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Influence of season and meteorological parameters on flight activity of *Culicoides* biting midges

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Summary

1. *Culicoides* biting midges are vectors of internationally important arboviruses including bluetongue virus (BTV). The ecological constraints imposed by the small body size of these insects strongly influence the epidemiology of the diseases they can carry. Bluetongue virus recently emerged in northern Europe, and atmospheric dispersion models have subsequently been employed to simulate vector movement (and hence likely spread of BTV). The data underlying such models, however, have hitherto either been obtained from small-scale studies or from outside the north-western Palaearctic.

2. The effects of seasonality and local meteorological conditions upon the daily presence and abundance of *Culicoides* vectors were examined using 2760 samples collected across a network of 12 different habitat types in England during 2008. Over 50 000 individuals were estimated to be in the samples with males constituting 62% of the total collection, allowing straightforward comparison between potential vector species in terms of their activity rates and seasonality. *Culicoides* abundance was linked to livestock density and land use. Farm-associated *Culicoides* species were recorded at all sites including species thought to be restricted to this ecosystem by larval habitat, suggesting a greater potential for dispersal over land than previously thought.

3. *Synthesis and applications*. The model developed has already been applied in a functional dispersion model to predict disease risk from wind-borne infected *Culicoides* incursion into the UK and elsewhere. The study has expounded the long-distance dispersal potential of *Culicoides*, essential for future prediction of the incursion and spread of *Culicoides*-borne pathogens. It has additionally contributed to the understanding of the ecology of highly dispersive insect vectors.

Key-words: bluetongue, dispersal, Rothamsted suction trap, surveillance, vector

Introduction

In 2006, a bluetongue virus (BTV) strain of sub-Saharan origin (BTV-8) entered northern Europe, initiating an epidemic that was to prove the most economically damaging outbreak of the virus ever recorded (Maan *et al*. 2008; Wilson & Mellor 2009). From approximately 2000 cases recorded in the Netherlands, Germany, mainland France and Belgium in 2006, the virus spread rapidly in subsequent years to cause tens of thousands of clinical cases over much of western Europe including the UK (Wilson & Mellor 2009). Outbreaks were eventually brought under control through the use of vaccination campaigns and zoosanitary measures; however, the probability of other strains entering this region remains poorly defined both for BTV and for other pathogens transmitted by *Culicoides*, including African horse sickness virus (AHSV) (Carpenter, Wilson & Mellor 2009a).

Understanding the ecology and behaviour of vector *Culicoides* species is a key element in predicting the epidemiology of those pathogens they transmit, and many *Culicoides* life cycle parameters are strongly related to meteorological conditions (Mellor, Boorman & Baylis 2000; Wittmann & Baylis 2000; Carpenter, Wilson & Mellor 2009b). The dispersal ability and the seasonality of *Culicoides* adults are of importance in this regard as they largely determine the pathogen spread in the absence of viraemic livestock movement. *Culicoides* are sensitive to desiccation and have low self-propelled flight speeds in comparison with many other vector groups. Appetitive flight is governed by temperature, humidity, and light intensity thresholds and appears to be inhibited by wind

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speeds > 3 ms^{-1} (Kettle 1957, 1969; Blackwell 1997; Carpenter *et al.* 2008b).

Flight distances recorded vary from only a few hundred metres (Kettle 1951; Lillie, Marquard & Jones 1981; Murray 1987) to several kilometres (Kettle 1960; Sellers 1980; Murray & Kirkland 1995) although cues and physiological limitations that restrict range are poorly understood. Many insects use the fast moving nocturnal, low-level jet stream at the top of the atmospheric boundary layer to assist long-distance migration (Chapman *et al.* 2004; Reynolds, Smith & Chapman 2008), and individual *Culicoides* have been caught at heights of several hundred metres (Glick 1939; Hardy & Cheng 1986; Johansen *et al.* 2003; Sanders *et al.* 2011).

Studies of *Culicoides* long-distance dispersal are usually inferred from incursions of *Culicoides*-borne pathogens onto islands and across large stretches of water in the absence of animal movement (Sellers 1980; Calistri *et al.* 2003; Alba, Casal & Domingo 2004; Gloster *et al.* 2008). Movement can be inferred over land in a similar way (Sellers 1980; Murray & Kirkland 1995; Braverman & Chechik 1996; Ducheyne *et al.* 2007); however, in such cases, confounding animal movements and intrinsic difficulties in modelling wind movement over topography at a local scale can be problematic. Nevertheless, models of the probability of movement of *Culicoides* have proved to be useful tools in the prediction of incursion routes and in the retrospective analyses of outbreaks (Gloster *et al.* 2008; Hendrickx *et al.* 2008; Agren *et al.* 2010).

The seasonal dynamics of adult *Culicoides* populations are important as they in part determine the timing of outbreaks of *Culicoides*-borne arbovirus outbreaks (Herniman, Boorman & Taylor 1983; Baylis *et al.* 1997). Studies of seasonality in European *Culicoides* have to date largely relied upon the collection of adults in light traps on a weekly sampling basis (Ortega, Holbrook & Lloyd 1999; Conte *et al.* 2007; Clausen *et al.* 2009; De Liberato *et al.* 2010). In the UK, *Culicoides* have been observed to occur in one, two or three seasonal abundance peaks depending upon species, location and the trapping methodology used (Hill 1947; Service 1971, 1974; Holmes & Boorman 1987; Blackwell *et al.* 1992; Blackwell 1997).

The Rothamsted Insect Survey routinely monitors aphids and other migrating insects in the UK by means of the Rothamsted suction trap (RST) (Macaulay, Tatchell & Taylor 1988; Harrington & Woiwod 2007) network, and *Culicoides* represent a part of the by-catch (Shortall *et al.* 2009). The 12·2 m height of these traps was originally chosen to minimize sampling of insects flying locally whilst sampling a dense layer of migrant insects (Macaulay, Tatchell & Taylor 1988). Whilst a previous, small-scale study of the abundance of *Culicoides* caught in two RSTs has been carried out in Belgium, the total number caught was too low ($n = 761$) and the sampling period too short to elucidate more than general trends in the effects of meteorological conditions on monthly activity (Fassotte *et al.* 2008).

The aim of the present study was to provide a more complete understanding of the effects of seasonal population dynamics and meteorological conditions on the daily flight activity of vector *Culicoides* as demonstrated from their abundance in RST catches. The data presented provide a significant advance in our understanding of parameters influencing *Culicoides* ecology, and hence pathogen dispersal and seasonality in the field.

Materials and methods

ROTHAMSTED SUCTION TRAPS

Each RST provided a continuous (24 h), standardized sample at a rate of 45 m^3 of air per minute through an inlet 12·2 m above-ground level (Macaulay, Tatchell & Taylor 1988). Briefly, the trap consists of an electric fan which pulls air down a vertical tube through an air expansion chamber, to reduce insect velocity, and into a collecting bottle containing methanol. Insect samples were stored in 95% ethanol plus 5% glycerol for identification. Twelve traps at sites across England (Fig. 1) were used in locations representing a variety of habitat types and livestock densities (Table 1). Traps were run continuously in 2008, and samples were collected once every 24 h from 31 March to 16 November. At other times, samples were collected weekly and the numbers divided by seven to create a daily count.

Culicoides recovered from RST samples were separated for further identification. In samples containing more than 50 *Culicoides*, the total number was estimated by assuming the remaining fraction of the sample volume contained a similar density of *Culicoides*. *Culicoides* were identified to species level by wing morphology where possible (Campbell & Pelham-Clinton 1960). Females of the *C. obsoletus* group (*C. obsoletus s.s.* (Meigen), *C. scoticus* (Downes & Kettle), *C. dewulfi* (Goetghebeur) and *C. chiopterus* (Meigen)) were not

Fig. 1. Map showing the location of the twelve Rothamsted suction trap sites. N = Newcastle, AB = Askham Bryan, P = Preston, K = Kirton, BB = Broom's Barn, We = Wellesbourne, H = Hereford, RT = Rothamsted Tower, Wr = Writtle, SP = Silwood Park, W = Wye, SX = Starcross.

Table 1. Rothamsted suction trap site locations with habitat type and cattle density [Cattle density extracted from RADAR (2008)]

Site	Latitude	Longitude	Altitude (m)	Habitat type	Cattle density (per square km)
Askham Bryan	53·992	−1·162	30	Arable	21–40
Broom's Barn	52·26	0·570	70	Arable	< 10
Hereford	52·125	−2·637	84	Mixed	41–80
Kirton	52·937	−0·070	3	Arable	< 10
Newcastle	55·213	−1·682	93	Mixed/woodland	21–40
Preston	53·854	−2·763	15	Pastoral	> 80
Rothamsted	51·807	−0·356	119	Arable	< 10
Silwood	51·408	−0·641	64	Mixed/woodland	< 10
Starcross	50·628	−3·454	12	Pastoral/saltmarsh	41–80
Wellesbourne	52·201	−1·600	45	Arable	21–40
Writtle	51·733	0·427	38	Mixed	< 10
Wye	51·185	0·939	43	Mixed	10–20

separated to species level because of the unsuitability of the samples for molecular identification techniques. Males of the *C. obsoletus* group were identified to species level by genital morphology (Campbell & Pelham-Clinton 1960) and were used as a proxy for the relative abundance of females of each species. Hourly meteorological data, including temperature, wind speed, wind direction, cloud cover, rainfall and solar radiation, were provided by the Met Office and were taken from meteorological stations at each trap site or within 20 km.

STATISTICAL ANALYSIS AND MODELLING

Summary statistics for the RST catches for each site (total caught, time of first appearance) were analysed using generalized linear models (assuming negative binomial errors and log link or normal errors and identity link, respectively) to identify potential associations with latitude, habitat type and cattle density.

To explore seasonal trends or the effects of meteorological parameters on the numbers of *Culicoides* caught, however, requires a more detailed analysis because of several features of the RST catch data. First, and most importantly, the RST catches can vary over several orders of magnitude from one day to the next, making it problematic to discern trends on the basis of a descriptive analysis of the data. Secondly, the trap catches are collected over time, so that catches from one day may depend on those for previous days. Thirdly, the trap catches are collected at a number of different sites, with potentially different seasonal dynamics at each. Consequently, to understand the influence of seasonal variation and meteorological conditions on the abundance of *Culicoides* requires a statistical approach that accounts for these features of the data.

Accordingly, the daily RST catch data were analysed using generalized linear models (assuming Poisson errors and a log link function) that incorporated seasonal components (with different periods) and meteorological parameters. Furthermore, the approach included overdispersion (to allow for the high day-to-day variability in catches), temporal autocorrelation amongst the observations (to allow for dependence between observations) and hierarchical structure in the model parameters (to allow for between-site differences). Parameters in the model were estimated in a Bayesian framework implemented using WinBUGS (Lunn *et al.* 2000).

Separate models were constructed for eight of the RST catch data sets: total *Culicoides*; *C. obsoletus* group females; *C. obsoletus s.s.* males; *C. scoticus* males; *C. dewulfi* males; *C. chiopterus* males; *C. pulicaris* males; and *C. punctatus* males. Full details of the models, their implementation, model checking and inference are provided in Appendix S1, Supporting Information.

Results

ROTHAMSTED SUCTION TRAPS

A total of 20 156 *Culicoides* were identified from the 2008 samples providing an estimated total catch of 51 552 *Culicoides* over the 12 sites. Standardization by estimating then counting all *Culicoides* in 35 of the large samples (> 50 *Culicoides*) demonstrated a good correlation between estimates and the total number of *Culicoides* in the sample ($r = 0{\cdot}9293$; error tended towards underestimation). Trap catches were dominated by the *C. obsoletus* group (48% of the total catch) and *C. pulicaris/C. punctatus* (44%) species groups, with the remainder (8%) being other *Culicoides* species (in order of abundance: *C. impunctatus* (Goetgh.), *C. circumscriptus* (Keiffer), *C. stigma* (Meigen), *C. festivipennis* (Keiffer), *C. achrayi* (Kettle and Lawson), *C. brunnicans* (Edwards), *C. nubeculosus* (Meigen), *C. duddingstoni* (Kettle and Lawson), *C. segnis* (Campbell and Pelham-Clinton), *C. vexans* (Staeger), *C. grisescens* (Edwards), *C. salinarius* (Keiffer), *C. maritimus* (Keiffer), *C. pictipennis* (Staeger), *C. fagineus* (Edwards)). *Culicoides impunctatus* was present only at Preston, Newcastle and Hereford and represented 1% of the total catch. Males of all four members of the *C. obsoletus* group were recorded at every trap site (Table 2). Large differences were recorded between trap sites in the abundance and species composition of *Culicoides* ($\chi^2 = 6013{\cdot}5$, d.f. = 33, $P < 0{\cdot}001$). There was a male bias at many sites ($\chi^2 = 3311{\cdot}5$, d.f. = 11, $P < 0{\cdot}001$), with 62% of the total catch being male.

Total abundance of *Culicoides* increased significantly ($P < 0{\cdot}001$) with the density of cattle in the locality of the trap. Higher abundances were also associated ($P < 0{\cdot}001$) with pastoral compared with mixed or arable habitat types (although habitat type and cattle density are correlated; Table 1). There was no significant association between total abundance and latitude ($P = 0{\cdot}09$). *Culicoides* were most abundant at Preston, with 64% of the total estimated catch derived from this trap (Table 2). *Culicoides punctatus* (Meigen) and *C. chiopterus* males represented a large proportion of the Preston samples (29·4% and 22·5% respectively) with *C. obsoletus* group females comprising just 20% at this site (Table 2). The trap at Starcross also exhibited a dominance

Table 2. Summary of *Culicoides* catches from Rothamsted suction traps at 12 sites in 2008. *Culicoides obsoletus* group males are split into the species (*C. obsoletus*, *C. scoticus*, *C. dewulfi*, *C. chiopterus*) and individuals too damaged for identification

Site	First appearance†	*C. obsoletus* group ♀	*obs* ♂	*scot* ♂	*dew* ♂	*chi* ♂	dam ♂	*C. pulicaris* ♀	♂	*C. punctatus* ♀	♂	Other *Culicoides* ♀	♂	Total
Askham Bryan	124	674	167	44	73	48	3	46	16	362	176	37	99	1745
Broom's Barn	128	97	17	3	5	4	0	9	2	60	11	8	5	221
Hereford	113	828	170	87	178	121	10	70	19	271	94	107	100	2055
Kirton	117	120	22	7	5	5	4	8	6	105	13	31	17	343
Newcastle	130 (115)	954	449	380	791	171	7	132	92	308	538	332	243	4397
Preston	121 (90)	6572	896	739	942	7403	32	575	797	3285	9675	702	1305	32 923
Rothamsted	117	233	23	23	9	2	8	10	0	95	23	9	10	445
Silwood	113	240	39	98	46	5	5	18	15	102	34	63	289	954
Starcross	127 (90)	771	81	238	73	8	12	110	395	549	3919	123	88	6367
Wellesbourne	117	428	47	39	33	22	7	30	16	351	95	29	16	1113
Writtle	117	128	63	23	7	3	3	1	3	67	30	25	3	356
Wye	116	107	40	5	5	12	0	10	17	220	156	26	35	633
Total		11 152	2014	1686	2167	7804	91	1019	1378	5775	14 764	1492	2210	51 552

obs, *obsoletus*; *scot*, *scoticus*; *dew*, *dewulfi*; *chi*, *chiopterus*.
†No. days after 1 January 2008 at which > 5 individuals first appeared; time shown is for *C. obsoletus* group, with *C. pulicaris* shown in brackets if earlier.

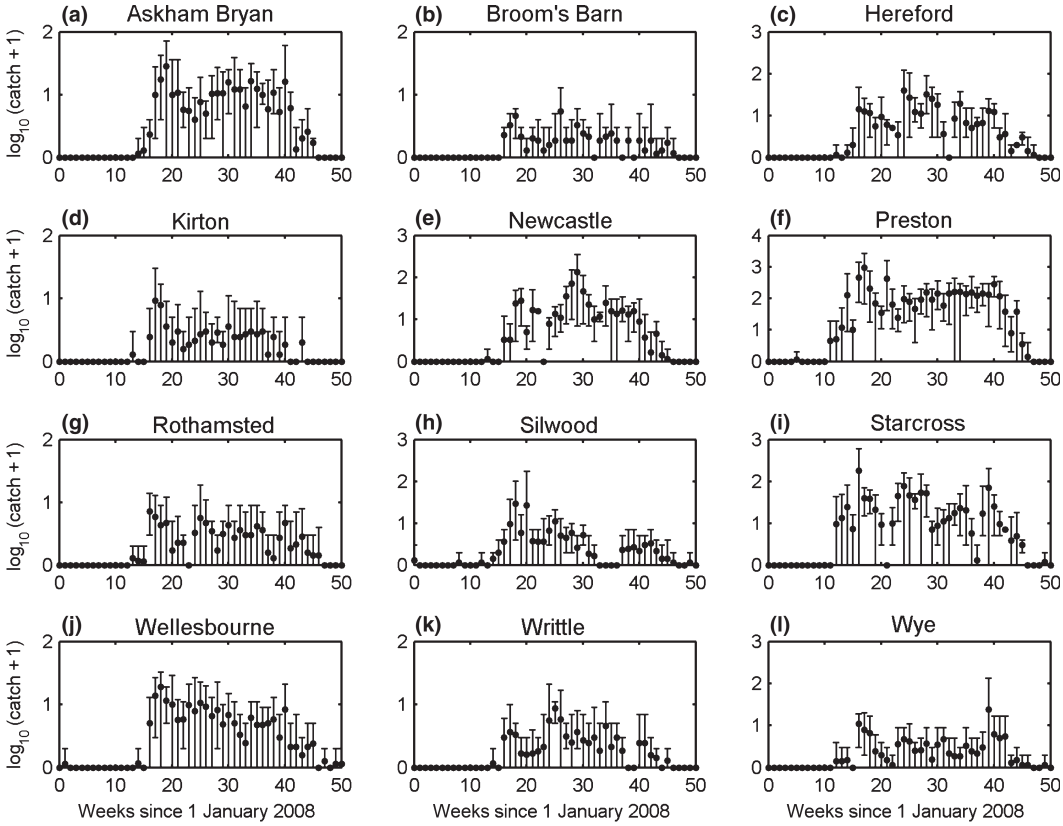

Fig. 2. Weekly summary of the numbers of *Culicoides* biting midges (total male and female) caught at the twelve Rothamsted suction trap sites during 2008: mean daily catch (circles) and minimum and maximum daily catches (error bars) for each week.

of *C. punctatus* males. At this trap, however, *C. scoticus* represented the largest proportion of the *C. obsoletus* group males (58%). The abundance of *C. punctatus* males at Newcastle, in addition to the large number of *C. obsoletus s.s.*, *C. scoticus* and *C. dewulfi* males at this site, also skewed the sex ratio towards males. At the remaining sites, where *Culicoides* were less abundant, *C. obsoletus* group females were dominant (Table 2).

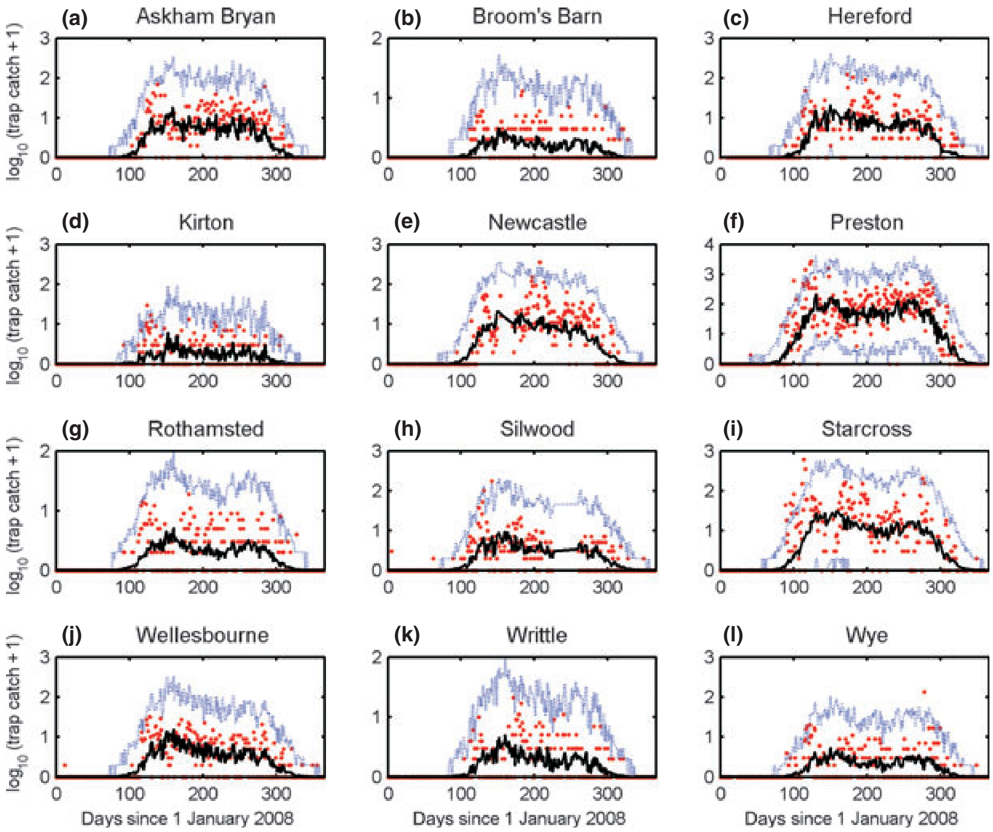

Fig. 3. Observed (red circles) and expected (black line: posterior median; blue dotted lines: 2·5th and 97·5th percentiles for the posterior predictive distribution) numbers of *Culicoides* biting midges (total male and female) caught each day for the twelve Rothamsted suction trap sites during 2008.

The first appearance of *Culicoides* (defined as a daily catch of greater than five individuals) was not significantly correlated with latitude ($F_{1,10}$ = 2·59, P = 0·14), habitat type ($F_{4,7}$ = 0·82, P = 0·56) or cattle density ($F_{4,7}$ = 0·40, P = 0·81) (Table 2). Daily abundance of *Culicoides* was highly variable at all sites, with day-to-day catches differing by several orders of magnitude (Figs 2 and 3). Even with daily data summarized to a weekly mean catch (Fig. 2), trends in abundance are difficult to ascertain visually. Most sites demonstrated greater *Culicoides* abundance during spring (April/May) and autumn (September/October) with the exception of Newcastle where abundance was greatest in mid-summer (Fig. 2). *Culicoides* abundance during the summer at the other sites was typically smaller and less sustained than the peaks earlier and later in the year (Fig. 2). A reduction in *Culicoides* abundance was noted at all sites in June.

The seasonal activity of *Culicoides* varied with the abundance of different species at each site (Fig. 4). *Culicoides punctatus* and *C. pulicaris* were caught for a longer period than the *C. obsoletus* group, emerging earlier in the year and staying later than many other species, and this was reflected in the extended *Culicoides* season length where these species were common (Fig. 4). At the Broom's Barn and Kirton sites where *Culicoides* abundance rarely exceeded five per catch, the season of activity was restricted (Fig. 4). *C. obsoletus* group females and males of each of the four species were present in catches for much of the season at Preston (Fig. 4). At other sites, different species showed shorter periods of activity. At Hereford, *C. obsoletus s.s.*, *C. scoticus* and *C. dewulfi* were more abundant earlier in the season than *C. chiopterus* (Fig. 4); however, at Newcastle and Askham Bryan, *C. dewulfi* appeared later in the season than *C. obsoletus s.s.* (Fig. 4).

STATISTICAL MODELLING

Full results for the statistical modelling are presented in the Supporting Information, including parameter estimates for the different models (Tables S1–S3) and comparison of the models and data (Fig. 3; Figs S1–S7). Model checking indicated that the models adequately captured the data (see, for example, Fig. 3) in terms of overall fit, total catch, maximum daily catch and time of first appearance (see Appendix S1 for details).

Seasonality

Statistical modelling did identify seasonal trends in abundance (Fig. 5), but ascribed any apparent peaks at short time-scales to variation in trap catches rather than anything systematic. Seasonal trends with bimodal peaks (in spring and autumn) were identified for total *Culicoides*, *C. obsoletus* group females,

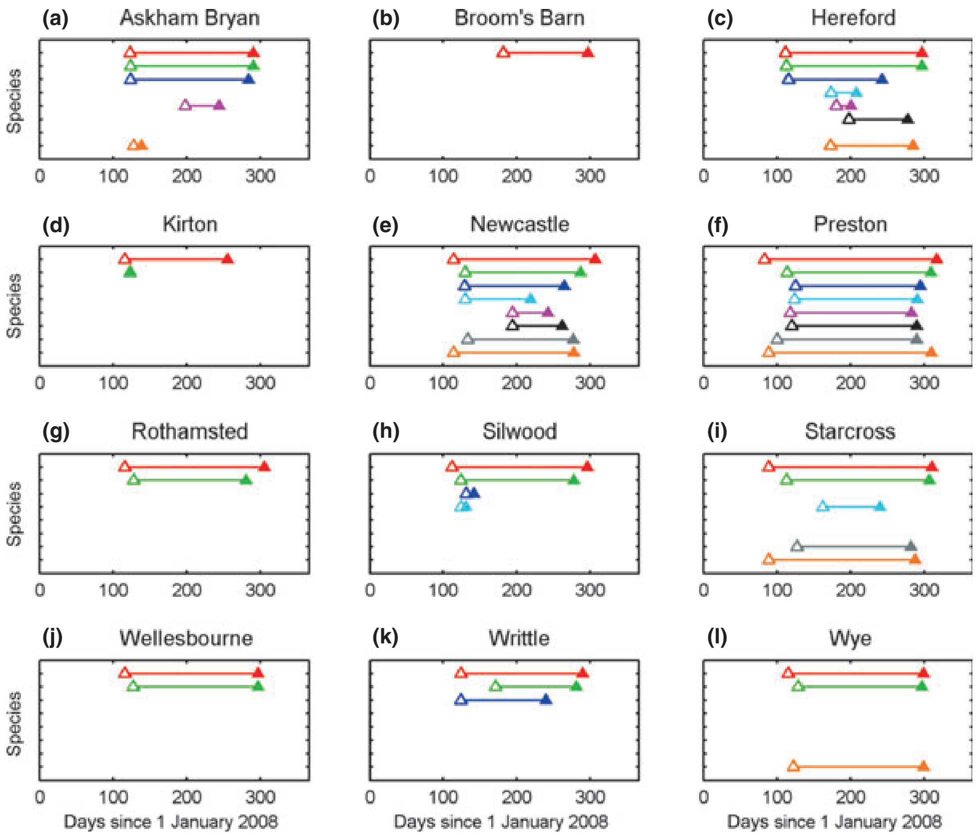

Fig. 4. Seasonal activity of *Culicoides* biting midges at each of the twelve Rothamsted suction trap sites. Open and closed triangles indicate the first and last days, respectively, on which each species appeared (defined as more than five midges caught); if more than five individuals per day were never caught at the site, no lines or symbols are shown. Colours indicate species: total *Culicoides* (red); *C. obsoletus* group females (green); *C. obsoletus s.s.* males (blue); *C. scoticus* males (cyan); *C. dewulfi* males (magenta); *C. chiopterus* males (black); *C. pulicaris* males (grey); and *C. punctatus* males (orange).

C. pulicaris males and *C. punctatus* males (Fig. 5); though, these peaks were only particularly pronounced for *C. pulicaris* and *C. punctatus*. By contrast, males of the *C. obsoletus* group exhibited only a single underlying peak in abundance (Fig. 5). The peaks in abundance for *C. dewulfi* and *C. obsoletus s.s.* typically occurred in spring (an exception being the peak for *C. obsoletus s.s.* at Preston which occurred in autumn), whilst that for *C. chiopterus* occurred in autumn; however, timing of the peaks for *C. scoticus* differed much more amongst sites.

The estimated seasonality in the total *Culicoides* abundance (Fig. 5a) was compared with that for the species-level abundance of male *Culicoides* (Fig. 5) by summing the individual species components weighted by their frequency in the trap catches (Fig. S8 Supporting Information). This suggested that the differences amongst sites in total *Culicoides* abundance reflect differences in the species composition at each site.

Meteorological parameters

The influence of meteorological parameters on trap catches was broadly consistent across species, with larger catches being associated with higher temperatures, lower wind speeds and days on which it was not raining at sunset (Tables S1–S3 Supporting Information); though, the magnitude of the effects did differ between species. There was, however, one exception to this pattern, with higher catches of *C. pulicaris* being associated with lower temperatures (Table S3 Supporting Information). Moreover, the effect of meteorological parameters was significant only at sites where large numbers of *Culicoides* were caught. For example, a significant effect of temperature was identified for *C. obsoletus s.s.* males at Askham Bryan, Hereford, Newcastle and Preston, but not at other sites.

Discussion

Using daily *Culicoides* data from 12 suction traps across an entire year, this study examines in unique detail the effects of meteorological conditions and seasonal dynamics on population abundance and dispersal. Although the vector status of *Culicoides* in northern Europe remains poorly defined (Carpenter *et al.* 2008a), trap samples were dominated by farm-associated species that have been implicated as potential vectors of BTV (Carpenter *et al.* 2006; Mehlhorn *et al.* 2007; Meiswinkel *et al.* 2007; Dijkstra *et al.* 2008; Carpenter, Wilson & Mellor 2009a). In contrast to most studies of *Culicoides* abundance which tend to concentrate on farms in proximity to livestock, the trap sites here were positioned across the UK in a variety of habitats. The abundance of vector species of

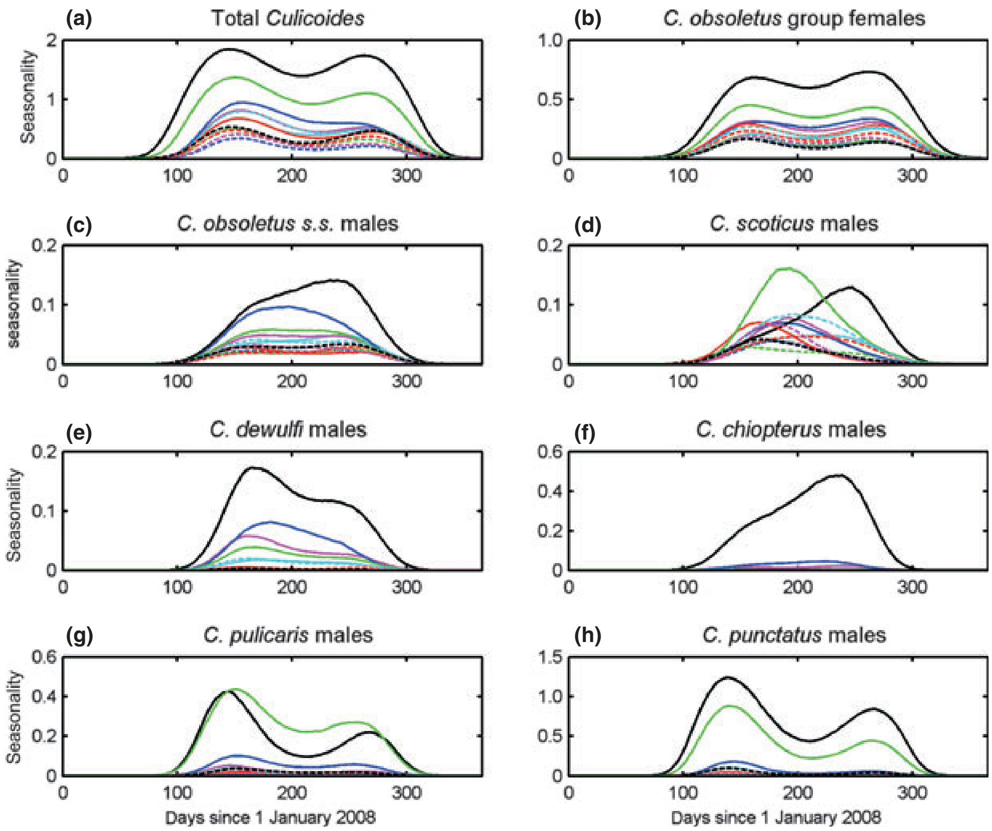

Fig. 5. Estimated seasonality components (posterior medians) in the species-level models for the number of male *Culicoides* biting midges caught each day for the twelve sites of the Rothamsted suction traps during 2008. (a) Total *Culicoides*; (b) *C. obsoletus* group females; (c) *C. obsoletus* s.s. males; (d) *C. scoticus* males; (e) *C. dewulfi* males; (f) *C. chiopterus* males; (g) *C. pulicaris* males; and (h) *C. punctatus* males. In each figure, sites are identified by the line style: Askham Bryan (solid cyan line); Broom's Barn (dashed blue line); Hereford (solid magenta line); Kirton (dashed green line); Newcastle (solid blue line); Preston (solid black line); Rothamsted (dashed red line); Silwood (solid red line); Starcross (solid green line); Wellesbourne (dashed cyan line); Writtle (dashed magenta line); and Wye (dashed black line).

Culicoides was strongly linked to land use and host density, with those areas surrounded by a greater density of livestock returning greater numbers. The dominance of livestock farm-associated *Culicoides* species in the RST samples is similar to that observed by Fassotte *et al*. (2008) and is typical of results using traps of other designs in England (Service 1971, 1974; Holmes & Boorman 1987).

The presence of *C. obsoletus* group species in traps in drier arable areas where livestock are rare implies a greater dispersal potential of *Culicoides* over land than previously thought. This was particularly evident from the presence, albeit in low numbers, of *C. chiopterus* and *C. dewulfi* which are restricted to cattle dung breeding sites (Kettle & Lawson 1952) in the traps in arable areas. The possibility of alternative breeding sites, such as the dung of horses and wildlife, within the arable areas, however, makes it difficult to suggest a dispersal range for *Culicoides* from RST sample data. The extent of movement of *Culicoides* over land may be further investigated with the use of hypervariable microsatellite markers and landscape data to examine the gene flow between populations, possible topographic barriers to dispersal and the use of habitat corridors between suitable areas (Cohuet *et al*. 2004; Storfer *et al*. 2007).

The date of first collection of five or more *Culicoides* at each site was remarkably similar considering the differences in habitat and latitude between sites, but was influenced by the abundance of *C. punctatus* and *C. pulicaris* at some sites, which emerged earlier than members of the *C. obsoletus* group. Analysis of male abundance suggests *C. pulicaris* and *C. punctatus* are bivoltine (two emergence peaks each year), whilst the emergence pattern of the *C. obsoletus* group is less clear. Distinct emergence periods for *C. pulicaris* and *C. punctatus* have not previously been recorded (Holmes & Boorman 1987).

Holmes & Boorman (1987) suggested that different species could be responsible for the three emergence peaks that they observed in the *C. obsoletus* group but they were unable to identify the individuals to species level. Here, *C. dewulfi* and *C. obsoletus s.s.* abundance peaked in spring and summer, respectively, whilst peak abundance in *C. scoticus* appears to be more variable, and following a brief spring flush, *C. chiopterus* peaked later in the year than the other three species. The abundance of *C. chiopterus* does not seem to be reflected accurately by UV light traps as this species has previously been found to be abundant at animal-baited traps. Consequently, its importance as a vector may be underestimated (Carpenter *et al*. 2008b). During the 2006–2008 outbreak of BTV in northern Europe, infection reached a peak in the autumn (Hoffmann *et al*. 2009). This increase, which correlates with the sustained abundance of *C. chiopterus* reported here, may be coincidental but may reflect the increased abundance of a more efficient vector at that time of year.

The risk of BTV entering the UK via wind-borne *Culicoides* from the near continent has been analysed since April 2007 using the NAME (Numerical Atmospheric-dispersion Modelling Environment) dispersion model (Jones *et al*. 2007) operated daily to predict incursion points and simulate likely spread patterns (Gloster *et al*. 2008). This model initially relied only upon a few quantitative studies often carried out in other countries to define activity rates, flight range and seasonality. The present Bayesian model for daily *Culicoides* abundance developed in this study has already been incorporated into the latest IAH-Met Office advisory service for the risk of infectious wind-borne *Culicoides* reaching the UK from continental Europe, the details of which will be published independently (L. Burgin, pers. comm.). The effect of meteorological conditions on *Culicoides* abundance was similar for all species at all sites, and the thresholds for temperature, wind speed and precipitation are similar to those seen in *Culicoides* caught in animal-baited traps (Zhdanova 1975; Olbrich & Liebisch 1987; Carpenter *et al*. 2008b). This suggests similar wind speed thresholds for flight of the *Culicoides* species and similar activity responses to temperature variation and precipitation.

In addition to their use in the IAH-Met Office advisory service, the statistical models could, in principle at least, be applied to other sites by making use of the hierarchical structure in the parameters (which allows for between site differences). In this case, we can generate parameter sets for new sites by sampling from the higher-order parameter distributions (see Tables S1–S3 Supporting Information) and use these to simulate *Culicoides* activity at the site, albeit with considerable uncertainty in any predictions if the models were to be applied in this way.

Conclusion

This study examined the influence of seasonal population dynamics and meteorological conditions on the daily abundance of potential vector *Culicoides* species. In addition to acting as a descriptive account of the 2008 season, this model allows the prediction of daily *Culicoides* abundance according to time of year and weather conditions, insights that are essential to assess the likely activity of *Culicoides*-borne viruses such as BTV and AHSV during outbreaks. Parameters generated in this study have been integrated into functional risk models of wind-borne infected *Culicoides* incursion into the UK and other countries, mapping areas of specific risk on a daily basis. The RST sample data suggest the dispersal of *Culicoides* species over large distances between suitable breeding sites. Understanding the seasonal dynamics and dispersal potential of *Culicoides* in northern Europe is essential in predicting and managing the continuing threat of incursion of BTV and other *Culicoides*-borne diseases.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Statistical methods.

Table S1. Parameter estimates for the model for total *Culicoides* biting midges.

Table S2. Parameter estimates for the model for female *Culicoides obsoletus* group biting midges.

Table S3. Parameter estimates for the species-level models for males of different *Culicoides* species.

Fig. S1. Observed and expected trap catches for female *Culicoides obsoletus* group biting midges.

Fig. S2. Observed and expected trap catches for male *Culicoides obsoletus s.s*.

Fig. S3. Observed and expected trap catches for male *Culicoides scoticus*.

Fig. S4. Observed and expected trap catches for male *Culicoides dewulfi*.

Fig. S5. Observed and expected trap catches for male *Culicoides chiopterus*.

Fig. S6. Observed and expected trap catches for male *Culicoides pulicaris*.

Fig. S7. Observed and expected trap catches for male *Culicoides punctatus*.

Fig. S8. Comparison of estimated seasonality components for total *Culicoides* and the sum of the species-level models for male *Culicoides* species.

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