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Sanders, C., Shortall, C. R., England, M., Harrington, R., Purse, B., Burgin, L., Carpenter, S. and Gubbins, S. 2019. Long□term shifts in the seasonal abundance of adult Culicoides biting midges and their impact on potential arbovirus outbreaks. *Journal of Applied Ecology.* 56 (7), pp. 1649-1660.

Long-term population monitoring of arbovirus vectors reveals a shift in adult phenology driven by site-specific heterogeneity

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Abstract

Viruses transmitted by arthropods (arboviruses) cause diseases of humans, livestock and wildlife across a broad geographic range that includes both tropical and temperate regions. It has been hypothesised that the incidence and intensity of outbreaks of such viruses should be particularly sensitive to climate change, due both to the poikilothermic physiology of their vectors and strong evidence for shifts in the phenology of non-vector arthropod species. A major limitation in testing this hypothesis, however, is the lack of relevant and consistently standardised data sets collected over a sufficient temporal span to detect shifts in the seasonal activity of vector species.

We use samples taken from a unique long-term insect survey, that has been carried out since the late 1970s in the United Kingdom (UK), to examine changes in the timing of the first and last appearance of adult *Culicoides* biting midges (Diptera: Ceratopogonidae). Using 2867 collections made at two sites in the UK separated by 400km we identify over 150 000 specimens of *Culicoides* caught between 1974 and 2012. These included all the putative vector species of *Culicoides* that have been identified as transmitting arboviruses in the UK. We then employ Bayesian modelling approaches to parameterise the impact of meteorological conditions, changes in host density and land use on their abundance at both sites. This approach leads to the discovery of site-specific variation in the first and last appearance of *Culicoides* adults, with no recorded change at one site and a 0.5-1.5 days per year shift over the course of the sampling period at the other. The shift in *Culicoides* adult phenology is driven by an overall increase in abundance and correlated with local increases in temperature and increased precipitation. We then simulate the impact of changes in the phenology of *Culicoides* on the temporal occurrence of arbovirus transmission and find that the period over which this could occur has been significantly extended in the period assessed.

Introduction

Arthropod-borne viruses (arboviruses) include some of the most important emerging and re-emerging pathogens of humans, livestock and wildlife worldwide (Gould, Pettersson, Higgs, Charrel, & de Lamballerie, 2017; Liang, Gao, & Gould, 2015; Weaver & Reisen, 2010). The seasonal incidence and abundance of arthropod vectors capable of transmitting arboviruses, alongside environmental temperatures enabling replication of the arbovirus in these vector, are key determinants of the timing, intensity and spread of outbreaks (Lafferty, 2009; Purse, Carpenter, Venter, Bellis, & Mullens, 2015; Rogers & Randolph, 2006). As poikilothermic organisms, the potential influence of climate on both arthropods and the arboviruses they transmit has been a key area of debate, in explaining both their current temporal and geographic incidence and in predicting what changes might be expected under future climate scenarios (Epstein, 2000; Gould & Higgs, 2009; Kovats, Campbell-Lendrum, McMichael, Woodward, & Cox, 2001; Lafferty, 2009; Tabachnick, 2016).

The unprecedented incursion and establishment of multiple strains and species of arboviruses transmitted by *Culicoides* biting midges (Diptera: Ceratopogonidae) across Western Europe is a spectacular example of a shift in global pathogen distribution and has been suggested to be driven by changing climate (Elbers, Koenraadt, & Meiswinkel, 2015; Gubbins, Carpenter, Baylis, Wood, & Mellor, 2008; MacLachlan & Guthrie, 2010; Purse et al., 2005). This hypothesis is underpinned by the fact that *Culicoides* are among the vector groups most likely to be affected by changes in temperature and precipitation, being small bodied (<1.5 mm body length) and entirely reliant on the presence of suitable semi-aquatic habitats for larval development (Purse et al., 2005). In addition, other competing hypotheses, including changes in livestock husbandry, distribution and abundance, have been discounted to date (Simon Carpenter, Wilson, & Mellor, 2009; MacLachlan & Guthrie, 2010; Purse et al., 2005).

Insect phenology is one of the strongest biological indicators for the impacts of climate change (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; Forrest & Miller-Rushing, 2010; Root et al., 2003) and therefore plays a key role in our understanding of changes in ecosystem processes (Diez et al., 2012; Rafferty, CaraDonna, Burkle, Iler, & Bronstein, 2013). In temperate regions, the magnitude and direction of response to shifts in climate varies with each species, but there is a general trend for spring-time events such as adult emergence, to take place earlier in response to shortening winters (Menzel et al., 2006; Parmesan & Yohe, 2003). It is therefore expected that changes in the timing of interactions between vectors, pathogens and hosts may also demonstrate similar adjustments that may promote or hinder pathogen transmission (Altizer et al., 2006).

The lack of relevant and consistently standardised data sets of vector species collected over a sufficient temporal span severely limits the ability to detect shifts in seasonal activity. Long-term studies of the seasonality of arthropods are dominated by charismatic insects such as large Lepidoptera and Coleoptera, where detailed historical records exist and have demonstrated dramatic shifts in phenology and distribution for some species (Altermatt, 2012; Roy, Rothery, Moss, Pollard, & Thomas, 2001; Roy & Sparks, 2000). Established in the 1970s, the Rothamsted Insect Survey network represents an invaluable resource as the longest continuous survey of insects in the world (Bell et al., 2015; Harrington et al., 2007). The 12m high suction traps collect a daily sample of aerial invertebrates that has been shown to be representative of the aerial population over a wide area (Bell et al., 2015). The collections from the trap network have been used to investigate changes in the population dynamics of pest aphid species (Harrington et al., 2007). Records of the first flight of pest aphid species show a significant change in the timing of first flight, with an average decrease of 0.6 days per year (Bell et al., 2015). The accumulated degree days above 16°C and milder winters were linked to this advancement whilst last flight observed and abundance in collections remained relatively constant (Bell et al., 2015).

The Rothamsted suction traps (RST) have been previously used to monitor *Culicoides* activity (Fassotte et al., 2008) and describe seasonality of *Culicoides* flight with meteorology over a single season (Sanders et al., 2011). These collections provide a unique opportunity within studies of vector ecology worldwide to examine the seasonal dynamics and abundance of adults over a period of time proportional to the long-term study of climate. Our aim is to utilise this resource to examine changes in the seasonality and abundance of *Culicoides*, including all putative vectors of bluetongue virus (BTV) in the Palearctic, at two sites over a period of nearly 40 years. We then assess the likely impact of these changes on the transmission of arboviruses using mathematical modelling approaches.

Methods

Trap collections, climatic variables and livestock density data

The climatic changes experienced across the Palaearctic region in the last 40 years are spatially heterogeneous (Fig. 1). Investigation of the impacts of this change required long-term collections of storage-resistant vector fauna at an abundance in collections from which deviance could be observed. The Rothamsted suction trap network across the UK represents sites in arable and pastoral regions. The Preston (53°51’16”N, 2°45’48”W) and Starcross (50°37’44”N, 3°27’13”W) trap sites were selected in the north and south of England respectively, where different changes in climatic conditions have been experienced (Figure 1). Land cover in the immediate vicinity (250m) of the Preston trap is a diverse mixture of broad leaved woodland (27%), improved grassland (18%) and heathland (21%) with smaller proportions of arable (10%) and sub-urban (14%) cover. Within 2km from the trap site the landscape is dominated by improved grassland (65%) and arable land (19%). The area around Starcross is largely a mix of arable (66%) and suburban (20%) land cover with small amounts of improved grassland (10%). Within 2 km of the trap site, arable (34%) and coastal (28%) dominate with some broadleaved woodland (11%) and improved grassland (11%). Soil types differs between the sites, with Starcross having a sandy soil that does not retain as much moisture as the clay loam at Preston. Suction traps at both largely pastoral sites had previously collected large numbers of *Culicoides* in 2008 (Sanders et al., 2011) and had near-complete, daily sample records from 1974 to 2012 from which *Culicoides* were identified. Samples were examined for *Culicoides* from every fourth day of every even year for Preston and every fourth day of every fourth year for Starcross. The daily samples for both sites from 2008 (Sanders et al., 2011) were also included in the analysis.

Culicoides were counted and identified according to morphological keys (Campbell & Pelham-Clinton, 1960; The Pirbright Institute., 2007) to species or species group level. Female *Culicoides* of the *Avaritia* subgenus were identified to the level of the polyphyletic Obsoletus group, described here as *Culicoides obsoletus* Meigen, *Culiocides scoticus* Downes and Kettle, *Culicoides dewulfi* Goetghebuer and *Culicoides chiopterus* Meigen. The long-term storage of these samples precluded molecular analysis to species level and separation of *C. dewulfi* and *C. chiopterus* by wing-pattern morphology in older samples was considered to be unreliable. Males of the Obsoletus group were identified to species level and have been used previously as a proxy for the activity of the females of each species (Sanders et al., 2011; Searle et al., 2014). The number of *Culicoides* present in large collections of more than 500 individual *Culicoides* were estimated using a randomised grid sampling method as described in (Sanders et al., 2011). Eleven species/groups of *Culicoides* were recorded: total *Culicoides*, Obsoletus group females, *C. obsoletus s.s.* males, *C. scoticus* males, *C. chiopterus* males, *C. dewulfi* males, *C. pulicaris* L. females, *C. pulicaris* males, *C. punctatus* Meigen females, *C. punctatus* males and other *Culicoides* (i.e. those species not listed).

Temperature and precipitation data for 1961-2011 were obtained from the UK Climate Projections (UKCP09) gridded observation data-sets. These cover the UK at 5 km × 5 km resolution with the data for each trap site extracted for the grid square in which it is located (Fig. S1a-e). Soil moisture data for the trap sites was provided from Grid to Grid hydrological model estimates (not observations) supplied by Centre for Ecology and Hydrology (need to provide attribution) (Fig. S1f). The North Atlantic Oscillation, an indicator of winter weather severity data was taken from the Hurrell station-based index, 1960-2011 (Figure S1g) (Hurrell, 2014). The numbers of cattle and sheep in each trapping area were taken from the corresponding 10x10km grid square extracted from the EDINA database of agricultural survey data 1972-2010 (Edina Agcensus, 2014) for census years (Fig. S2). A linear interpolation was used for years without data. Fine scale spatial information (25m^2 land parcels) on land cover during the latter half of the study period was derived from the CEH Land Cover Maps for 1990 (Fuller, Groom, & Jones, 1994), 2000 (Fuller, Smith, Sanderson, Hill, & Thomson, 2002) and 2007 (Morton et al., 2011) (Fig. S3).

Statistical methods

Five measures of phenology and abundance of *Culicoides* biting midges were considered: (i) time of first appearance (defined as >5 individuals caught); (ii) time of last appearance (defined as >5 individuals caught); (iii) season length (i.e. time between first and last appearance); (iv) maximum daily catch; and (v) mean daily catch. Annual trends in each of the measures were explored by computing them from the RST data, fitting a straight-line relationship to the computed measure for each year by linear regression and testing whether the slope differed significantly ($P<0.05$) from zero. Because data for all years (except one) are based on a subsample of the daily catches, the robustness of these trends was assessed by fitting a generalised linear model (GLM) to the full RST data-set for the species/group and site in a Bayesian framework (cf. Sanders et al. 2011). In the model, the trap catch on day t was assumed to follow a Poisson distribution with mean $\mu(t)$ given by,

$$\log(\mu(t)) = b_0 + \sum_{n=1}^{2} \left\{ a_n \sin\left(\frac{2n\pi}{365}t\right) + b_n \cos\left(\frac{2n\pi}{365}t\right) \right\},$$

where b_0 scales the abundance and the a_ns and b_ns are the seasonality parameters (i.e. they control phenology). The model parameters were allowed to vary between years (to allow for variation in seasonality and abundance between years) and the model also included temporal autocorrelation (to allow for dependence between observations) (see Text S1 for details). The fitted models were then used to generate replicated simulated phenology and abundance measures with the trends in these replicated measures analysed by linear regression (see Text S1 for details). In addition to assessing the robustness of the trends, this approach also allows a more detailed exploration of the underlying trends in the RST data and, in particular, to disentangle the roles of abundance and phenology from one another.

The relationship between the five phenology and abundance measures and climate was assessed for twenty summary climate variables) and for density of two livestock species (Table S1). Linear regression was used to fit a straight line relationship between each measure and the variable of interest and testing the significance of the slope. As with the annual trends, this was done using the measures computed from the data and using replicated simulated measures to assess the robustness of any relationships.

Implications for arbovirus transmission

To explore the possible consequences of changing *Culicoides* phenology on the transmission of *Culicoides*-borne viruses we used a simple model for viral replication inside the adult midge vectors based on cumulative thermal time (S. Carpenter et al., 2011; A. Wilson, Carpenter, Gloster, & Mellor, 2007). In the model a *Culicoides* midge is able to transmit BTV once the accumulated degree-days since it was infected equals or exceeds the level required for completion of the extrinsic incubation period. Assuming no infected midges survive from one season to the next (A. Wilson, Darpel, & Mellor, 2008), we used the model to estimate the earliest time at which newly infected midges would first become infectious (because they have accumulated sufficient thermal time) and so the earliest time at which transmission could occur.

Results

Trap collections

A total of 2867 collections from both sites were examined for *Culicoides*. At Preston, the 1628 samples contained a total of 139,861 *Culicoides*; at Starcross the 1239 samples contained 19,193 *Culicoides*. Collections at Preston were dominated by the Obsoletus group (65.0%), the Pulicaris group contributed 21.2%, with other species including *C. circumscriptus* Keiffer, *C. achrayi* Kettle and Lawson, *C. brunnicans* Edwards, *C. stigma* Meigen, *C. nubeculosus* Meigen, individually not exceeding 1% of the total catch and together accounting for 13.9% (Fig. 2). At Starcross, the trap collections were dominated by the Pulicaris group (54.1%) and the Obsoletus group contributed 19.6%. Other species of *Culicoides*, including *C. circumscriptus* (3.8%), when combined contributed 26.2% to the total catch. At both sites the traps collected a greater proportion of male (68.4% at both sites) than female *Culicoides* (31.6%) (Fig. 2).

Annual trends in phenology and abundance

Between 1974 and 2012 at Preston times of first appearance were earlier, times of last appearance were later, seasons were longer and abundance (maximum and mean daily catch) greater, though these trends were not significant for all eleven *Culicoides* species/groups (Table 1; Figure 3). By contrast, no significant trends were identified in any of the measures of phenology or abundance for any of the eleven species/groups at Starcross over the same time period (Figure 4). These conclusions are robust to uncertainty in the phenology and abundance measures (Figure 5).

At Preston, the time of first appearance decreased by around 0.5-1.5 days per year for total *Culicoides*, *C. obsoletus* group females, *C. scoticus* males, *C. dewulfi* males and *C. punctatus* males (Table 1). Furthermore, the time of last appearance increased by a similar amount for these species/groups (Table 1). Accordingly, the length of the active season for these species/groups increased by around one to three days per year (Table 1). In addition, the time of last appearance increased by around two days per year and season length increased by about three days per year for *C. punctatus* females (Table 1). There were increases in abundance of between 5% and 13% per year for seven (out of 11) species/groups as measured by maximum daily catch and of between 2% and 10% per year for ten (out of 11) species/groups as measured by mean daily catch (Table 1).

In the underlying statistical models used to infer the annual trends in phenology and abundance measures, there were no significant trends in any of the seasonality parameters (i.e. the a_ns and b_ns) for any of the species at either Preston or Starcross, nor were there significant trends in the abundance parameter (i.e. b_0) for any of the species at Starcross (Figure S4). By contrast, the abundance parameters increased significantly over time for nine (out of 11) species at Preston (Figure S4). This suggests that the earlier times of first appearance and later times of last appearance (Table 1) are a result of increased abundance (and, hence, an increased chance of being trapped) rather than to changes in phenology.

The full results of the statistical modelling are presented in the supporting information, including assessment of the fit of the model to data (see Text S1 and Figs S5-S26). In particular, model checking indicated that the models adequately captured the data in terms of overall fit, total catch and maximum daily catch.

Climate, host and land use variables

There was a significant increase in annual mean temperature at Preston (b=0.03; P<0.001) between 1974 and 2012 (Fig. S1a) and in annual total precipitation (b=4.0; P=0.005) (Fig. S1c), but no significant trend in annual mean soil moisture (P=0.46) (Fig. S1f). There was a significant decrease in cattle (b=-0.05, P=0.05) density and a significant increase in sheep density (b=0.44, P=0.01) between 1974 and 2012 at the site (Fig. S2). At Starcross, there was a significant increase in annual mean temperature (b=0.02; P<0.001) over the same time period (Fig. S1a), but no significant trends in annual total precipitation (P=0.08) (Fig.

S1c) or in annual mean soil moisture (*P*=0.32) (Fig. S1f). Over the same time period there was a significant decrease in cattle density (*b*=-0.1, *P*<0.001), but no significant trend in sheep density (*P*=0.64) (Fig S2).

Since 1990, there has been a large decrease in the proportion of semi-natural grassland (-23%) in the Preston site area, with an increase in imporved grassland (+15%) and small increases in arable and broad leaf woodland (1% and 2% respectively) (Fig. S3). Since 1990, in the area 2km from the Starcross trap has experienced a decline in semi-natural grassland (-10%), an increase in broadleaf woodland (8%) and arable land (6%).

Variables driving the trends in phenology and abundance measures

At Preston, higher annual mean temperatures, annual total precipitation and annual mean soil moisture were associated with earlier times of first appearance and later times of last appearance (and, hence, longer seasons), as well as with higher maximum daily catch and mean daily catches (Figure 6). Furthermore, these associations were significant and consistent across a number of *Culicoides* species/groups (Figure 6). For the remaining climate variables at Preston and all climate variables at Starcross there was little evidence for any significant relationships with the abundance or phenology measures, though in some cases there was a significant relationship for one or two *Culicoides* species/groups. None of the phenology and abundance measures were significantly associated with cattle or sheep densities at Preston or Starcross.

Implications for transmission of Culicoides-borne viruses

Comparison of the model for viral replication and time at which newly infected *Culicoides* would become infectious, the with the times of first appearance shows that midges are active for several months before virus transmission could occur (Figure 7). Consequently, earlier first appearance is unlikely to influence the spread of BTV, at least at Preston or Starcross. Once midges become infectious, they remain so for the rest of their life. As a result the transmission season will end only once adult vectors cease to be active and complete gonadotrophic cycles. Accordingly, a later time of last appearance does result in a longer transmission season (Figure 6).

Discussion

The impact of the changes observed in the climate of northern Europe on vector fauna seasonality and abundance is likely to reflect the spatial heterogeneity of changes in the abiotic population drivers. In utilising a unique, continuous dataset of insect vector collections, we provide evidence that a significant change in the first and last appearance of *Culicoides* species in the UK has occurred in response to observed changes in climate over 40 years. The change in timing of first and last collection was driven by a significant increase over time in the abundance, from the mean and maximum daily catches, at the site for most of the *Culicoides* species. This is the first evidence for the impact of climate change on the long term population dynamics of an arbovirus vector as the observations include the putative *Culicoides* vectors of bluetongue and Schmallenberg viruses in northern Europe. Increased abundance and seasonal activity period of vectors would increase the likelihood of arbovirus transmission in the region and may have contributed to the emergence of *Culicoides*-borne arboviruses into Europe in recent years.

Changes in phenology in response to recent climate warming have been observed in many organisms across marine, freshwater and terrestrial ecosystems. Biological events studied in the northern hemisphere spring have occurred earlier, with the mean rate of advance calculated at -0.23 to -0.55 days per year (Parmesan & Yohe, 2003; Root et al., 2003). At -0.5 to -1.5 days per year, the observed rate of advancement in the first capture of adult *Culicoides* at Preston are greater than the previously reported average for phenological events of terrestrial invertebrates of -0.4 days per year (Thackeray et al., 2016; Thackeray et al., 2010). A similar change in first flight has been observed in some Lepidoptera and Heteroptera (Bell et al., 2015; Roy & Sparks, 2000).

The northern Palaearctic putative vector species of BTV, with the exception of *C. chiopterus*, demonstrated significant changes in first appearance, last appearance or increases in mean catch at the Preston site. The changes were associated with increased annual mean temperature and precipitation, with no other associations with the climate, host and land use variables examined. At Starcross significant changes in precipitation were not observed, and no significant trends in *Culicoides* abundance or phenology were observed, reflecting the heterogeneity of changes in climate observed between the sites. Local variation in the direction and extent of climate change will therefore impact populations differentially and blanket statements suggesting changes in vector abundance and phenology across broad spatial scales are an overly simplistic representation of complex interactions.

Attributing changes in phenology to climate change is problematic due to the plasticity in response of species to short-term changes in factors independent of meteorological conditions (Diez et al., 2012). We investigated the biotic and abiotic factors that drive *Culicoides* population dynamics that could potentially account for the differential response of *Culicoides* at the two sites, including land-use and host (domestic livestock) population density (Searle et al., 2014). In addition, the differences in *Culicoides* abundance and fauna between the sites were not responsible for the changes observed. Mean temperature and precipitation were the only significant explanatory variables associated with the increase in activity and changes in phenology seen at Preston. Despite the geographical separation of the Preston and Starcross sites (435 km), a similar change in average temperature occurred over the period 1974-2012 at both sites. The significant increase in precipitation observed at Preston was not observed at Starcross. The major land use changes seen at both trap sites of conversion to arable land, loss of semi-natural grassland and increase in improved grassland is likely to have, if any, a negative impact on breeding site and host availability for *Culicoides* (Purse et al., 2015; Purse et al., 2005). Livestock density, in particular that of sheep and cattle, is a key driver of vector *Culicoides* abundance in providing hosts and associated breeding habitats (Searle et al., 2014). Declines were observed in cattle density at both trap sites which would have a neagtive impact on the abundance of *Culicoides*, especially obligate dung breeders, such as *C. dewulfi*. Sheep density rose at Preston, increasing the availability of hosts and yet our analysis demonstrated that changes in host livestock density were not associated with the changes in *Culicoides* abundance and seasonality observed at Preston.

Soil type and soil moisture determine *Culicoides* larval habitat suitability and availability (Mellor, Boorman, & Baylis, 2000; Purse et al., 2015). The sandy soil at Starcross retains lower soil moisture than that at Preston and no significant increase in precipitation was observed at the Starcross site. This implies that ephemeral larval habitats may dry more quickly and therefore habitat suitability and availability rather than temperature may be limiting the *Culicoides* population at the site. The *Culicoides* population at Starcross may not have been able to exploit the rise in temperature in the same way as the population in Preston where precipitation, soil moisture and therefore larval habitat suitability would not limit population growth. Although the *Culicoides* population at Starcross was an order of magnitude smaller than that at Preston, our analysis suggests that there was sufficient *Culicoides* data from Starcross to identify similar degrees of change to that observed at Preston. The species compliment at each site was not responsible for the difference in observed changes. The first appearance of Pulicaris group species in the Preston was observed to have shifted significantly, yet this trend was not observed at Starcross where the species group dominated collections.

Analysis of the underlying statistical models that were used to examine the data suggests that the observed changes in phenology of *Culicoides* at Preston are a result of increased abundance of *Culicoides*. Increased abundance increases the likelihood of collection, extending the period when the number of actively flying adults is great enough for them to appear in collections. No evidence for changes in the timing or pattern of peaks in activity of

Culicoides, or impacts of previous year’s meteorological conditions were found. The increase in abundance of *Culicoides* at Preston was driven by the impact of warmer temperatures and increased precipitation experienced at the site over time. There was no evidence from the current data, however, that *Culicoides* abundance at Preston increased as a result of increased larval survival during mild winters as has been suggested for other insects (Bale & Hayward, 2010), as no associations between the severity of the winter weather and *Culicoides* population were observed.

In contrast to *Culicoides*, pest aphid species showed no increase in the autumnal activity period over time within the same collections (Bell et al., 2015). Overwintering activity and the environmental triggers of winter ‘diapause’ in *Culicoides*, whether facultative diapause or quiescence in the larval stage, are poorly understood (Luhken, Steinke, Hoppe, & Kiel, 2015; White, Sanders, Shortall, & Purse, 2017). In many insects the induction of diapause is triggered by a temperature-regulated response to photoperiod (Bale & Hayward, 2010). Temperature-mediated plasticity in response to photoperiod may enable persistence and adaptation to local conditions throughout an insect’s distribution (Sgro, Terblanche, & Hoffmann, 2016). The degree to which photoperiod contributes as an induction cue is unclear, as suggested by mechanistic modelling of *Culicoides* population dynamics (White et al., 2017). The proportion of the *Culicoides* population entering diapause or delaying development may therefore be reduced in warmer winters, allowing greater activity and a prolonged season, even if the timing of peaks in activity are unchanged (Bale & Hayward, 2010). The increase in adult activity season observed in the present data suggest that the proportion of the *Culicoides* population entering diapause or quiescence is temperature dependent and some individuals emerge later in the year, or that adults survive and are active for longer. The presence of nulliparous adults in later catches suggests these individuals are newly emerged, although age grading of *Culicoides* adults by pigmentation may not reflect the age of the insect (Harrup, Purse, Golding, Mellor, & Carpenter, 2013). Whilst termination of diapause and synchronised emergence in the spring is more likely to be more dominated by temperature (Luhken et al., 2015; Tauber & Tauber, 1976), the lack of change in the peak of adult activity in Spring over the 40 year period suggests that other factors including photoperiod may also play a significant role.

The extension of the active period of approximately 40 days over the study period has significant implications for the transmission of viruses by *Culicoides*. The transmission of *Culicoides*-borne disease can only occur during periods of adult vector activity. The emergence of *Culicoides* earlier in the spring may not lead to increased or earlier transmission as activity occurs below the replication threshold temperature of the virus. The increased activity season of *Culicoides* observed at Preston would allow additional cycles of transmission at the end of the season as infected *Culicoides* would be active for longer. In temperate areas, the ‘seasonal vector-free period‘ is used to delineate periods of low risk of transmission (A. J. Wilson & Mellor, 2009). At Preston, this period has effectively reduced by 40 days over the period 1974 to 2012, reducing the time over which a virus such as BTV would have had to survive in vertebrate hosts. Warming winter temperatures may also promote survival of infected *Culicoides* adults and potential transmission of viruses in microclimates such as large animal holdings (Sarvasova, Kocisova, Liptakova, Hlavata, & Mathieu, 2016). The end of season extension of adult *Culicoides* activity would increase the impact and occurrence of clinical signs of Schmallenberg virus in Scotland and N England where the critical seasonal window of infection during pregnancy that result in birth defects overlaps with end of adult vector season (Bessell et al., 2013; Searle et al., 2014).

There was variation in the response of *Culicoides* species at Preston to the change in temperature and precipitation. Whilst significant differences were observed in the timing of first and last appearance in total *Culicoides*, *Obsoletus* group females, *C. scoticus* males, *C. dewulfi* males and *C. punctatus* males, trends in timing were not significant for *C. pulicaris*, *C. obsoletus* males and *C. chiopterus* males. *Culicoides pulicaris* typically appear in trap catches earlier than the Obsoletus group (Searle et al., 2014) and may therefore not exhibit an altered phenology if the temperature threshold for activity is lower in this species than for other *Culicoides*. All species, except for *C. chiopterus* showed an increase in mean daily catch at Preston. Collections of *C. chiopterus* in the RSTs are typified by the appearance of large numbers of individuals in the collections at discrete points in time, suggesting a flush of activity or emergence that occurs late in the season (Sanders et al., 2011). This later period of activity and the highly stochastic nature of captures of *C. chiopterus* males may reflect the differences in size and diel periodicity of *C. chiopterus* to other *Avaritia* (S. Carpenter et al., 2008; Sanders et al., 2012) and explain the lack of changes observed in this species.

The present study is the first to examine long-term changes in the phenology and abundance of arbovirus vectors, using a unique data set of standardised trapping over 40 years with observed climatic changes. Such datasets over which the impact of climate change over an period of decades can be investigated are unavailable for other vector groups at present time (Hoekman et al., 2016). The study demonstrates species- and site-specific heterogeneity in response to changes in climate that in turn show heterogeneity in local effects and impacts. Large scale projections of the response of a vector group to climate change using a functional relationship between vector biology and climate are likely to underestimate the variability both in local population response and the local effects of climate change. The impact of future changes in climate on the population dynamics of arbovirus vectors such as *Culicoides* will be regulated by local biotic and abiotic factors that govern the capacity of a site to support the population.

Acknowledgements

The UK Climate Projections data have been made available by the Department for Environment, Food and Rural Affairs (Defra) and Department for Energy and Climate Change (DECC) under licence from the Met Office, Newcastle University, University of East Anglia and Proudman Oceanographic Laboratory. These organisations accept no responsibility for any inaccuracies or omissions in the data, nor for any loss or damage directly or indirectly caused to any person or body by reason of, or arising out of, any use of this data. This study was funded by Defra (grant numbers SE4211, SE4113 and ref lab), with additional support provided by Biotechnology and Biological Sciences Research Council (BBSRC) grant BBS/E/I/00001701. And Rothamsted Research and CEH…

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Table 1. Summary of annual trends in measures of *Culicoides* phenology and abundance at Preston, 1974-2012 (posterior median and 95% credible interval).

Species	change (days per year)†			% increase per year†	
	time of first appearance	time of last appearance	season length	maximum daily catch	mean daily catch
total *Culicoides*	-0.5 (-0.8, -0.2)	0.5 (0.2, 0.8)	1.0 (0.5, 1.5)	5.8 (2.7, 9.2)	5.6 (3.9, 7.6)
C. obsoletus group (♀)	-0.5 (-0.8, -0.1)	0.5 (0.2, 0.8)	1.0 (0.5, 1.4)	4.8 (2.2, 7.4)	4.4 (3.2, 5.6)
C. obsoletus s.s. (♂)	n.s.	n.s.	n.s.	4.8 (0.7, 9.1)	3.2 (1.4, 5.0)
C. scoticus (♂)	-1.6 (-2.7, -0.2)	1.2 (0.3, 2.4)	2.9 (1.2, 4.4)	8.3 (3.8, 12.9)	3.7 (2.1, 5.6)
C. chiopterus (♂)	n.s.	n.s.	n.s.	n.s.	n.s.
C. dewulfi (♂)	-1.1 (-2.2, -0.3)	1.2 (0.5, 2.2)	2.4 (1.3, 3.7)	7.8 (4.5, 11.4)	4.1 (3.0, 5.5)
C. pulicaris (♀)	n.s.	n.s.	n.s.	n.s.	2.1 (0.9, 3.6)
C. pulicaris (♂)	n.s.	n.s.	n.s.	n.s.	2.6 (0.5, 5.3)
C. punctatus (♀)	n.s.	1.6 (0.5, 2.9)	2.8 (1.3, 4.3)	9.1 (5.1, 13.3)	6.1 (4.4, 8.3)
C. punctatus (♂)	-1.1 (-2.3, -0.4)	1.3 (0.6, 2.6)	2.5 (1.3, 4.1)	12.8 (8.0, 18.3)	9.8 (7.6, 12.6)

other *Culicoides*	n.s.	n.s.	n.s.	n.s.	2.9 (1.6, 4.4)

† n.s.: not significant (posterior-predictive *P*-value>0.05)

Figure 1. Geographical variation in the slope values for the 1974-2011 trend in annual mean temperature (a) and annual total precipitation (b) per pixel. All UK pixels show an increasing trend in annual mean temperature over the study period and that most pixels show an increasing trend that is as strong as that seen in Preston (b=0.04) and Starcross (b=0.03), with warming being most pronounced in the south and east of the UK. Most UK pixels show an increasing trend in annual total precipitation, but pixels with a strong increasing trend (b >= 4), equivalent to that seen in Preston tend to be confined to Scotland, Cumbria and upland areas of N and S Wales.

Figure 2. Mean daily catches of *Culicoides* biting midges in the Rothamsted Insect Survey suction traps at (*a*) Preston and (*b*) Starcross between 1974 and 2012. The colours indicate different *Culicoides* species/groups caught (see legend).

Figure 3. Annual trends in *Culicoides* phenology and abundance at Preston, 1974-2012. Results are presented for five measures: time of first appearance (t. first app.); time of last appearance (t. last app.); season length (seas. length); maximum daily catch (max. catch); and mean daily catch (mean catch). In each figure the observed measures calculated from the trap catches are shown as red circles. The simulated measures generated from the generalised linear models fitted to the RST data are shown as box and whisker plots (median: horizontal black line; interquartile range: grey box; and 2.5th and 97.5th percentiles: whiskers).

Figure 4. Annual trends in *Culicoides* phenology and abundance at Starcross, 1974-2012. Results are presented for five measures: time of first appearance (t. first app.); time of last appearance (t. last app.); season length (seas. length); maximum daily catch (max. catch);

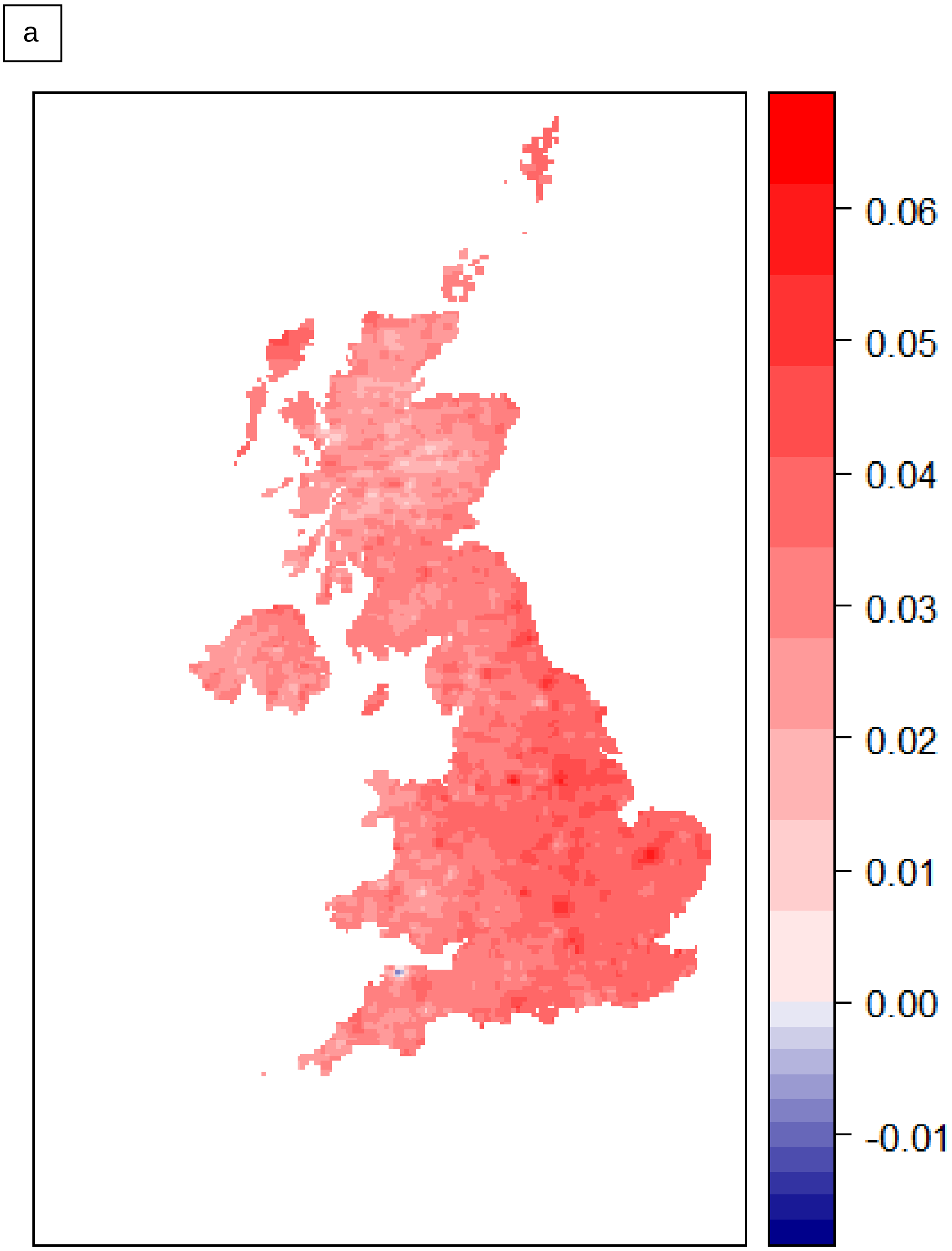
and mean daily catch (mean catch). In each figure the observed measures calculated from the trap catches are shown as red circles. The simulated measures generated from the generalised linear models fitted to the RST data are shown as box and whisker plots (median: horizontal black line; interquartile range: grey box; and 2.5th and 97.5th percentiles: whiskers).

Figure 5. Summary of the annual trends in *Culicoides* phenology and abundance at (*a*) Preston and (*b*) Starcross, 1974-2012. Results are presented for five measures: time of first appearance (t. first app.); time of last appearance (t. last app.); season length (seas. length); maximum daily catch (max. catch); and mean daily catch (mean catch). Each figure shows the regression coefficients for the trend line for the measure estimated in two ways. First, the black circles and error bars show the estimate and 95% confidence interval, respectively, based on the measures computed directly from the Rothamsted Insect Survey suction trap data. Second, violin plots show the posterior density (shape), median (circle) and interquartile range (line) for the regression coefficient inferred from the posterior predictive distribution for the data. Plots are coloured red where evidence for the trend is robust (median posterior *P*-value<0.05) and blue where it is not (median posterior *P*-value>0.05). Where a plot is missing for Starcross, insufficient individuals were caught to be able to define the times of first and last appearance.

Figure 6. Relationship between (*a*) annual mean temperature, (*b*) annual total precipitation and (*c*) annual mean soil moisture and measures of *Culicoides* phenology and abundance at Preston, 1974-2012. Results are presented for five measures: time of first appearance (t. first app.); time of last appearance (t. last app.); season length (seas. length); maximum daily catch (max. catch); and mean daily catch (mean catch). Each figure shows the posterior predictive distribution for the regression coefficient in a straight-line relationship between the climate variable and the measure. Violin plots show the posterior density (shape), median (circle) and interquartile range (line) for the coefficient. Plots are coloured red where

evidence for the trend is robust (median posterior *P*-value<0.05) and blue where it is not (median posterior *P*-value>0.05).

Figure 7. Transmission season for bluetongue virus at (*a*) Preston and (*b*) Starcross, 1974-2012. Each plot shows the posterior median (circles) and 95% credible interval (error bars) for the time of first appearance (red), the earliest time at which a newly infected midge could become infectious (blue) and the time of last appearance (black). Results are based on the total number of *Culicoides* biting midges caught.


a
0.06
0.05
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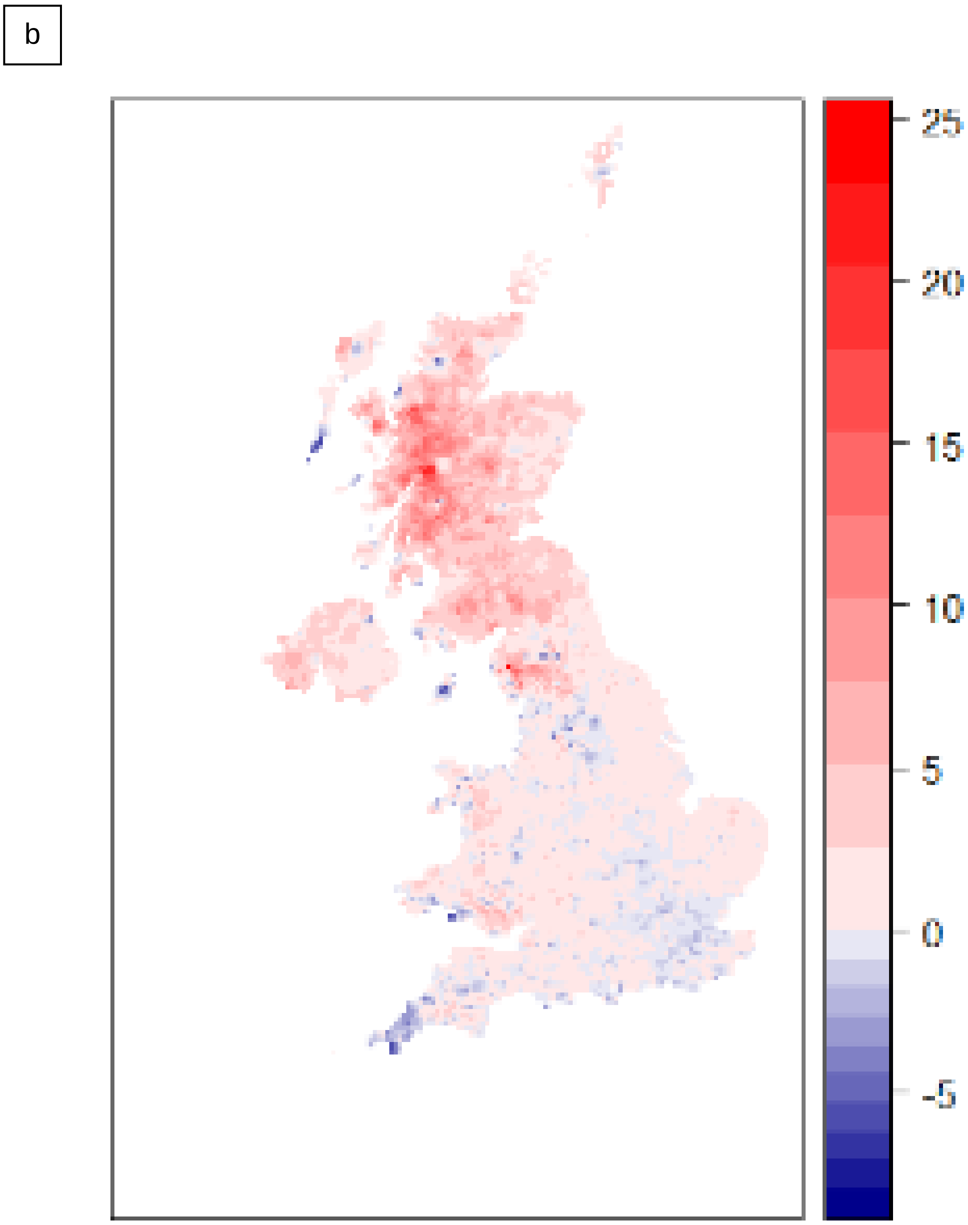

Figure 1 a) and b).

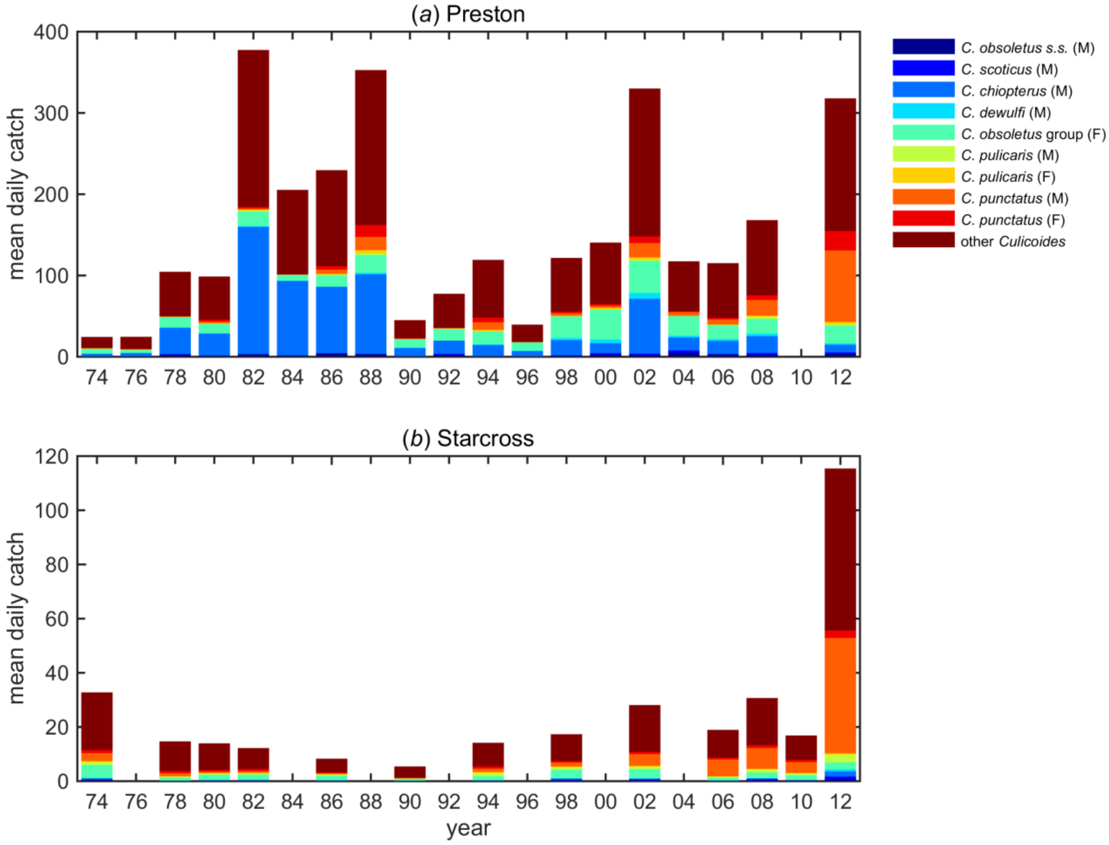
(a) Preston
(b) Starcross
mean daily catch
0
100
200
300
400
20
40
60
80
120
74
76
78
80
82
84
86
88
90
92
94
96
98
00
02
04
06
08
10
12
year
C. obsoletus s.s. (M)
C. scoticus (M)
C. chiopterus (M)
C. dewulfi (M)
C. obsoletus group (F)
C. pulicaris (M)
C. pulicaris (F)
C. punctatus (M)
C. punctatus (F)
other *Culicoides*

FIGURE 2

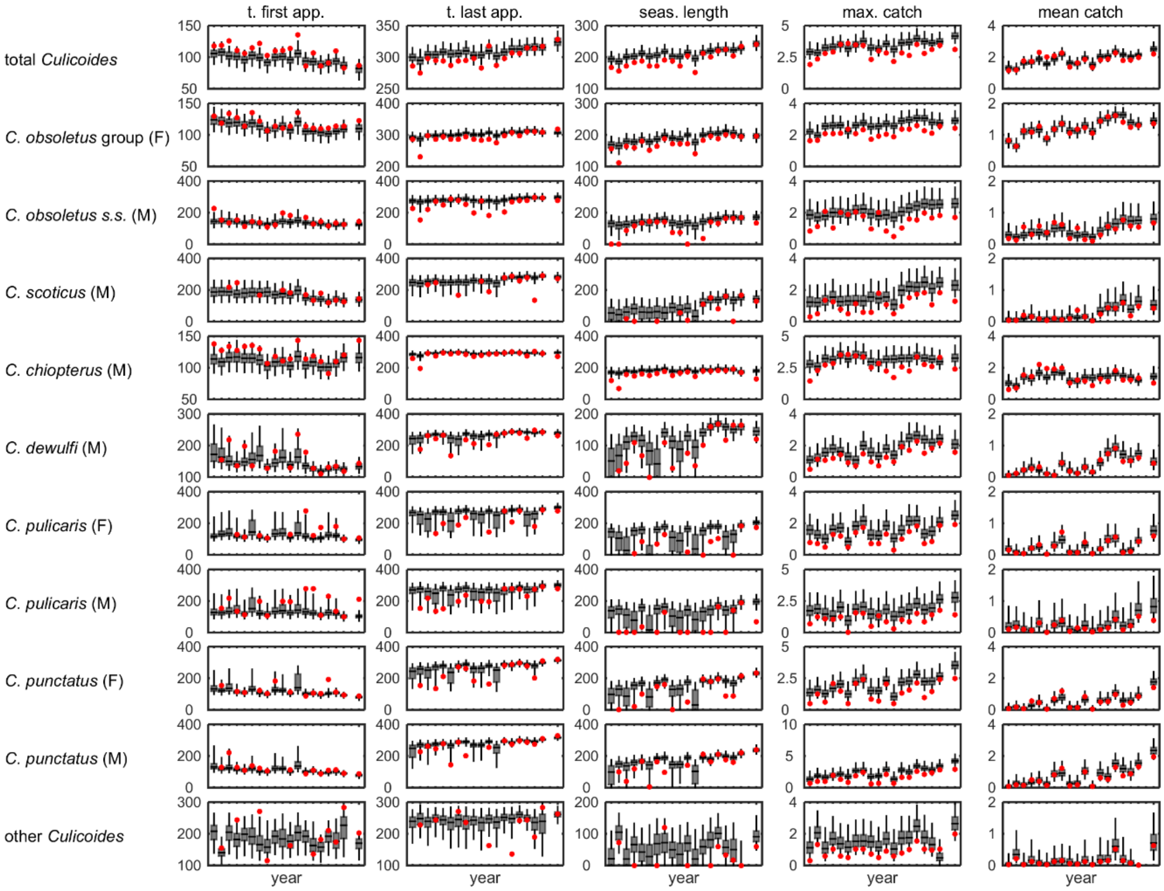
t. first app.
t. last app.
seas. length
max. catch
mean catch
total *Culicoides*
C. obsoletus group (F)
C. obsoletus s.s. (M)
C. scoticus (M)
C. chiopterus (M)
C. dewulfi (M)
C. pulicaris (F)
C. pulicaris (M)
C. punctatus (F)
C. punctatus (M)
other *Culicoides*
150
100
50
350
300
250
300
200
100
5
2.5
0
4
2
0
400
200
0
1
10
year
year
year
year
year

FIGURE 3

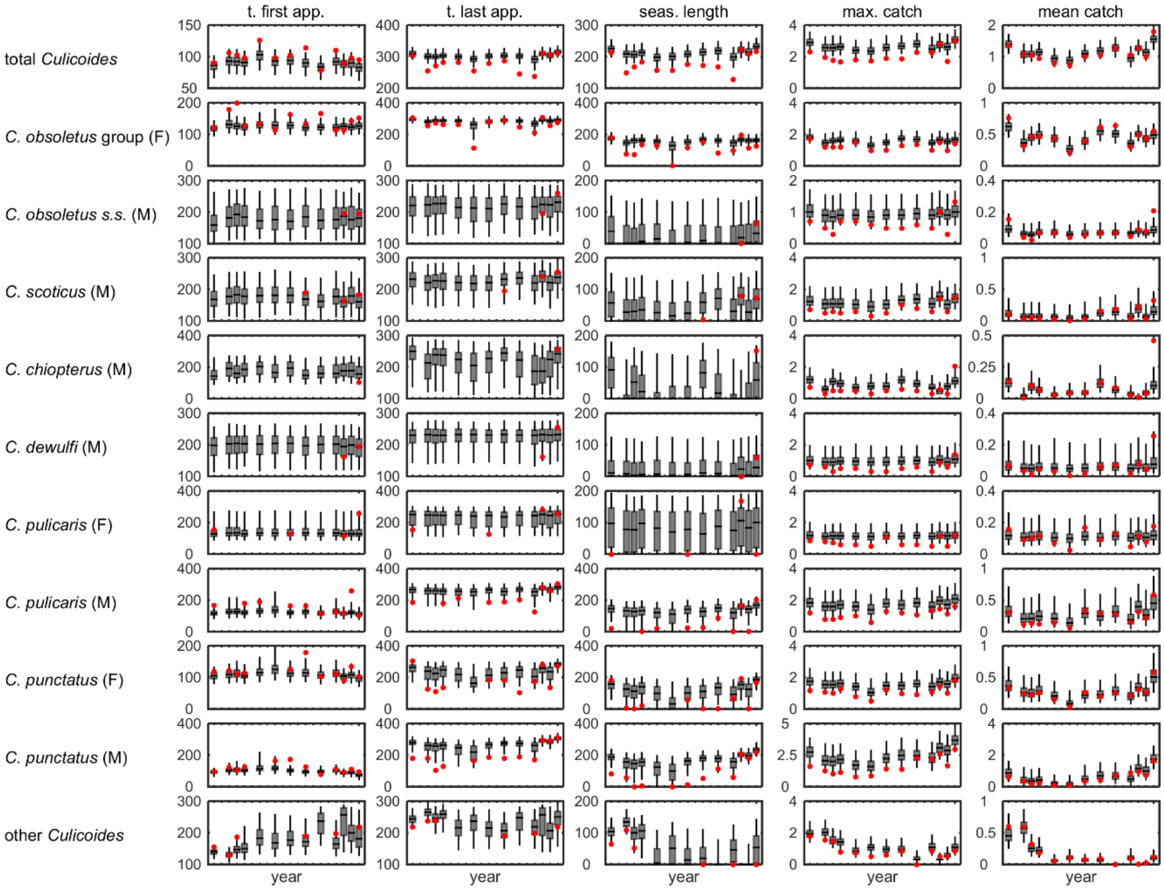
t. first app.
t. last app.
seas. length
max. catch
mean catch
total *Culicoides*
C. obsoletus group (F)
C. obsoletus s.s. (M)
C. scoticus (M)
C. chiopterus (M)
C. dewulfi (M)
C. pulicaris (F)
C. pulicaris (M)
C. punctatus (F)
C. punctatus (M)
other *Culicoides*
year
year
year
year
year

FIGURE 4

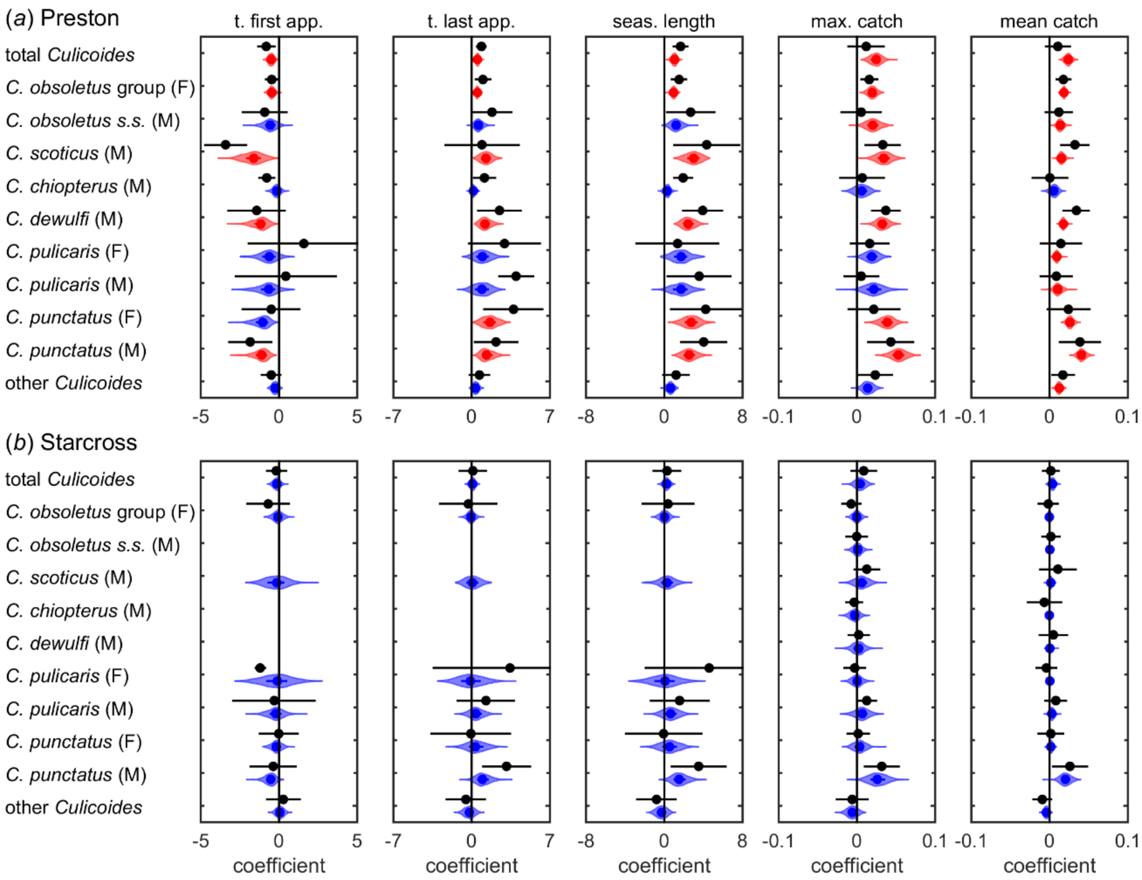
(a) Preston
t. first app.
t. last app.
seas. length
max. catch
mean catch
total Culicoides
C. obsoletus group (F)
C. obsoletus s.s. (M)
C. scoticus (M)
C. chiopterus (M)
C. dewulfi (M)
C. pulicaris (F)
C. pulicaris (M)
C. punctatus (F)
C. punctatus (M)
other Culicoides
-5
0
5
-7
0
7
-8
0
8
-0.1
0
0.1
-0.1
0
0.1
(b) Starcross
total Culicoides
C. obsoletus group (F)
C. obsoletus s.s. (M)
C. scoticus (M)
C. chiopterus (M)
C. dewulfi (M)
C. pulicaris (F)
C. pulicaris (M)
C. punctatus (F)
C. punctatus (M)
other Culicoides
-5
0
5
-7
0
7
-8
0
8
-0.1
0
0.1
-0.1
0
0.1
coefficient
coefficient
coefficient
coefficient
coefficient

Figure 5

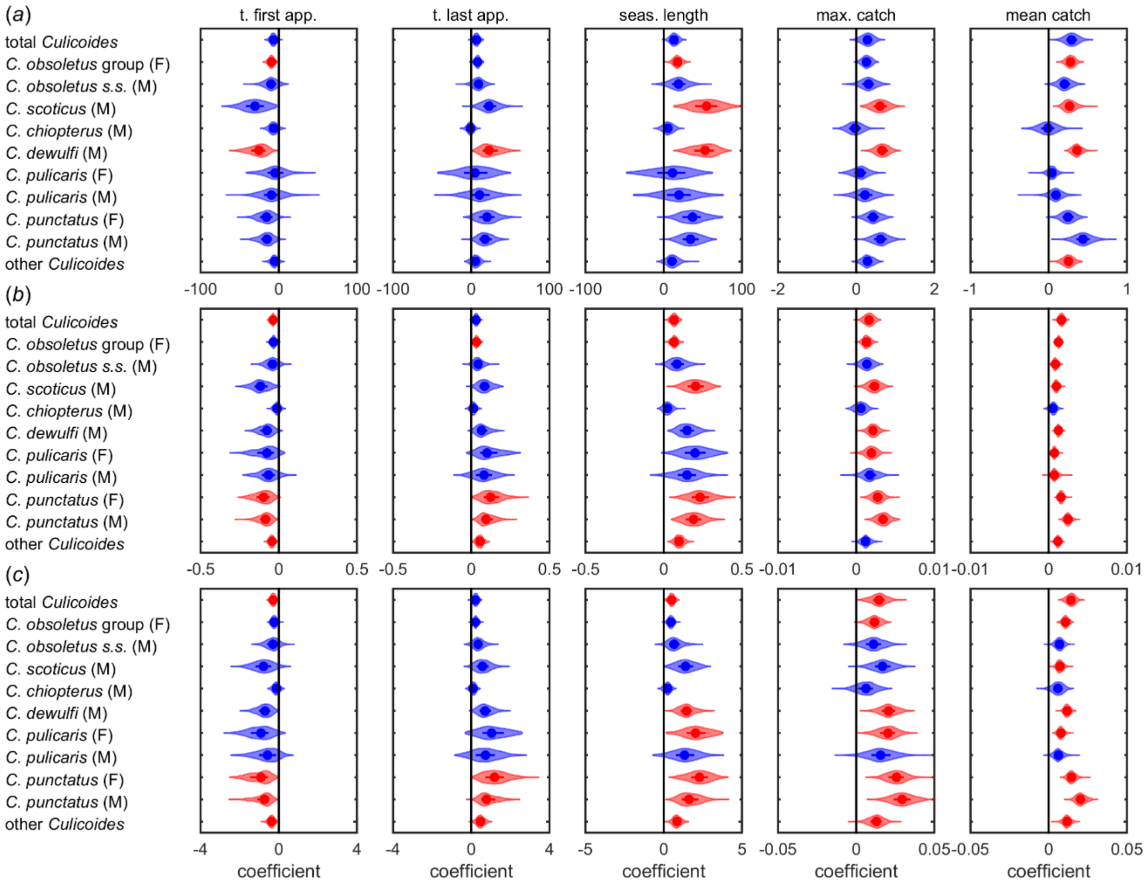
(a)
t. first app.
t. last app.
seas. length
max. catch
mean catch
total Culicoides
C. obsoletus group (F)
C. obsoletus s.s. (M)
C. scoticus (M)
C. chiopterus (M)
C. dewulfi (M)
C. pulicaris (F)
C. pulicaris (M)
C. punctatus (F)
C. punctatus (M)
other Culicoides
-100
0
100
-100
0
100
-100
0
100
-2
0
2
-1
0
1
(b)
-0.5
0
0.5
-0.5
0
0.5
-0.5
0
0.5
-0.01
0
0.01
-0.01
0
0.01
(c)
-4
0
4
-4
0
4
-5
0
5
-0.05
0
0.05
-0.05
0
0.05
coefficient

Figure 6

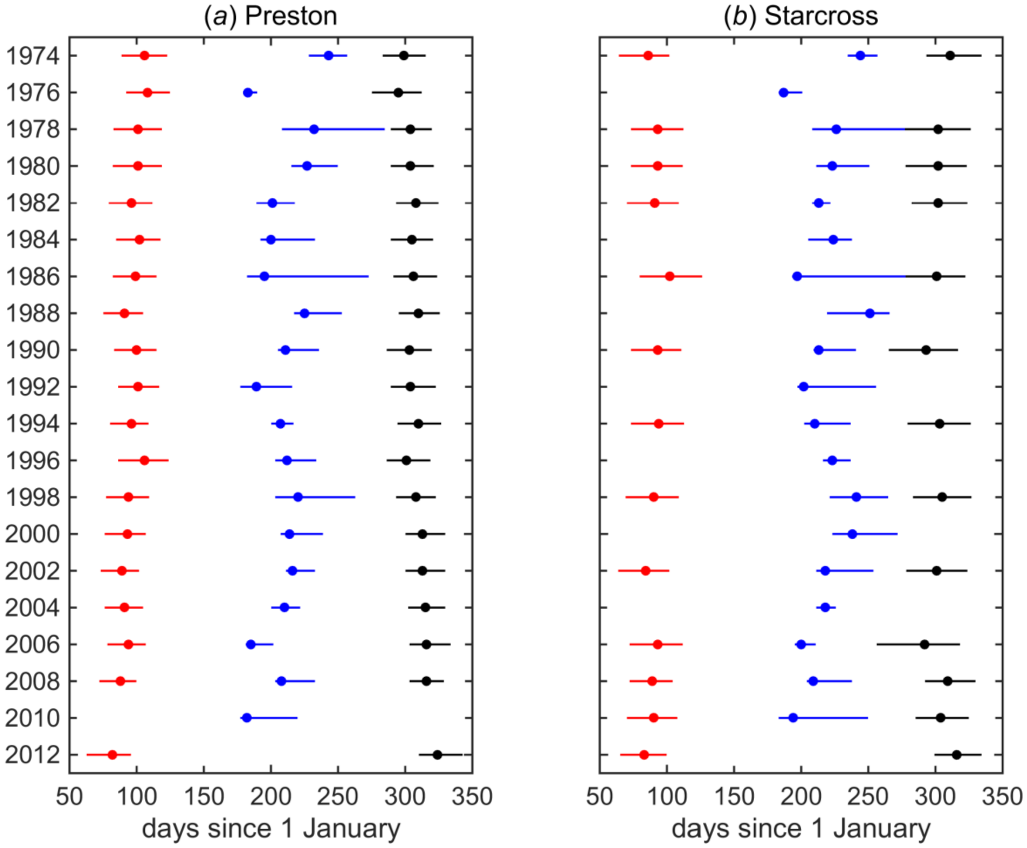
(a) Preston
(b) Starcross
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
50
100
150
200
250
300
350
days since 1 January

Figure 7