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ORIGINAL PAPER

Do surveys of adult dragonflies and damselflies yield repeatable data? Variation in monthly counts of abundance and species richness

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Abstract

There is considerable debate over the most appropriate method for surveying dragonflies and damselflies (odonates). Using data from 62 survey locations nested within 26 waterbodies at 15 sites (discrete parcels of common ownership) in West Suffolk, UK, we show that short (20 m line transects or 3 min duration point counts), monthly counts of adults are repeatable. Correlations between predictions from models accounting for variation in ambient conditions and time of day and 52 separate counts used for validation equalled $r = 0.87$ for total abundance and $r = 0.75$ for species richness. Correlation coefficients between observed and modelled abundance exceeded 0.5 for eight of fourteen species modelled individually. Ambient temperature was the most important weather variable that influenced survey results, affecting the abundance of nine species, total abundance and species' richness. Most of the spatial variation in survey results was between waterbodies, rather than between sites or at individual survey locations, suggesting that adult counts may indicate aspects of waterbody quality, although differences in these patterns were observed between dragonflies (Anisoptera) and damselflies (Zygoptera). Encouraging relatively infrequent and rapid counts of flying adults may therefore be used to increase volunteer participation in citizen (community) science odonate monitoring schemes whilst also providing repeatable abundance and species richness data that can contribute to research and monitoring programmes.

Keywords Citizen science · Freshwater · Methods · Monitoring · Odonata · Temperature

Introduction

Recent reports of large-scale declines in insect populations (e.g. Hallmann et al. 2017; Sanchez-Bayo and Wyckhuys 2019) have generated considerable interest, with potential implications for a range of ecosystem services, such as pollination (Potts et al. 2010; Oliver et al. 2015). However, despite recent headlines, there remains considerable uncertainty over the magnitude of these declines, with many insect groups and most parts of the world poorly monitored (Thomas et al. 2019). The monitoring of insects is much neglected, but yet vital to understand environmental change (Thomas 2005). Not only are insects important determinants of ecosystem function (Weisser and Siemann 2004), and deliver a wide-range of ecosystem services, they are also keystone species important for the maintenance of populations of many insectivorous species (e.g. Kristin and Patocka 1997; 2010).

Although some groups of insects, such as butterflies, are relatively well-monitored (Thomas 2005) many others are poorly covered. One relatively poorly covered group is Odonata (dragonflies and damselflies; hereafter odonates). They have aquatic larval life-stages susceptible to mortality in response to changes in the quality and extent of freshwater habitats, but aerial/terrestrial adult stages which are highly detectable by observers. As a result, they have the potential to indicate variation in the quality of aquatic systems (Clark and Samways 1996; Martin and Maynou 2016; Berquier et al. 2016; Golfieri et al. 2017), climate change

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impacts (Bush et al. 2013) and the success of habitat restoration (Modiba et al. 2017). However, with the exception of the Netherlands (Bouwman et al. 2009), odonate population trends have not been routinely monitored through national monitoring schemes in the same way as achieved in many countries for butterflies which have similarly visible adult life stages (van Swaay et al. 2008). Instead, for example in the UK, odonate trends are tracked through long-term changes in distribution, variation in the occurrence of biological records, or through occurrence in complete lists (Cham et al. 2014; Border et al. 2019; Outhwaite et al. 2020). This is a significant global gap given that wetlands, including freshwater habitats, cover less than 1% of the world's surface area but support 6% of species (Dudgeon et al. 2006) and deliver a large number of ecosystem services, ranging from water and food to recreational activities (Zedler and Kercher 2005). Wetlands are highly threatened, and in line with this, globally, odonate populations are thought to be declining as a result of the loss and deterioration of freshwater habitats (IUCN 2009). For example, in the UK, three species have become extinct since the 1950s, a further six species are red-listed as endangered or vulnerable and six are listed as near-threatened (Daguet et al. 2008), largely based on range contractions or restricted range-extent, although more recently, six species have colonised as breeding species from continental Europe, one of which is a recolonization by a previously extinct species (Cham et al. 2014).

There is considerable debate about the relative efficacy of different methods for sampling odonates. Quantitative information about odonate abundance may be obtained from the sampling of larval stages in the aquatic environment, for example using sweep nets (Raebel et al. 2010; Golfieri et al. 2017), sampling of exuviae (Raebel et al. 2010; Hardesen et al. 2017) or counting emerged adults (e.g. Giuglioano et al. 2012; Berquier et al. 2016; Simaika et al. 2016). Given their mobility, some have suggested that adults do not necessarily signal that viable populations may be supported at a site, leading to recommendations that the sampling of exuviae is the most effective method for surveying odonates (Raebel et al. 2010; Hardersen et al. 2017). However, the low detectability of exuviae and the risk of under-estimation of occurrence, has led others to favour the sampling of adults (Bried et al. 2012; Giuglioano et al. 2012), counts of which have been shown to correlate with exuviae and teneral occurrence, two indicators of locally successful completion of the life-cycle (Bried et al. 2015; Pattern et al. 2019).

If the aim of monitoring is to achieve large-scale and long-term abundance and trend information, for example to inform conservation prioritisation and to understand drivers of change, and to provide background monitoring against which more intensive site-specific trends can be compared, then using volunteers to support a citizen science (sometimes known as community science) monitoring scheme provides significant potential (Pocock et al. 2018). In the Netherlands, some 250 transects have been surveyed annually, largely by volunteers (Bouwman et al. 2009), but within the UK a pilot citizen science scheme requiring two visits per month had limited uptake (Smallshire pers. comm.). For information to be obtained from a sufficient sample of representative sites in a cost-effective manner, a relatively large number of volunteers are required. For this to be achievable, the methods used and the requirements for identification need to be accessible to hundreds of potential surveyors (Pocock et al. 2015). Achieving this may require a trade-off between intensive sampling at individual sites which only a relatively small number of volunteers may be able to commit to, and a less-intensive survey method that may result in a greater number of sites being monitored.

This principle is demonstrated by the impact that the switch from the intensive Common Bird Census (CBC) mapping methodology to the Breeding Bird Survey (BBS) had on participation and geographical coverage of bird surveys in the UK. The CBC method required seven to ten visits to a site during the bird breeding season, and enabled breeding bird abundance at about 250 sites per year, located mainly in southern England, to be censused with a high degree of accuracy. In contrast, the BBS requires only two-visits sampling breeding bird abundance using line-transects. Although the resulting data from BBS are more stochastic than CBC at the site level, the resulting order of magnitude increase in the number of participants delivers improved coverage of data from across the country, and therefore much more representative and precise national trends (Freeman et al. 2007). Similarly, the adoption of a method with a minimum of two visits in July and August for surveying butterflies as part of the UK Wider Countryside Butterfly Survey (WCBS), has opened up butterfly surveying to a wider-range of volunteers and increased representation across the wider countryside (Brereton et al. 2011) compared to the more intensive Butterfly Monitoring Scheme with an ideal of weekly counts across a six-month survey period (BMS; Pollard 1977). The aim of this paper is to assess whether a similarly rapid approach to odonate monitoring with fewer visits than has been previously tried, can deliver repeatable results of either abundance or species' occurrence, as indicated by species richness, as a contribution to the debate about the most appropriate approach for surveying odonates. Secondarily, by describing how the results of such counts vary spatially and temporally with method and ambient conditions, we assess the value of such information to address particular conservation and policy questions, and make some suggestions about how a citizen science odonate monitoring scheme may be taken forward.

Table 1 Summary of conditions suitable for odonate surveys (yes) as described by Smallshire and Benyon (2010) using a combination of temperature, time of day and cloud cover. In addition, surveys should not be undertaken in rain or winds greater than force 4

Temperature\time	09:30–10:00	10:00–16:00	16:00–16:30
< 15 °C	No	No	No
15–17 °C	No	Yes if cloud cover < 60%	No
17–22 °C	No	Yes	No
22–30 °C	Yes	Yes	Yes
> 30 °C	No	No	No

Methods

Survey methodology

We adapted the pilot methodology of the British Dragonfly Society Dragonfly Monitoring Scheme (Smallshire and Beynon 2010) which advocated the use of two complementary methods. For linear waterbodies and larger ponds, line-transects were recommended, following the methods of the Dutch Monitoring Scheme (Bouwman et al. 2009) but for smaller waterbodies, or sites with limited visibility or access to the water, Smallshire and Benyon suggested the use of point counts. Although both Smallshire and Benyon (2010) and Bouwman et al. (2009) advocated up to fortnightly counts being undertaken, or weekly counts for selected rare species during their main flight periods, here we consider the information that can be gained from monthly counts at sites from the months of May to September inclusive. This is greater than the intensity of the WCBS which has improved the uptake and coverage of butterfly monitoring in the UK, but half the intensity advocated by existing dragonfly monitoring schemes.

Smallshire and Beynon (2010) recommend the use of 100 m transects split into two 50 m sections. Whilst appropriate for large waterbodies and rivers, such an approach would not work for the many small waterbodies which can form the majority in many landscapes and are important for some species. Given the small size and limited accessibility/visibility of many of the ditches and rivers covered in our study, the minimum transect length was reduced to 20 m, whilst many ponds were covered by one to three point counts only. Points and transects were non-overlapping with most from the same waterbody separated by tens of metres. As recommended by Smallshire and Beynon (2010), transects were walked slowly, and all individuals observed by eye or using binoculars, counted to a width of 5 m. Point counts had a duration of 3 min and all individuals counted within a 5 m

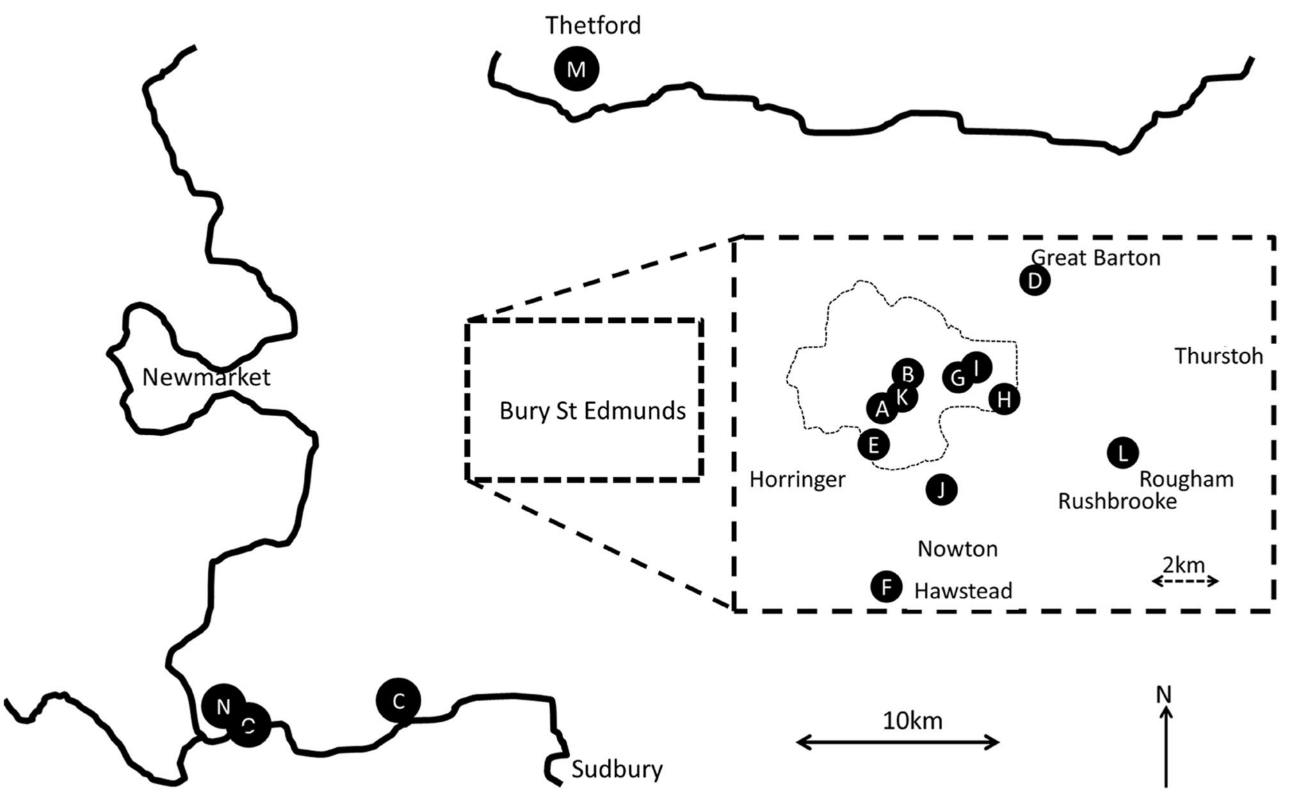

Fig. 1 Map of sites (letters within circles) within the West Suffolk area. Major towns and county boundaries are shown on the large map, whilst the inset delineates the extent of Bury St Edmunds (dashed polygon) and surrounding villages. The letters cross-reference to the sites in Table 2 that summarises coverage

Table 2 Summary of coverage by site and year

Site code	2015	2016	2017	2018
A				3/4
B				1/2
C	2/4	2/5	4/10	4/10
D				1/1
E			1/2	1/2
F		1/2	1/2	1/2
G				1/2
H			1/3	1/3
I				1/2
J	2/4	2/4	2/4	2/4
K			2/2	2/2
L	1/5	2/7	2/7	2/7
M		4/11	4/13	4/16
N				1/3
O				1/2
Totals	5/13	11/29	17/43	26/62

Each cell denotes the number of waterbodies/number of locations covered in each year, for each site. Site codes match those shown in Fig. 1

radius, although when large numbers of individuals were observed, or identification was challenging, counts took up to 10 min to ensure accurate counts and identification. Most difficult to identify individuals were photographed and either confirmed in the field, or subsequently. Where large numbers of difficult-to-identify individuals were recorded, such as blue damselflies, it was sometimes necessary to split these into estimates per species, based on the proportion of the different species identified whilst accounting for behavioural differences between species, such as their association with terrestrial vegetation or open water, that may differentially affect their detectability. All counts used in this study were undertaken by a single observer (JPH).

The start time of each count was recorded, as was ambient temperature (°C), wind speed (Beaufort scale) and cloud cover (8-point Okta scale). Weather data were either recorded directly in the field or taken from local met station observation data available at an hourly resolution. Ideally, surveys were conducted under the recommended conditions of Smallshire and Benyon (2010; Table 1), but in some cases this was not possible. Recording the weather enabled the potential impact of recording odonates in unfavourable conditions to be accounted for analytically. Waterbodies were classified as either still or flowing.

Coverage

Data were collected from 2015 to 2018 inclusive from a total of 62 survey locations nested within 26 waterbodies and 15 sites (defined by common ownership), concentrated around Bury St Edmunds (52°14′ N, 0°42′ E) in West Suffolk (Fig. 1). Sites ranged in size from 1 waterbody with 1 location, to four waterbodies with 16 locations, and all were open to the public or adjacent to public rights-of-way (footpaths). Over time, more sites were surveyed each year (Table 2). From the year they were first included, 69% coverage of a possible 735 location × month combinations was achieved (n = 503). Note that only six waterbodies at three sites were surveyed in all of the five months in one year or more. In addition to these monthly counts, 52 duplicate counts were undertaken, in order to provide a separate check for validation, 23 of which were on the same day as other counts, whilst 29 were repeats of counts within the same month, but on different days.

Analysis

We summarised the results of each survey as (i) the total numbers of individuals recorded across all species, and separately the total number of individual dragonflies (Anisoptera) and damselflies (Zygoptera), (ii) the total number of species observed (species richness), also presented separately for dragonflies and damselflies, and (iii) the total numbers of individuals recorded per species. These data also reflect the two main approaches employed to monitor odonates, that of counting adults to monitor changes in abundance (e.g. Bouwman et al. 2009), and of recording occurrence within lists (e.g. van Grunsven et al. 2020), as employed by the British Dragonfly Society.

Using a mixed model we examined how counts varied between sites, waterbodies and individual survey locations, to quantify the extent that multiple locations at individual waterbodies, or separate waterbodies within sites, might be regarded as independent. Given that counts are likely to vary according to the ambient conditions and with time of day, we modelled the extent to which changes in conditions affect survey results, and then used that model to predict the number of individuals or species recorded during each of the validation counts, in order to test the repeatability of our survey method. This approach will be similar to, but more robust than, simply correlating observations across pairs of original and validation counts because it allows us to control for predictable variation due to changes in ambient conditions. We are therefore able to i) quantify the scale at which odonate survey results vary, ii) quantify the factors affecting survey results and how those factors vary across species, and iii) describe the repeatability of the survey method. In combination, this provides information to inform the design of any future odonate monitoring scheme, with particular reference to increasing accessibility to citizen scientists.

Given the nested distribution of the study, with surveys undertaken from selected sites, some of which included

Table 3 Mean values for each predictor variable and inter-correlations between them, as given by Pearson Correlation Coefficient (r) and *P* values

	Mean (range)	CLOUD	WIND	TEMPERATURE
CLOUD	4.8 (0–8)			
WIND	2.3 (0–6)	$r = 0.038$ $P = 0.34$		
TEMPERATURE	22.1 (14–31)	$r = -0.21$ $P < 0.0001$	$r = -0.28$ $P < 0.0001$	
TIME	14.8 (11.4–16.7)	$r = -0.097$ $P = 0.014$	$r = 0.059$ $P = 0.013$	$r = -0.094$ $P = 0.017$

multiple waterbodies, most of which had counts from multiple locations, the resulting data are inherently non-random. To account for this, we used a generalised linear mixed model (GLMM) in which location, waterbody and site were specified as random effects. Individual days were also modelled as a separate random effect with a unique identifier to account for the reduced independence of counts from the same day. All models were undertaken in SAS 9.4 using PROC GLIMMIX, specifying a Poisson error distribution and log-link function, and applying the Kenward–Rogers correction for the estimation of the degrees of freedom (Littel et al. 1996). Random effects which failed to account for any covariance were removed to improve convergence. We also tested for over-dispersion, which was a potential issue when modelling total numbers of individuals across all species only (scale parameter 2.02 for the full model). In this model only, over-dispersion was corrected for using the 'random _residual_;' command.

The following predictor variables were considered when modelling total abundance, species richness and the abundance of individual species recorded on more than 20 occasions. METHOD (point count or line-transect) and HABITAT (still or flowing water) were both included as two-level factors. TIME (start-time, in which minutes were converted into the proportion of an hour), and variables describing variation in ambient conditions (TEMPERATURE, CLOUD and WIND), were considered as covariates with both linear and quadratic terms included together. Models were simplified by backwards deletion of non-significant ($P > 0.05$) terms, although non-significant linear terms were retained alongside a significant quadratic term. None of these predictors were closely correlated (Table 3).

The strength of the correlation (r) between observed and expected richness or abundance across the 52 validation counts gave a measure of survey consistency. Expected values were derived from the GLMM and therefore are based upon the predictor variables and random effects. For species recorded fewer than 5 times in the validation counts, a random selection of initial counts were removed from the modelling dataset when used to make these predictions and were treated as validation counts, so that for each species, there was a minimum of five non-zero records in the validation counts for this correlation. Following Pearce-Higgins et al. (2011), we regard models with $r < 0.25$ as poor, $0.25 \le r \le 0.50$ as moderate and $r > 0.5$ as good. All error estimates in the text, tables or figures are standard errors.

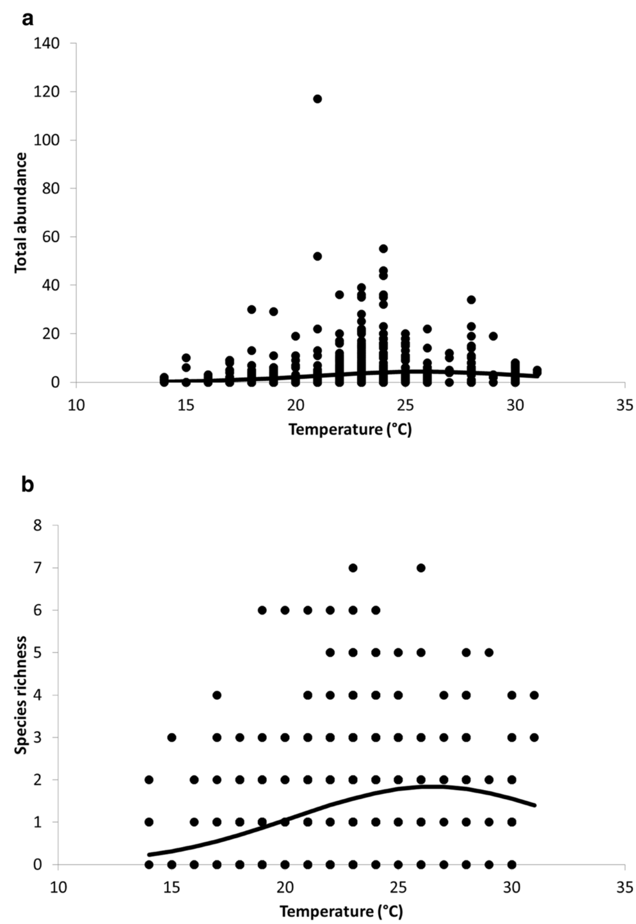

Fig. 2 Variation in **a** the total number of odonate individuals counted and **b** odonate species richness, as a function of ambient temperature across the 503 individual samples used to build the models. The fitted curves are based on the coefficients given in Table 4, and therefore do not account for spatial variation in abundance attributed to the random effects

Table 4 The effect of weather variables upon the abundance and richness of odonates recorded

	All Odonates	Dragonflies	Damselflies
a. ABUNDANCE			
Intercept	− 10.08 ± 3.19	− 2.64 ± 0.73	− 48.40 ± 10.46
Time	− 0.20 ± 0.061**		4.29 ± 1.38**
$Time^2$			− 0.16 ± 0.048**
Temperature	1.13 ± 0.27****	0.103 ± 0.027***	1.68 ± 0.36****
$Temperature^2$	− 0.022 ± 0.0059***		− 0.034 ± 0.0079****
Cloud		− 0.133 ± 0.039***	
b. RICHNESS			
Intercept	− 8.52 ± 1.90	− 2.71 ± 0.65	− 13.05 ± 2.49
Time			
Temperature	0.71 ± 0.17****	0.10 ± 0.024****	1.05 ± 0.22****
$Temperature^2$	− 0.013 ± 0.0037***		− 0.021 ± 0.0047****
Cloud	− 0.051 ± 0.023*	− 0.12 ± 0.035***	

Shown are coefficients for the significant (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$) terms in the final minimum adequate model

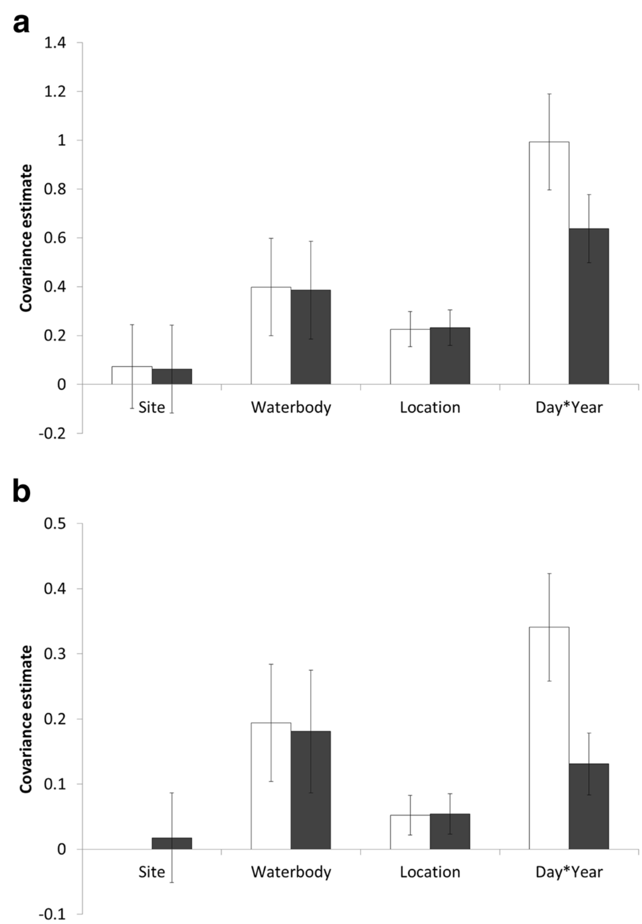

Fig. 3 Variation in the allocation of unexplained variation in **a** total odonate count and **b** total species richness, both spatially (across Sites, Waterbodies and Locations), and between dates (Day*Year). Estimates (± SE) are given before (white) and after (grey) accounting for significant predictor variables (Table 4). The difference between the two shows at which scale those variables have the greatest impact

Results

Models of abundance and richness

Total odonate abundance was negatively correlated with TIME ($F_{1,332.5} = 11.10$, $P = 0.0010$) and quadratically with TEMPERATURE showing a mid-range peak around 26 °C (linear, $F_{1,104.5} = 17.59$, $P < 0.0001$; quadratic, $F_{1,101.9} = 13.90$, $P = 0.0003$; Fig. 2a). When split by Suborder, the model for dragonfly abundance contained a positive association with TEMPERATURE ($F_{1,79.14} = 14.63$, $P = 0.0003$; Fig. S1a) and negative association with CLOUD ($F_{1,106.6} = 11.73$, $P = 0.0009$). The separate model for damselflies contained quadratic relationships with both TIME (linear, $F_{1,496} = 9.69$, $P = 0.0020$; quadratic, $F_{1,496} = 10.99$, $P = 0.0010$) and TEMPERATURE (linear, $F_{1,114.8} = 21.38$, $P < 0.0001$; quadratic, $F_{1,112} = 18.41$, $P < 0.0001$; Fig. S1b). Model coefficients are given in Table 4a.

Species richness showed a quadratic relationship with TEMPERATURE (linear, $F_{1,90.65} = 17.65$, $P < 0.0001$; quadratic, $F_{1,84.79} = 13.30$, $P = 0.0005$; Fig. 2b) and a weak negative relationship with CLOUD ($F_{1,87.73} = 4.80$, $P = 0.031$). The same variables were associated with the number of dragonfly species recorded, but in this instance the relationship with TEMPERATURE was positive (TEMPERATURE, $F_{1,82.25} = 17.07$, $P < 0.0001$; Fig. S2a; CLOUD, $F_{1,90.71} = 12.05$, $P = 0.0008$), whilst variation in damselfly species richness showed a quadratic correlation with TEMPERATURE only (linear, $F_{1,100.9} = 23.42$, $P < 0.0001$; quadratic, $F_{1,94.94} = 19.66$, $P < 0.0001$; Fig. S2b). Model coefficients are given in Table 4b.

Forty-one percent of the variation in the null model of total odonate abundance was attributable to spatial random effects and 59% to survey date (Fig. 3a). More than half (57%) of the spatial variation occurred at the level of waterbodies, with relatively little explained by site. Incorporating covariates of TIME and ambient conditions reduced the residual variation attributed to date by 36%, but did not affect differences between locations, waterbodies or sites. These patterns differed between Suborders, with 56% of variation in dragonfly abundance attributed to spatial random effects compared to 37% of variation for damselflies (Fig. S3). Of these spatial terms, 74% of spatial covariation in dragonfly abundance was attributable to waterbodies, whilst spatial variation in damselflies was relatively evenly spread across the three spatial random effects. The inclusion of covariates reduced residual variance in temporal abundance attributable to date by 45% in dragonflies but only by 22% in damselflies.

As with the abundance data, 41% of the null variation in species richness was spatial rather than temporal, although with a greater percentage (79%) apportioned to the waterbody random effect, rather than to site or location (Fig. 3b). The inclusion of TIME and weather variables reduced the residual variation attributed to date by 62%. Again, these covariance patterns differed between dragonflies and damselflies (Fig. S4), with almost double the proportion of variation attributed to spatial random effects in dragonflies (60%) compared to damselflies (32%), although similar majority proportions of this were attributed to the waterbody random effect (82% and 75% respectively), instead of site or location. The inclusion of explanatory variables in the models significantly reduced variance attributed to sample date by just over half (54% in dragonflies and 55% in damselflies).

In combination, these results indicate that both abundance and richness vary considerably between different waterbodies at the same sites, but that these patterns are much stronger in dragonflies, with damselfly abundance in particular much less spatially variable. Daily variation in abundance and species richness is significantly reduced (by up to 60%) in all models by the inclusion of survey time and weather covariates.

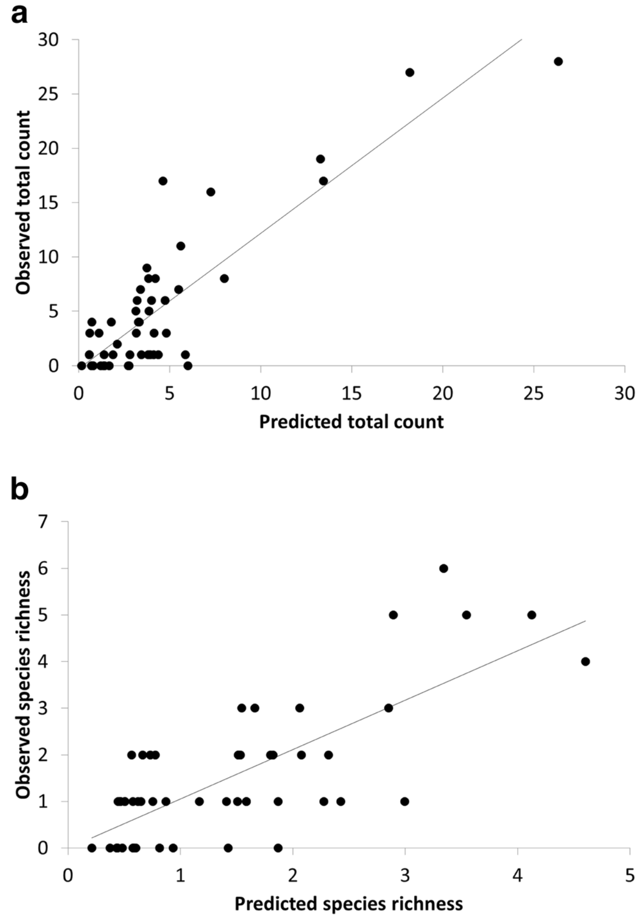

Fig. 4 Correlation between observed and predicted total odonate count (**a** $y = 1.25x - 0.28$, $r = 0.87$) and richness (**b** $y = 1.06x - 0.0033$, $r = 0.75$)

When used to predict abundance and richness across the 52 validation counts not used to construct the models, both models of total odonate abundance and species richness showed good predictive ability, predicting 76% and 57% of the observed variation respectively (Fig. 4). There was no difference in the size of the residuals between observed and expected values according to whether the validation counts were taken on the same day as other counts or were duplicates of counts from other days within the same month (abundance, $t = -0.88$, $df = 50$, $P = 0.38$; richness, $t = -0.92$, $df = 47.7$, $P = 0.36$; The test for richness used the Satterthwaite method to account for unequal variance $P = 0.028$ between the two samples). When split by Suborder, models accounted for 32% and 65% of observed variation in dragonfly and damselfly count, and in 27% and 53% of dragonfly and damselfly richness respectively.

Table 5 The effect of weather variables upon the abundance of individual species

Damselflies Zygoptera	BanDem *C. splendens*	WilEme *C. viridis*	LarRedDam *P. nymphula*	AzuDam *C. puella*	ComBluDam *E. cyathigerum*	BlutaiDam *I. elegans*	RedeyeDam *E. najas*
Intercept	− 141.50 ± 45.55	− 3.23 ± 0.37	− 57.62 ± 27.58	− 125.97 ± 32.40	− 16.16 ± 5.43	− 4.42 ± 1.20	− 30.04 ± 12.49
Habitat (Still vs Flow)	− 3.62 ± 0.74**						
Method (Point vs Transect)							
Time (quadratic)	13.74 ± 6.33* − 0.48 ± 0.22*			12.25 ± 4.23** − 0.44 ± 0.15**	− 0.21 ± 0.076**		
Temperature (quadratic)	3.65 ± 1.07** − 0.074 ± 0.022**		5.19 ± 2.58* − 0.12 ± 0.060*	3.33 ± 1.22** − 0.069 ± 0.027*	− 1.38 ± 0.46** − 0.025 ± 0.0099*	0.12 ± 0.04**	2.46 ± 1.12* − 0.053 ± 0.025*
Wind speed (quadratic)			− 0.68 ± 0.27*	0.71 ± 0.42 − 0.16 ± 0.076*			− 1.23 ± 0.46** 0.19 ± 0.087*
Cloud cover (quadratic)							
Predictive ability (r)	0.80	0.33	0.74	0.72	0.80	0.42	0.83
Dragonflies Anisoptera	**MigHaw *A. mixta***	**SouHaw *A. cynanea***	**BroHaw *A. grandis***	**EmpDra *A. imperator***	**FouspoCha *L. quadrimaculata***	**ComDar *S. striolatum***	**RudDar *S. sanguineum***
Intercept	− 3.58 ± 0.38	− 2.00 ± 0.60	− 6.59 ± 1.32	− 9.30 ± 1.77	− 60.81 ± 22.23	− 72.48 ± 36.19	− 3.58 ± 0.64
Habitat (Still vs Flow)			− 1.27 ± 0.32****				
Method (Point vs Transect)				0.92 ± 0.42*			
Time (quadratic)						10.71 ± 5.18* − 0.40 ± 0.18*	
Temperature (quadratic)			0.21 ± 0.053***	0.23 ± 0.067***	4.93 ± 1.94* − 0.10 ± 0.042*		
Wind speed (quadratic)							
Cloud cover (quadratic)		− 0.27 ± 0.11*				− 0.23 ± 0.096*	
Predictive ability (r)	0.30	0.05	0.44	0.53	0.91	0.34	0.71

Shown are coefficients for the significant (*$P<0.05$, **$P<0.01$, ***$P<0.001$, ****$P<0.0001$) terms in the final minimum adequate model for each species, and the ability of that model (r) to predict abundance across 52 validation counts

Species-specific models

Species-specific models could be produced for fourteen odonate species recorded on 20 or more occasions (Table 5). Two species (brown hawker *Aeshna grandis* and banded demoiselle *Calopteryx splendens*) showed significant associations with HABITAT, being more abundant over flowing than still water, as indicated by the negative coefficients. One species, emperor dragonfly *Anax imperator*, tended to be more abundant when recorded from point counts vs line-transects, although this relationship was weak ($P=0.036$), and therefore similar to the level of significance expected by chance across fourteen species. The abundance of four species varied significantly with TIME of survey (common blue damselfly *Enallagma cyathigerum*, azure damselfly *Coenagrion puella,* banded demoiselle and common darter *Sympetrum striolatum*), with azure damselfly, common darter and banded demoiselle each showing evidence of a mid-range peak in abundance at 13:55, 13:22 and 14:18 respectively.

Of the weather variables, the most important by far was TEMPERATURE which positively affected the abundances of nine species in either a positive linear (emperor dragonfly, blue-tailed damselfly *Ischnura elegans,* brown hawker) or quadratic manner (common blue damselfly, azure damselfly, four-spotted chaser *Libellula quadrimaculata*,, large-red damselfly *Pyrrhosoma nymphula*, banded demoiselle, and red-eyed damselfly *Erythromma najas*). The abundances of three species were negatively associated with WIND speed (azure damselfly, large-red damselfly and red-eyed damselfly) and two negatively with CLOUD cover (southern hawker *A. cyanea* and common darter).

These models had variable ability to predict abundance across the validation samples (average $r = 0.57 \pm 0.069$, range 0.05 to 0.91) with an average predictive ability (r^2) of 0.38. For eight species (common blue damselfly, azure damselfly, emperor dragonfly, four-spotted chaser, large-red damselfly, banded demoiselle, ruddy darter and red-eyed damselfly), model performance was regarded as good ($r > 0.5$), and for five (blue-tailed damselfly, brown hawker, migrant hawker *A. mixta*, common darter and willow emerald *Chalcolestes viridis*), moderate. The model for willow emerald also showed good predictive ability if one outlying zero count when 3.5 individuals were expected to be recorded was removed ($r = 0.33$ vs 0.80).

Although there was a tendency for damselfly species models to have a better predictive ability than dragonfly models ($r = 0.66 \pm 0.08$ vs 0.47 ± 0.11 respectively), this difference was non-significant ($t = 1.48$, $df = 12$, $P = 0.16$). Predictive ability was also not significantly correlated with the prevalence of each species, as measured by the proportion of samples used to build the model with the species present ($r_s = 0.38$, $P = 0.18$), but was correlated with the number of predictor variables included in the model ($r_s = 0.63$, $P = 0.02$), which in damselflies (mean = 3.1 predictors per species) tended to be double that of dragonflies (mean = 1.4 predictors).

Discussion

We describe the factors that influence the abundance of adult odonates, and consider the potential for a rapid method of surveying adults to produce repeatable and predictable counts of total abundance, species richness and the abundance of many individual species. Importantly, there were strong correlations between both modelled odonate abundance and richness, and observed values across 52 validation counts not used to construct the models. This suggests that given a similar set of conditions even repeated short counts of abundance and species richness are likely to be strongly correlated. Such tests of the repeatability of biological survey data are relatively rare, but the findings here are similar to those found for both vascular plant and breeding bird surveys (Renwick et al. 2012; Loos et al. 2015). In combination, this provides confidence in the meaningful nature of relatively rapid surveys of odonate communities, and opens the potential for rapid assessment methods that can be applied extensively to surveying adults across large areas with relatively few resources.

Although there was more variation in the ability of our method to produce repeatable counts of individual species, over half of the species models were regarded as good, able to account for at least 25% of the variation in observed abundance in the validation data ($r = 0.50$). There was a tendency for models of damselfly abundance to have greater predictive ability than dragonflies, both at the individual species level, although this difference was not statistically significant, and when totalled across all species. Whilst more work is required to better understand the factors that influence the relative detectability of different odonate species, our models suggest that counts of the majority of species are significantly influenced by ambient conditions. The fact that the dragonfly models tended to contain fewer covariates than damselflies may therefore contribute to the differences in model fit between the two Suborders. Whether this is due to biological differences in the sensitivity of dragonflies and damselflies to ambient conditions, or a function of the reduced power of the dragonfly models due to the smaller numbers of individuals encountered on any one survey (Fig. S1), requires further examination.

Our models support the recommendations of Smallshire and Beynon (2010) that high levels of cloud cover, strong winds and particularly cold temperatures do indeed have a negative impact on at least some odonates, and that activity also varies significantly with time of day, with a peak early in the afternoon and declining later. These constraints are similar to the requirements for butterfly counts (Pollard 1977; Brereton et al. 2011). However, there was wide variation in the extent to which these factors affect the counts of individual species, suggesting that surveys outside of these parameters may still contain useful information. If weather conditions and time of day are recorded by the observer, either directly in the field or from nearby weather-station data widely available on the internet, it may therefore be possible to use models to reduce the impact of weather conditions upon estimates of abundance (e.g. Renwick et al. 2012). Thus, although counts in sub-optimal conditions are likely to be under-estimates of abundance or richness, they may still contribute useful data for a wider monitoring scheme, a key conclusion with respect to the design of potential citizen science monitoring schemes for odonates, or even other similarly active insect groups.

The partition of variation in counts between different levels of spatial resolution, and time, can inform the design of any odonate monitoring programme and help understand the value of any resulting data. Approximately half of the variation in both total abundance and richness was explained spatially, and half between different survey visits during the course of the season. Over half of the spatial variation in both abundance and richness was a function of waterbody, rather than site or location, although this was much stronger in dragonflies than damselflies; abundance of the latter appeared equally distributed between sites, waterbodies and locations. In the context of previous studies of odonates, where there is an ongoing debate over the value of sampling adults compared to exuviae or larvae (Raebel et al. 2010; Giuglioano et al. 2012; Golfieri et al. 2017; Hardersen et al. 2017), these results demonstrate that significant variation in odonate abundance and richness occurs at the level of waterbodies, particularly for dragonflies, supporting the inference of Kietzka et al. (2017). Thus, adult counts can provide useful information about the quality of those individual waterbodies, although precisely how that measure of quality relates to aspects of odonate biology, such as the ability of species to reproduce successfully, remains unclear (Raebel et al. 2010, although see Bried et al. 2015; Pattern et al. 2019), and more intensive methods may be required for particular species. The fact that species richness also followed this pattern provides evidence that the list-based approach to odonate recording promoted by the British Dragonfly Society, and the trends recently produced for Dutch dragonflies using occupancy modelling (Van Grunsven et al. 2020) are indeed likely to provide valuable information about the quality of different waterbodies (see also Kietzka et al. 2017).

In the context of long-term monitoring, the role of temperature in influencing odonate counts is important, particularly as odonates are regarded as good indicators of climate change impacts (Bush et al. 2013; Rappaccuilo et al. 2017). If the generally positive or quadratic associations between both abundance and richness and temperature are a function of individual activity and behaviour being positively related to warmth, rather than a population-level response to warmer conditions, then care needs to be taken in attributing long-term population changes to climate change. Further work is required to assess the mechanisms underlying these associations.

When designing any large-scale monitoring scheme, there is a trade-off between the intensity of surveys at particular locations, and the number of locations surveyed. Is it better to maximise the accuracy of counts at particular sites, or to maximise coverage at the cost of increasing the error of estimates from any one location? A similar trade-off exists around the spatial scale of sampling. Is it better to maximise the number of waterbodies covered, or the number of locations at each waterbody? If the aim of a survey is to monitor particular odonates at specific waterbodies, then the most appropriate methods for that species should be used, maximising the number of survey locations at key waterbodies and the frequency of coverage of those locations as required. However, if large-scale and long-term monitoring of a range of species is the aim, then it is best to use a method that is repeatable across many species, and to maximise the representativeness of the samples, which may best be achieved through more rapid and extensive approaches. Based on our method, we suggest that a single observer could undertake counts at five to ten locations at an individual site within an hour, depending on how far apart those individual locations are, the duration of the counts and the level of difficulty in counting or identifying the species encountered. On this basis, once an observer is at a particular waterbody, it is probably worthwhile them undertaking a number of separate counts to minimise any impact of fine-scale variation in habitat or changes in ambient conditions on the counts, although further data collection and analyses would better quantify this trade-off.

This same debate also applies to butterflies, where extensive surveys of flying adults provide national-level estimates of abundance and trend (Brereton et al. 2011), and can be used to monitor responses to large-scale drivers such as climate change (Martay et al. 2017), but for other purposes, more detailed surveys are required (Kral et al. 2018). In practice, the level of monitoring applied at sites, for species, or across large-scales, will often be resource dependent. If resources are limiting, then short monthly odonate surveys may provide a good minimalist approach, whilst also increasing the potential for large-scale engagement by volunteers (citizen scientists) to monitor annual variation in the abundance of flying adults, in a manner similar to transect surveys for butterflies (Pollard 1977; Brereton et al. 2011). At present, the British Dragonfly Society encourages observers to track changes using complete lists (https://british-dragonflies.org.uk/recording/monitoring/; see also van Strien et al. 2010), but there is not currently a scheme that monitors changes in odonate *abundance*, in the UK (Border et al. 2019). The Dutch monitoring scheme has successfully employed volunteers to count odonates fortnightly across 250 sites annually whilst also producing sufficient data for occupancy modelling (Van Grunsven et al. 2020), but a trial of these methods in the UK had insufficient take-up (Smallshire pers. comm.).

Citizen science is increasingly used as a means for undertaking biodiversity monitoring, not only because it provides a mechanism for large-scale and long-term data collection, but also because of the benefit of engaging local people with environmental change and promoting engagement with the natural world (Pocock et al. 2018). It is our experience that a citizen scientist could reasonably undertake surveys at freshwater sites in their local area as part of their daily routine, such as during a lunch-break at work or at weekends in amongst other duties, subject to the travel-time required. Our results suggest that relaxing the criteria for fortnightly recording, or facilitating an additional tier of sites with monthly coverage on top of more intensively monitored sites, may be worth considering as a means of increasing engagement and the number of sites monitored, in much the same way as the Wider Countryside Butterfly

Survey outlined above (Brereton et al. 2011) has achieved for wider countryside butterflies. Although the precise methodologies of any such development would require further piloting, in order to increase opportunities for engagement, the collection of data outside of optimal conditions could be enabled providing that volunteers also provide standardised information about ambient weather conditions and the time of survey. These could either be estimated or measured in the field with an appropriately designed survey form to prompt this, or derived from observations from a nearby weather station, many of which are readily accessible on the internet. Annual variation in abundance, occurrence or richness could then be modelled using a year-term, whilst accounting for the relevant covariates and potentially geographical variation in coverage by giving greater weight in the analysis to samples from areas with poorer coverage. Unidentified odonates should also be counted, perhaps separated into a number of ecologically relevant groups such as 'blue damselflies', potentially providing useful additional information for trend calculation.

However, before a specific methodology and approach can be recommended, a number of key questions remain for large-scale odonate monitoring, particularly about the field methods and sampling protocols. Firstly, we have counted individuals to a transect width of 5 m, although we suspect that individuals of many species may be identifiable at greater distances than these, potentially increasing the number of individuals that could be surveyed, and therefore the data collected. Further work should attempt to assess the distance over which different species are likely to be detectable (e.g. Oppel 2006), which may further improve count accuracy whilst also enabling densities along water margins to be estimated. Secondly, detection is not just a function of distance, but also the behaviour of individuals. Occupancy modelling approaches provide a means for assessing the likelihood of detecting individuals at a location if they are there, and it would be worth considering whether surveyors at individual sites should undertake two or three consecutive counts in order to separate detection probability as a result of behaviour, from detection probability as a result of distance (van Strien et al. 2010). Longer duration counts of 5 or 10 min, rather than 3, may also be desirable to reduce any effect of the number of individuals or the difficulties of identification in extending the time required to count them. Thirdly, although we have based our assessment on monthly counts, it should be possible to use models that accounted for variation in sample effort for trend production, thus allowing for missed visits or enabling the incorporation of data from more frequently monitored sites. As outlined earlier, it may be that an optimal scheme could have two tiers of effort. One with a relatively low frequency of counts (e.g. monthly) to maximise coverage and engagement, and a second based on more frequent monitoring from particular sites which may be required for more accurate assessments of the abundance of adults with relatively short flight periods (Smallshire and Benyon 2010; Bouwman et al. 2009), and to maximise the chance of recording breeding behaviour (Patten et al. 2019). More analytical work may be required to determine the optimal strategy for this. Finally, the consistency of counts between different observers should be assessed, in order to consider the robustness of spatial variation between counts by different people (Buchanan et al. 2006). We hope that by publishing these results, we will stimulate further work to consider the potential for establishing odonate monitoring programmes at particular sites, regions or countries, particularly using citizen scientists to monitor changes in abundance, occurrence and communities. Given global concerns about wetland conservation and insect populations, such data are much needed.

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Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

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Research involving human and animal participants No insects were harmed during the course of this project and no human participants were involved in the work.

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