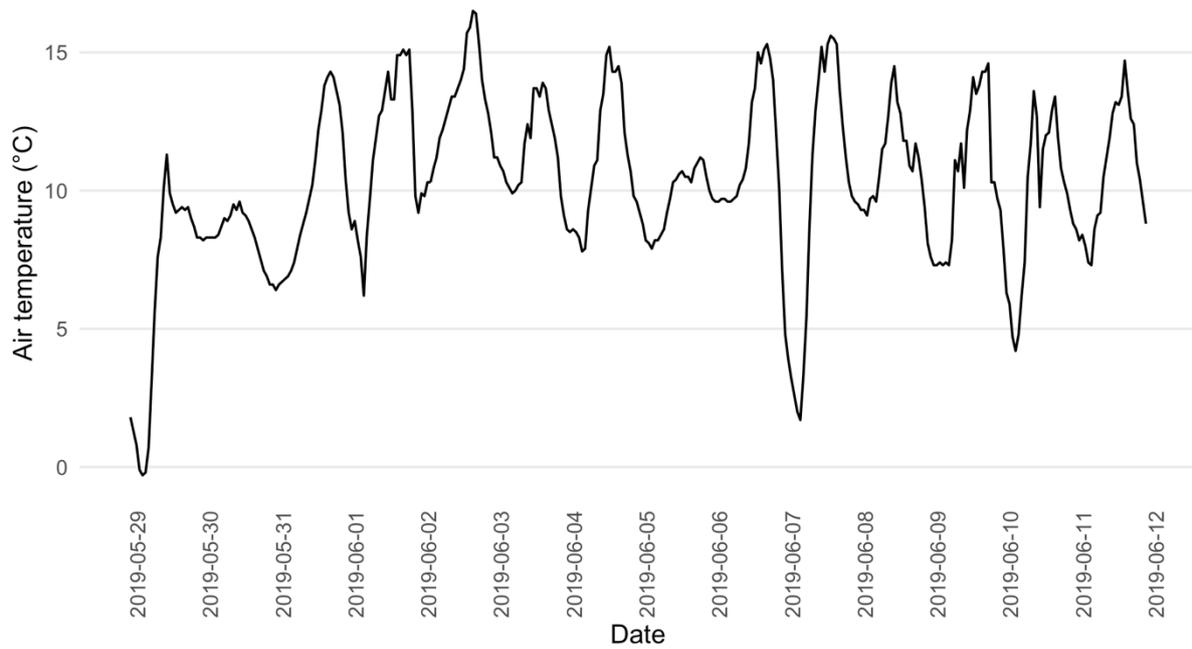


Figure 14: Time series displaying hourly values for air temperature (°C) across the study period

Temperature ranges from -0.3°C to 16.5°C . The start of the study period sees the lowest temperature which rises steeply to the highest recorded temperature on June 2nd. Large drops in air temperature below 5°C are recorded on June 7th and 10th.

Figure 15 shows hourly values for precipitation (mm) and wind speed (knots) throughout the study period.

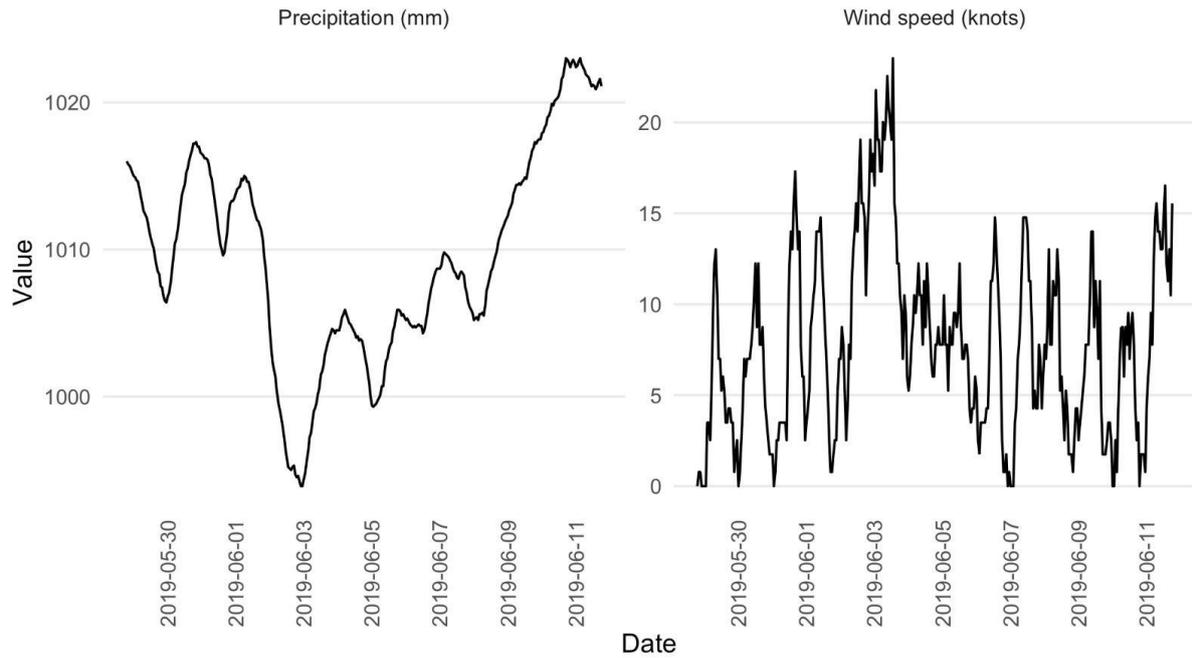


Figure 15: Time series of hourly values for precipitation (mm) and wind speed (knots) across the study period

Precipitation sees an overall decrease from 1014 mm to 994 mm between 30th May and June 3rd. From here it gradually increases over the study period. Peak precipitation of 1022 mm is seen on June 11th before it declines to 1016 mm on June 11th.

Wind speed fluctuates greatly ranging from 0 knots to 23.5 knots with highest speeds observed on the 3rd June.

3.2.4 Bird survey data

In total 116 observations of birds feeding at beaver sites were recorded (Figure 16).

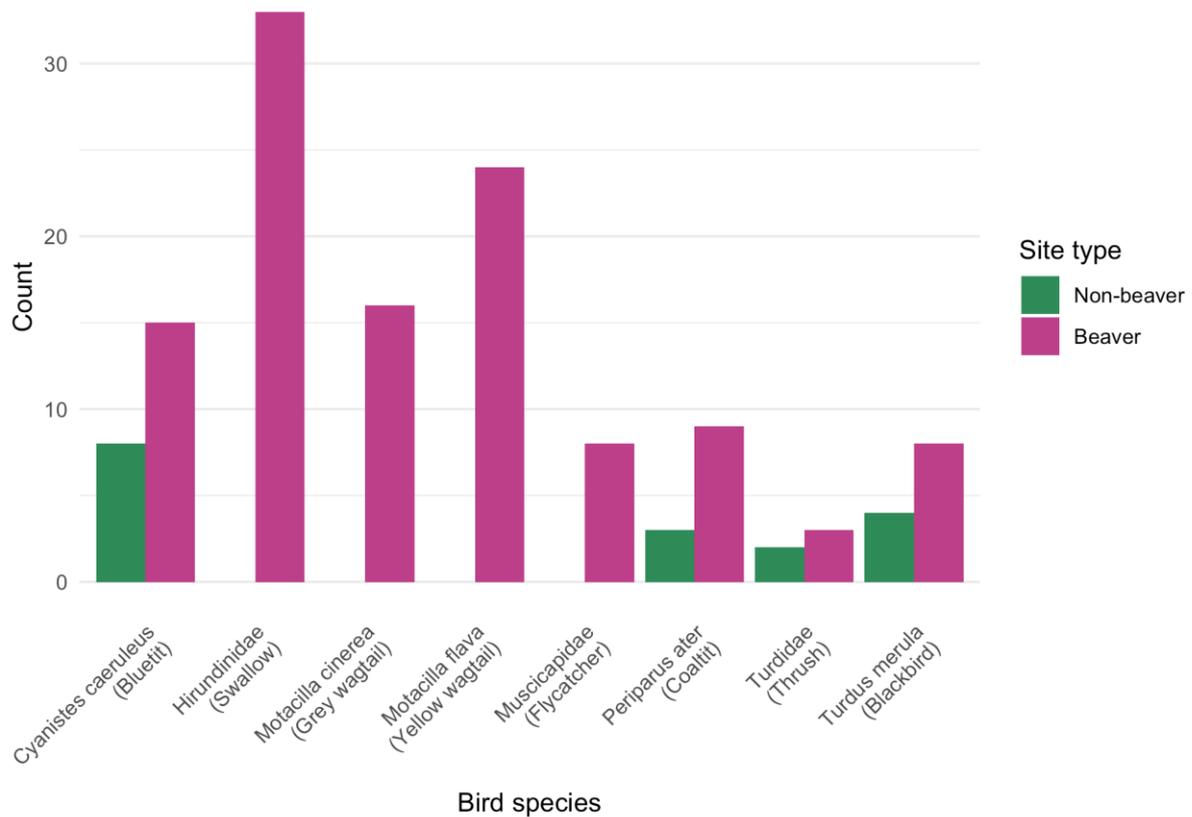


Figure 16: Total bird survey counts from beaver and non-beaver sites

Observations were much lower at non-beaver sites with just 17 recorded. Beaver sites also saw more species feeding which included insectivorous birds such as *Hirundo rustica* and *Muscicapa striata*. The species with the most observations were *Hirundo rustica* and *Motacilla flava*. At non-beaver sites the most observed species was *Cyanistes caeruleus*.

4. Discussion

4.1 Abundance, biomass, and diversity of emergent insects

Abundance, biomass and diversity of aquatic insects are influenced by a multitude of factors which have been studied extensively (Hershey *et al.* 2010). They include water chemistry, dissolved oxygen, water temperature, pollution, substratum, vegetation, flow and air temperature (Bell 1970, Nebeker 1972, Hershey *et al.* 2010). This study aims to investigate the effect that beavers have on some of these factors, and the extent to which their habitat modifications can be deemed to influence emergent insect communities and their avian predators.

Previous studies have shown clear relationships between beavers and an increase in species richness and abundance (Wright *et al.* 2002, Law *et al.* 2016). The findings in this study largely agree with this showing an increase in species abundance, biomass and species richness. Significant differences in abundance and biomass were seen between beaver and non-beaver sites allowing us to accept H_1 that beaver sites harbour a higher abundance and biomass of emergent insects. No significant difference was seen in species richness between beaver and non-beaver sites, so it is not possible to reject the null hypothesis that beaver sites do not harbour a higher diversity of emergent insects (H_2).

Mean emergent insect counts at beaver sites were observed to be ten-fold higher than counts at non-beaver sites and biomass was four times higher. However, there were large diurnal variations in total emergent insect abundance ranging from 0 – 368 (Figure 6). Zero counts were recorded across all sites on the 29th May and 31st May suggesting prevailing environmental conditions were unsuitable for emergence. Counts were present at non-beaver sites on some days (30th May) but absent from beaver sites, and conversely on 3rd June counts were recorded at beaver sites but absent from non-beaver sites. This suggests there were contrasting in-stream variables on these days. A clear increase in emergent insect counts was seen at both site categories from the 5th June onwards indicating there was a shift towards more favourable emergence conditions.

Although we cannot accept H_2 , there are some clear observations in diversity between the sites. Diptera are seen to dominate counts from most sites which is to be expected as they are often the most abundant group of invertebrates in freshwater

habitats and are tolerant to a wide range of environmental conditions (Cornette *et al.* 2015). Although low in numbers at beaver sites, Plecoptera and Odonata were absent from non-beaver sites which could be associated with contrasting in-stream variables.

One explanation for the difference in abundance and diversity seen between beaver and non-beaver sites is the contrast in environmental characteristics, which is reflected in the GLMM output for the binary beaver variable. It is widely accepted that habitat heterogeneity alters aquatic insect communities directly affecting diversity and abundance (McDowell and Naiman 1986).

All sites in this study were located within agricultural streams. However, the non-beaver sites had poor lateral connectivity and lacked variation in vegetation, depth, substratum, and velocity. This is due to historical straightening, the removal of debris and blockages, and the encroachment of agriculture into their riparian zone. At beaver sites, beavers had increased heterogeneity by engineering a habitat consisting of a series of dams and ponds linked by running streams.

The subsequent sections of this discussion will consider the influence of environmental characteristics at beaver and non-beaver sites on the observed differences in abundance and diversity of emergent insects. While environmental observations such as macrophyte abundance and woody debris were not accounted for in the statistical analysis, in order to address H₃, their potential influence will be considered. This will be followed by an exploration of the further analysis undertaken on the influence of water temperature and dissolved oxygen. Finally, the effect of the observed differences in insect emergence on the feeding activity of birds will be discussed.

4.2 Differences in environmental characteristics between beaver and non-beaver sites

The main environmental observations of each site are listed in Tables 7 and 8 with clear differences seen between beaver and non-beaver sites. At macroscopic scales, beavers add habitat heterogeneity to streams by the addition of at least two habitat types; ponds and dams (Rolauffs *et al.* 2001). These habitats drive changes in vegetation, woody debris, velocity, substratum and stream width.

4.2.1 Macrophytes

Beaver ponds support extensive aquatic vegetation which plays a key role in the diet and habitat for aquatic insects (Rolauffs *et al.* 2001). In this study vegetation abundance and diversity varied between all sites but overall, beaver sites were observed to have more submergent, emergent and floating vegetation compared to non-beaver sites. The greatest diversity of emergent insects was observed at the site with the highest diversity of aquatic macrophytes; site 6 where 11 species were recorded. This complements findings from a previous study of macroinvertebrates undertaken by Law *et al.* (2016) on a separate stream on the Bamff estate. They found that vegetated areas of beaver modified habitat had the greatest mean species richness of macroinvertebrates compared to other areas of both beaver modified habitat and unmodified habitat.

The complex macrophyte structure created by beavers increases food resources and provides shelter from predators (Declerck *et al.* 2011). The diversity of species provides feeding material for a wide range of aquatic insects with different feeding mechanisms (Merritt and Wallace 1981). For example, shredders such as species of the Plecoptera and Diptera orders, who feed directly from living vascular plants and coarse pieces of organic matter (CPOM). Scrapers such as some species of Trichoptera and Ephemeroptera have mouthparts adapted to scrape off materials such as periphyton and algae attached to macrophytes (Brittain 1982, Cummins *et al.* 1989). Diptera *spp.* rely more heavily on decomposing fine particular organic matter (FPOM) which they filter out from the water column or gather from the sediment (Merritt and Wallace 2009).

Low counts of emergent insects were observed at site 3. However, it had a relatively high biomass due to the presence of a higher diversity of species. This included larger and heavier species of caddisfly and mayfly that were not present at other sites. This could be attributed to the presence of varying macrophyte species that not only provide a food source for caddisflies but also important material for case building (Figure 17).



Figure 17: Cased caddisfly larvae observed from site 6, note case constructed from macrophyte material

Although high numbers of Diptera were observed across all sites, the disparity between non-beaver sites and beaver sites could be influenced by an increase in vegetation; Diptera species not only feed from macrophytes but are also known to use them for egg laying and feeding (Kondo and Hamashima 1992).

Odonata species use submerged vegetation for foraging and refuge (Goertzen and Suhling 2013). Throughout the study, the presence of Odonata species was recorded only at site 4a, although many were observed in the wider surrounding area. This site had large masses of submerged vegetation which may have been preferred by this species over other sites where submergent vegetation was minimal.

4.2.2 Woody debris

Accumulations of wood are a major natural feature on streams and rivers due to the mortality of riparian trees. Unfortunately, woody debris is frequently removed from lotic systems for navigational and channelisation purposes (Benke and Wallace 2003). However, the incorporation of woody debris into watercourses brings many ecological benefits and in recent times has been used as a form of river restoration to reinstate natural processes (Thompson *et al.* 2017). A key effect resulting from beaver activities such as damming and tree felling, is the input of woody debris to the watercourse (Saarenmaa 1978).

In this study, the highest counts of emergent insects were recorded at the beaver sites which were located next to dams. Non-beaver sites were absent of dams and woody debris. This correlates well with previous studies that found emergent insect density to be higher at beaver dams compared to beaver ponds and free flowing stream sections (Rolauff *et al.* 2001).

Similarly to macrophytes, beaver dams are a source of refuge and food for aquatic insects. Consisting of large quantities of fine woody debris (1 – 10 cm), dams have a large inner surface that extends habitat availability for aquatic insects (Naiman *et al.* 1986). The incorporation of organic material into the dam as well as allochthonous and autochthonous resources provide a valuable food source (Everett and Ruiz 1993, Roni *et al.*, 2015, Cashman *et al.* 2016).

Food resources are increased at dams by their ability to trap leaf litter thus enabling it to be broken down by microbes and mechanical processes. This makes it more palatable for species such as Diptera and Ephemeroptera (Merritt and Wallace 1981).

At non-beaver sites, the absence of dams and woody debris results in leaf litter being transported downstream and unable to decompose. Baillie *et al.* (2019) note how fresh leaf litter is unpalatable and undesirable as a food source due to its high carbon:nitrogen ratio.

4.2.3 Velocity and substrate

The addition of woody debris to streams influences the velocity, stream width, stream depth and substratum (Lehane *et al.* 2002). At beaver sites, flow velocity was much lower than at non-beaver sites which is to be expected because beaver dams dissipate stream energy within their structure. Dams also increase stream width thereby reducing unit stream power (Marston 1994).

Changes in velocity can also modify substrate type which is known to influence the composition of aquatic insect communities (Hodkinson 1975). With the presence of beavers, erosional environments normally present in swift flowing waters see a shift to depositional environments. This impacts on the substratum which changes from a hard, rocky substrate to a soft, sediment-rich substrate (Naiman *et al.* 1984). A transition was evident between the study sites with beaver sites differentiated from non-beaver sites by their lower velocities and sediment-rich, soft substrates. These conditions are favourable to Diptera *spp.* who were present at beaver sites in high numbers. They are known to prefer softer substrates and feed on fine particular organic matter within the sediment (Naiman *et al.* 1984). Low velocity also enhances the availability of suspended organic matter in beaver ponds improving habitat for filter feeders and probably providing a higher count of Diptera at the beaver sites in this study (Naiman *et al.* 1986).

An absence of Plecoptera from non-beaver sites is perhaps a surprise as they are often observed in high flow habitats, however this could be caused by a lack of food resources resulting from minimal macrophyte abundance and leaf litter abundance (Hershey *et al.* 2010).

4.3 Water chemistry

It is widely accepted that water chemistry plays an important role in the ecology and evolution of aquatic insects. The timing and duration of insect emergence are known to respond to changes in water temperature and dissolved oxygen (Ward and Stanford 1982).

4.3.1 Water temperature

Water temperature is an important attribute of water quality and is known to play a critical role in the ecology and evolution of aquatic insects (Ficklin *et al.* 2013). Aquatic insects respond to the entire thermal regime which includes patterns of absolute temperatures, diel and seasonal amplitudes and rates of change (Ward and Stanford 1982). This is crucial to their survival, influencing many aspects of their existence including distribution, reproduction, feeding, growth rates and emergence (Precht *et al.* 1973, Dallas 2008).

Results from this study show that water temperature differed significantly between non-beaver sites and beaver sites. The GLMM analysis revealed that at beaver sites it was an important predictor in insect emergence abundance, but this was not the case at non-beaver sites (Table 3). Figure 18 shows the relationship between abundance and water temperature split between beaver and non-beaver categories revealing the disparity, and therefore the value of the interaction term.

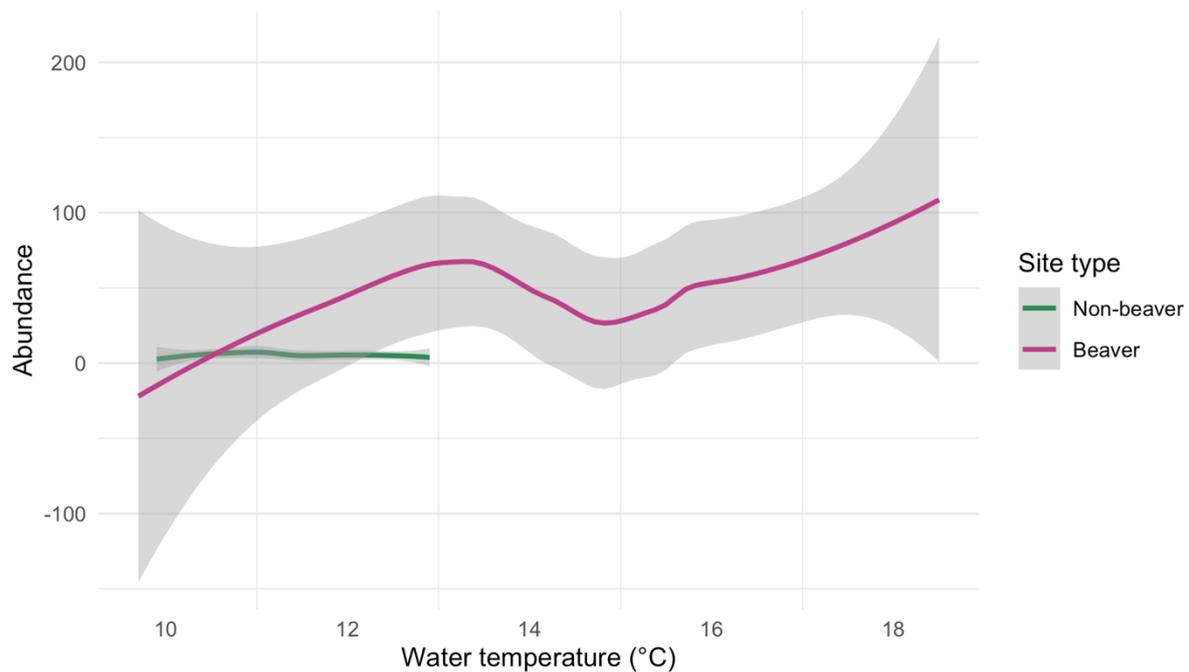


Figure 18: Relationship between water temperature and abundance between non-beaver and beaver sites

This difference is likely due to the warmer temperatures observed at beaver ponds which is known to be an important cue for insect emergence and a key factor in emergence patterns (Egan *et al.* 2016). Fluctuations observed at beaver sites were very high and displayed an overall range of 9.1°C compared to a much smaller range at non-beaver sites of 3.1°C. Emergent insect abundance and biomass at beaver sites responded well to these fluctuations with increases in abundance and biomass recorded where there were peaks in water temperature. Low counts of emergent insects were seen when water temperature decreased, for example at the start of the time series (Figure 12). Here water temperature was low across all sites and counts were very low or zero. June 1st saw a rise from a count of zero on the previous day to a total count of 43 with 77% of these emerging from beaver sites. Water temperatures at beaver sites on this day were seen to increase from an average of 11.5°C to 15°C.

The greatest abundance and biomass of emergent insect were recorded between 5th-11th June which coincided with the highest recorded water temperatures. Although the majority of counts on these days are comprised of samples from beaver sites, counts from non-beaver sites are significantly higher than earlier in the study. This suggests that although water temperature was not significant in predicting insect emergence at non-beaver sites, there was some degree of correlation.

Water temperature not only affects the number of insects emerging but also the biomass as they can grow more rapidly in warmer water (O’Gorman *et al.* 2012). Throughout the warmer period (5th-11th June), biomass increased at all sites apart from site 5. In particular, site 3 saw large peaks in biomass throughout this period despite showing very low emerging insect counts. That said, there was more diversity amongst the insects emerging during this period from site 3 including Ephemeroptera, Megaloptera and Trichoptera. These all have a higher individual weight than Diptera *spp.* which are seen to dominate most sites (Smock 1980).

Each species observed has its own thermal tolerance range which is the range over which the species can survive (Vannote *et al.* 1980). The tolerance range is maintained by a consistent thermal regime within the stream and is important to regular timing of insect emergence. This must coincide with conditions suitable to their survival, including appropriate food resources and the emergence of suitable mating partners (Vannote and Sweeney 1980). In this study, species with a wider thermal tolerance range, for example Diptera *spp.* are seen to emerge from varying water temperatures throughout the time series, whereas other orders recorded show an increase in emergence on days where water temperature was higher. This is not an unusual observation and has been noted in previous studies of insect emergence where water temperatures were seen to influence community composition. Nordlie and Arthur (1981) investigated the effect of water temperature on different species of emerging insect. They revealed that Chironomids were the only species emerging at temperatures of 10°C-13°C with Ephemeroptera, Trichoptera and Odonata only seen to start emerging when temperatures increased by 5-10°C. Increases in temperature of this magnitude were observed at beaver sites and although counts of Ephemeroptera, Trichoptera, Plecoptera and Megaloptera were not very high, they were higher than the non-beaver sites, suggesting the larger temperature range had some influence.

Fluctuations in water temperature are driven by natural and anthropogenic processes. One of the strongest factors in determining water temperature is air temperature, and a strong linear relationship often exists between the two (Wetzel 2001).

Crisp and Howson (1982) reported that mean air temperature alone accounted for 87-95% of the variance seen in water temperature across six north Pennine streams.

In this study, air temperature was seen to increase throughout the time series correlating closely with rises in water temperature. The almost immediate response observed in water temperature is influenced by the depth at each site. All sites apart from Site 4a are classified as shallow (<60 cm) and therefore respond better to air temperature because of their smaller thermal inertia (Stefan and Preud'homme 1993).

Although fluctuations in water temperature were observed at non-beaver sites, they are much smaller than those recorded at beaver sites which suggests that additional factors may have influenced the temperature at beaver sites. Beavers are known to influence water temperature as a result of the changes they create in flow velocity, surface area and depth. By building dams, beavers inundate riparian areas which increases channel surface area and subsequently influences surface heat fluxes which are scaled with the area (Neilson *et al.* 2010). Beaver dams are also known to reduce flow velocity upstream, which was noticed at beaver sites in this study (Majerova *et al.* 2015). Water temperature is generally observed to be higher where flow velocity is low, particularly in shallower streams (Sinokrot and Gulliver 2000).

Shade from vegetation is a factor that influences variation in water temperature (Brown 1969). Although in-stream vegetation was sparse at non-beaver sites, bankside vegetation was fairly dense, particularly at Sites 1 and 5 which had the narrowest channels. Although shade is important in preventing stream temperatures from rising too much, these sites saw completely shaded stream sections which would have reduced heating and fluctuations in temperature (Caissie 2006). In this study, beaver sites saw a much higher abundance of macrophytes which are known to increase shade, but they had wider channels allowing for open water areas too. Sites 4a and 6 had the most macrophyte abundance but also showed high water temperatures and fluctuations. This is probably due to the ability of macrophytes to increase the amplitude of water temperature fluctuations through energy fluxes during photosynthesis (Dale and Gillespie 1977, Crisp and Howson, 1982).

Overall, emergent insects were seen to respond well to an increase in water temperature as a result of the effects of the beaver's engineering abilities.

4.3.2 Dissolved oxygen

Oxygen is fundamental to all life in freshwater habitats and is essential to the metabolism of aerobic aquatic organisms (Wetzel 2001). Dissolved oxygen (DO) varies spatially and temporally and is a large factor in influencing the distribution of aquatic species (Connolly *et al.* 2004).

In this study, DO concentration was significantly different between non-beaver and beaver sites, with overall concentrations lower at beaver sites. These observations are in line with results from other studies which showed that concentrations of DO in beaver ponds were lower than in unmodified stream sections (Snodgrass and Meffe 1998, Rozhkova-Timini *et al.* 2018). As observed in the AICc analysis, DO concentrations were not seen to be an important predictor in insect emergence at either beaver or non-beaver sites. Despite this, it is widely acknowledged that DO concentration, alongside a number of other factors, plays a critical role in the development and emergence of aquatic insects (Ambuhl 1959).

Sites 4a and 6 are seen to have much lower DO concentrations than the other sites, and these were also observed to have some of the highest water temperatures. The relationship between these two parameters is well understood with water temperature playing a significant role in the solubility of oxygen in freshwater habitats (Ambuhl 1959, Davis 1975). There is an inverse relationship between the solubility of oxygen and water temperature with higher temperatures resulting in lower DO concentrations (Dallas and Day 2004). This is evident at site 4a where a large drop in water temperature between the 2nd and 3rd June results in a significant spike in DO concentration. It is also observed at site 6 which overall saw the highest water temperatures throughout the time series, and also saw consistently low DO concentrations. Across the non-beaver sites, water temperature was consistently lower and fluctuated less. This was reflected in the DO concentrations which remained fairly high and showed very little fluctuation. These sites also saw higher flow velocities which are known to influence DO concentration as demonstrated by Coble (1961). The study by Coble (1961) presented a clear relationship between the two parameters with a positive correlation seen between DO and flow velocity (Figure 19).

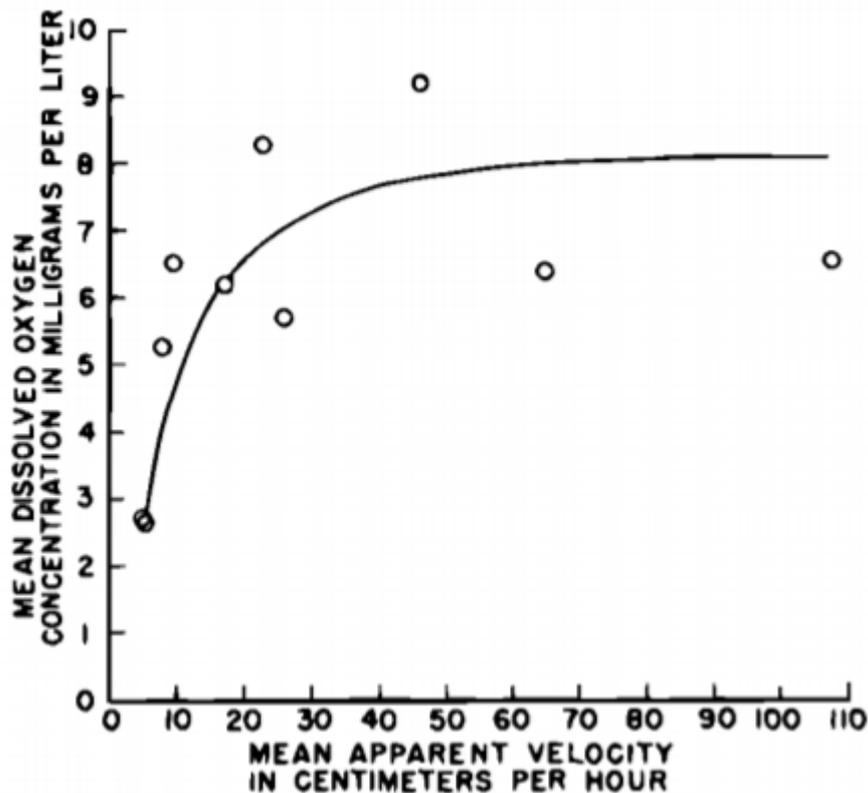


Figure 19: Observed relationship between mean velocity and mean dissolved oxygen by Coble (1961)

This positive relationship can be attributed to water renewal rates which are increased during high flow velocities thereby increasing oxygen availability (Genkai-kato *et al.* 2004).

The evidence presented here suggests that at non-beaver sites, high flow velocity and low water temperature maintained the relatively high and consistent DO concentrations. The absence of macrophytes may also have contributed to higher DO concentrations as extensive cover of emergent and floating vegetation can impede oxygenation (Angélibert *et al.* 2004). This may have been the case for sites 4a and 6 that had the most abundant macrophyte cover. Sites 3 and 4b saw similar DO concentrations to the non-beaver sites and although they had some areas of open water, macrophytes were present in a fairly high density. This could be attributed to the difference in macrophyte species between sites. Floating macrophyte abundance was low at site 3 and absent at site 4b, however the submergent species *Elodea Candensis* was present at both sites. DO concentrations have been seen to increase where this species is present in a higher abundance than emergent or floating species (Frodge *et al.* 1990).

Availability of oxygen influences species diversity as each species have different tolerance ranges owing to variations in their respiratory adaptations and behaviour (Eriksen 1984). Diptera *spp.* have a large range of tolerances to harsh environmental conditions including hypoxia because they possess haemoglobins (Pinder 1986, Panis *et al.* 1996). Although Diptera dominated counts at all sites apart from site 1, they were particularly high at site 6 where DO concentrations were lowest. This was the youngest beaver pond in the study, having been created approximately 2 years ago; as quick colonisers, Diptera are often found in high abundances at newly established sites (Nilsen and Larimore 1973). Decomposition rates are often higher in newly established sites as a result of the large input of inundated material and decaying wood which contribute to low levels of DO (Rozhkova-Timina *et al.* 2018). Older and more established sites, such as 3 and 4b, would already have experienced the initial increase in decomposition rates that occur when beavers inundate an area and were likely experiencing lower and more stable decomposition rates.

The other orders recorded in this study were fairly low in numbers making it difficult to draw conclusions about the factors influencing their distribution. However, Ephemeroptera, Plecoptera and Trichoptera are known to be more sensitive to DO concentrations and are often limited in abundance where concentrations are low (Hepp *et al.* 2013). That said, Plecoptera was only present at site 6, suggesting that DO concentration is not the most important factor influencing its distribution. Similarly, Ephemeroptera were seen in higher numbers at site 6 than site 3 which had consistently higher DO concentrations. There is contrasting literature on the tolerance range of Ephemeroptera to DO concentrations, with Nebeker (1972) suggesting they are very sensitive to low levels and Hepp *et al.* (2013) suggesting they are less so. However, some emergence patterns can be observed within this study, with the highest numbers of Ephemeroptera emergence taking place during peaks in DO concentrations.

It is difficult to identify patterns in emergence and distribution within the other orders recorded in this study as the numbers are so low. Further sampling over a longer time frame would help to establish patterns and to confirm whether they are indeed low in abundance or whether the timing of this study did not coincide with their emergence.

4.2.4 Bird data

This study found that there were significant differences between the number of birds feeding at beaver and non-beaver sites, with increased counts recorded at beaver sites. There were also notable differences in species with beaver sites seeing more insectivorous birds. Swallows dominated counts at beaver sites which also saw numbers of yellow wagtail and flycatcher; both listed on the BTO red list of birds of conservation concern (BTO 2015). These increases are likely to have been driven by the increased abundance of emergent insects which serve as an important food resource (Epanchin *et al.* 2010).

These results are in line with observations from other studies investigating the relationship between emergent insects and insectivorous birds. Gray (1993) reported that flycatcher densities were highly correlated with total insect emergence, and Rosenberg *et al.* (1982) reported on the concurrence between feeding and peaks in insect availability. This study did not correlate bird feeding activity with insect emergence peaks due to the nature of the bird surveys which were not conducted daily. More research is needed in order to investigate the effect beavers have on the timing of bird feeding activity, however the evidence presented here indicates that bird feeding activity increases at beaver sites.

Birds have been observed to choose nesting sites where food abundance and biomass is higher and this is an important factor in their reproductive success (Gibbs 1991, Burke and Nol 1998). Extra food can reduce nest predation rates as less time is spent away from the nest foraging, leaving more time for nest guarding (Rastogi *et al.* 2006). Chicks also spend less time begging when their food supply is regular which ensures that they are less readily detected by predators (Haskell 1994).

Food quantity may not be the only important factor in the observed increases in bird counts at beaver sites. Recent research has found that food quality, including caloric density, nutrient composition and digestibility is also of key importance to the survival of birds (van Gils *et al.* 2005). Highly unsaturated omega-3 fatty acids (HUFA) have been found to have a greater effect than calorific content alone on the developmental performance of birds, including immune function and neural development (Twining *et al.* 2016). Whilst HUFA are found in abundance in aquatic primary producers, they are absent from many terrestrial plants likely due to their

sensitivity to oxidation (Shepinov *et al.* 2014, Hixson *et al.* 2015). Long-term field studies show that tree swallow nestling success was positively correlated with higher aquatic insect availability, whereas little effect was seen by the availability of terrestrial insects (Twining *et al.* 2018). In this study, DO concentrations were observed to be lower at beaver sites than non-beaver sites which could potentially result in increased availability of HUFA. Further research is required in order to investigate how beavers influence HUFA availability and the effect this has on food quality for birds.

Whilst food availability and quality are the most likely explanations for the increased bird counts at beaver sites, differences in habitat may also be a contributing factor. Habitat surrounding the non-beaver sites was mostly open agricultural land with few trees and vegetation to hide and nest in. At these sites, they were more open to predation and feeding would have been riskier than at the beaver sites where there was plenty of refuge (Rastogi *et al.* 2006).

4.3. Limitations and considerations

The findings above must be considered in light of the following limitations.

Firstly, due to funding constraints, fieldwork could only be undertaken within the noted timeframe (29th May – 12th June). The first two weeks of June have historically seen great peaks in emergence of aquatic insects in Scotland (Willby pers. commun) however the weather, particularly at the start of the study, was unusually cold for the time of year and few insects emerged. Similarly, inclement weather at the end of the study resulted in the traps being blown over and consequently data was lost for the last day of the study. The weather also limited the number of bird surveys that could be conducted because of poor visibility. This resulted in a limited dataset and ideally, the study would have been extended in order to capture more emergence peaks and bird activity.

Secondly, although care was taken to place the emergent traps in the middle of the beaver pond in order to keep consistency with the non-beaver sites, this may have resulted in an under estimation of aquatic insects that require a physical structure for emergence. The majority of vegetation at beaver sites was at the pond margins and emergence may have been greater here, and therefore been a better representation of these sites. Alternatively, the traps themselves do present a physical structure and

could have provided an overestimation of insects emerging through the water column, namely *Diptera spp.* (Naiman *et al.* 1984).

Thirdly, due to the time constraints, insects were identified to order. Identifying the insects to species level would have provided a more in-depth understanding of the effect beavers have on the diversity of emergent insect communities. It would also have allowed for further statistical analysis such as a Redundancy Analysis (RDA). Amongst insect species, there is variation in their requirements and tolerance ranges to environmental conditions. Although generalisations about preferences for orders can be made, these do vary at species level and are worth investigating. For example, within Trichoptera, preferences towards channel substrate and case building material vary, with some preferring harder substrate and others preferring soft substrate (Mackay and Wiggins 1979). Understanding these interactions would make conclusions on environmental preferences and distribution of this species clearer. Within Ephemeroptera, there is variation in feeding mechanisms with some species adapted to scraping and others to filter feeding (Wallace and Merritt 1980). Understanding which species were present at each site would help to make a more substantiated interpretation of their distribution, for example if there was a higher abundance of scrapers at beaver sites this would suggest they were benefitting from the increase in macrophytes and woody debris, whereas at non-beaver sites a dominance in filter feeding species may reflect a lack in suitable substrate for periphyton and algae (Ouahsine *et al.* 1996). Additionally, it may have been beneficial to measure nitrogen and phosphorus concentrations at each site as these are known to have a great influence on aquatic insect assemblages (Parr and Mason 2003).

4.4. Implications for conservation and conclusions

Whilst there is some controversy regarding the reintroduction of beavers to the UK, the benefits they bring to ecosystems are clear. This study investigated the aquatic-terrestrial links restored by beavers on the Bamff Estate, Scotland. The main aim was to investigate the extent to which their habitat modifications can be deemed to influence emergent insect communities and their avian predators.

Through their engineering abilities, beavers have transformed once hostile, homogenous streams into ones full of heterogeneity. Increases in macrophyte

abundance and woody debris have enhanced habitat availability, whilst a softer substrate and low flow velocity have made the streams more hospitable. Evidence suggests beavers have also altered water chemistry; increasing water temperature, reducing dissolved oxygen concentration and enhancing diurnal fluctuations in both variables. It is worth noting that without the acquisition of pre-beaver data on insect emergence, environmental characteristics and bird activity, the differences between non-beaver and beaver sites cannot be attributed unequivocally to the presence of beavers. That said, this conclusion can be made on the basis of similar observations made by studies into beaver activity on the Bamff Estate (Law *et al.* 2016).

The abundance and biomass of emergent insects was higher at beaver sites than non-beaver sites and appears to be influenced by the interaction between environmental characteristics. Water temperature is seen to be a significant predictor in insect emergence with peaks in emergence correlating with increased temperatures. There was no significant difference in species richness between beaver and non-beaver sites, however more orders were observed at beaver sites. It would be valuable to explore this further by sampling insect emergence from different habitats across beaver modified landscapes. For example, from wetlands in the riparian zone created by inundation as these are known to harbour different species from the beaver ponds and dams (Rolauff *et al.* 2001).

The increases in emergent insects appear to have had a positive influence on bird feeding activity which was higher at beaver sites. Insectivorous birds such as swallows and flycatcher were found to be present at beaver sites but absent from non-beaver sites. Although there were some clear differences in bird feeding activity between beaver and non-beaver sites, bird survey data was limited in the number of recordings due to inclement weather. Therefore, to affirm the results from this aspect of the study, further bird surveys should be conducted in order to obtain a larger, more reliable dataset. Furthermore, with emerging research into the difference in quality between aquatic and terrestrial insects, future studies should investigate the effect beavers have on HUFA availability and food resource quality (van Gils *et al.* 2005, Twining *et al.* 2016).

The findings from this study further validate the existing corpus of literature suggesting that rewilding can be an effective measure for ecosystem restoration. The reintroduction of beavers to the Bamff Estate has had a transformative effect not only

on the specific locality but also to the wider ecosystem; something that traditional restoration measures have failed to do. In light of the recent reintroduction of beaver communities in sites across the UK, this is a wholly positive sign for many facets of British wildlife, from macrophytes, emergent insects, bird communities and everything in between. With this in mind, UK conservation plans need to focus less on human intervention and have more faith in the ability of one of our greatest ecosystem engineers; the beaver.

Auto-critique

I chose to undertake this study as my earlier work has focused on measures in which to restore rivers using human intervention. As my awareness of the scale of ecosystem degradation has increased, I have become more interested in exploring ways in which whole landscapes and catchments can be restored. A particular interest of mine is connectivity between ecosystems and the links between aquatic and terrestrial habitats. This led me to study rewilding and species reintroduction as a form of ecosystem restoration. Subsequently I discovered the benefits beavers provide as ecosystem engineers. Having discovered a gap in the literature on the effect beavers have on emergent insects and how this relates to the feeding activity of birds, I was keen to address this missing research. The opportunity to study the beavers on the Bamff Estate in Scotland was particularly exciting as they have recently received protection status, and I strongly believe it is more important than ever to understand the benefits they bring to ecosystems in order for their reintroduction across the UK to be successful.

I believe the main strength of this study is the originality of the research topic and the gap it fills in current literature. Overall, the project was successful in its aim and has provided key research that was lacking in previous studies of beavers. The study was able to answer the presented hypotheses and provides evidence that abundance and biomass is increased at beaver modified habitat. Results also show that bird feeding activity is increased at beaver sites. Analysis of the environmental variables reveals how beavers have modified their habitat, making it more favourable for emergent insects and birds. At a personal level, one of the key skillsets I wanted to improve during this study was my species identification skills of both aquatic insects and birds. This has developed throughout the fieldwork and analysis, and I now feel much more confident in my identification abilities.

There were some weaknesses in the study, notably gaps in both the insect and bird data. Poor weather limited some of the conclusions that could be made, particularly around the diversity of emergent insect communities. Furthermore, identifying the insects to order made interpretations of their distribution less clear because of the differences in environmental tolerances at species level. If I were to undertake this research again, I would identify the insects to species level. This would also enable

more statistical analysis, such as an RDA on the species distribution. I would undertake bird surveys daily to ensure they coincided with peaks in emergence, which would enable me to identify patterns in the feeding activity of birds. Despite this, the study did show some interesting initial patterns and as a unique research project, it provides a basis for further studies into this topic. It has also opened doors onto opportunities to investigate whether beavers influence the quality of food resources, and how this influences the feeding activity of birds.

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Appendices

Appendix 1

Abundance:

Prepare initial model with all non-correlated variables

```
model <- lme4::glmer(abundance ~ beaver + temp + o2 + (1 | site), data = df, family = "poisson")
```

Run AICc using glmulti

```
aicc <- glmulti::glmulti(
```

```
  formula(model, fixed.only = TRUE), # take our model (from above)
```

```
  random = "(1 | site)", # add random effect for site
```

```
  data = df_z, # specify data
```

```
  fitfunc = lmer.glmulti,
```

```
  crit = "aicc"
```

```
)
```

Identify most parsimonious model on the basis of AICc

```
glmulti::weightable(aicc)
```

Implement most parsimonious model

```
lme4::glmer(abundance ~ 1 + beaver + temp + beaver:temp + (1 | site), data = df, family = "poisson")
```

Biomass:

Prepare initial model with all non-correlated variables

```
model <- lme4::lmer(biomass ~ beaver + temp + o2 + (1 | site), data = df)
```

Run AICc using glmulti

```
aicc <- glmulti::glmulti(
```

```
  formula(model, fixed.only = TRUE), # take our model (from above)
```

```
  random = "(1 | site)", # add random effect for site
```

```
data = df_z, # specify data
fitfunc = lmer.glmulti,
crit = "aicc"
)

# Identify most parsimonious model on the basis of AICc
glmulti::weightable(aicc)

# Implement most parsimonious model
lme4::lmer(biomass ~ 1 + beaver + temp + (1 | site), data = df)
```