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DRAGONFLY SPECIES-RICHNESS AND TEMPERATURE: NATIONAL PATTERNS AND LATITUDE TRENDS IN BRITAIN

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The pattern of Odonata species-richness in Britain is mapped at 10 km resolution. This is strongly correlated with mean air temperatures. The relationship with seasonal and monthly mean temperatures is explored: summer temperatures are better predictors of overall dragonfly richness than are winter temperatures. However, there appears to be some latitude variation in the relationship. Thus, in northern Britain, increasing Odonata richness is correlated with increasing summer temperatures for non-boreal species, and with decreasing winter temperatures for predominantly-boreal species; physiological adaptations of individual species are proposed as a possible explanation.

INTRODUCTION

The geographic distribution of individual dragonfly species in Britain has been documented since the early nineteenth century (LONGFIELD, 1960). Of the 40 currently resident species, 36 had been recorded in Britain by 1900, and national distribution maps showing the occurrence of each species within the 112 vice-counties were published by CORBET et al. (1960). A national recording scheme was launched in 1968, and preliminary national maps, using as the mapping unit the 2860 10 km squares of the British Ordnance Survey grid, have been published at intervals from 1971 onwards. A comprehensive set of species maps, with descriptive text, has recently been published (MERRITT et al., 1996), and it is this dataset, summarised at 10 km square resolution, which provides the basis for the analyses which follow. At the same time as recording of dragonflies has advanced, the precision and reliability of interpolations of climate data for Britain, derived from 356 meteorological stations, has improved, so that accurate climate data at 10 km square resolution are now available (VINER & HULME, 1994).

NATIONAL PATTERNS OF SPECIES-RICHNESS AND CLIMATE

It has long been known that more species of dragonfly occur in southern England than in the north of Britain. This is an example of a common trend in many parts of the world, whereby species richness declines at higher latitudes (SCHALL & PIANKA, 1978). The thoroughness of recording has only recently become sufficient for more detailed patterns of species richness to be explored. The general pattern, of a decline in species-richness from S or SE to N or NW, is found in many taxa, and is correlated with several environmental factors (LAWTON et al., 1994). In Britain, many physical variables — temperature, rainfall, sunshine, topography, geology and soils — show a strong SE to NW gradient, the SE being warmer, drier, sunnier, predominantly lowland, with more basic rocks and alluvial soils (VINCENT, 1990; EVERSHAM & ROY, in press). Probably as a result of these trends in environmental factors, Odonata diversity 'hotspots' are concentrated in southern England, although several of the scarcer species are confined to the north (PRENDERGAST et al., 1993). Large-scale patterns in species-richness have thus been explained in terms of major gradients, whereas smaller-scale variations are considered to be due to current and historical land use (EVERSHAM, 1993; LAWTON et al., 1994). Diversity 'hotspot' distribution is probably caused by an interaction between the two.

Phytogeographers have previously suggested that the effects of climate are much greater than other factors (such as soil) in determining large-scale patterns of species distribution (CAIN, 1944; HILL & DOMINGUEZ-LOZANO, 1994). Some zoologists have proposed that solar energy input is the single factor responsible for latitude gradients in species-richness (TURNER et al., 1987). Recent concern about possible future climate change has focused attention on the relationship between species distribution and climate (United Kingdom Climate Change impacts Review Group [UK CCIRG], 1991; ASPINALL & MATTHEWS, 1994). Previous studies have illustrated a correlation between dragonfly species-richness and temperature (WATT et al., 1990), noting that the smoothed species-richness followed closely the pattern of April mean daily temperatures in southern England. For instance, all areas containing over 20 species were within the 9°C April mean isotherm (UK CCIRG, 1991). A correlation with spring temperatures made sense in terms of species ecology, because the season could be seen as a time-window between larval diapause and adult emergence. Many British species undergo a winter diapause, broken by temperature rise in spring (the threshold for recommencement of development varying between species) (CORBET, 1962). The main flight period of all but one British species, including 'boreal' species (see definitions below), begins between early May and mid-June; the exception is a recent colonist with a southern distribution, *Aeshna mixta*, which usually emerges from early July onward (MERRITT et al., 1996).

As a preliminary to a study modelling the patterns of species-richness in the flora and fauna of Britain with respect to a wide range of environmental variables (EVERSHAM et al., in prep.), the relationship between Odonata species-richness and temperature was examined. This was partly for its intrinsic interest, and partly as a sensitivity test of the choice of temperature variables for modelling.

RESULTS

MONTHLY TEMPERATURES AND DRAGONFLY RICHNESS

Figure 1 shows the recorded pattern of dragonfly species-richness in Britain, based on data summarised in MERRITT et al. (1996). It also indicates 4 latitude bands used in later analyses. Figures 2 and 3 show the pattern of temperature in summer (July--September mean) and winter (January-March mean), the choice of temperature variables following HILL & DOMINGUEZ-LOZANO (1994). The main difference between summer and winter spatial patterns of temperature in Britain is that summer shows a clear SE-NW gradient, which is confused in winter by a warm-coast (especially in the west), cold-interior effect. Thus, the SE has warmer summers but colder winters than the SW.

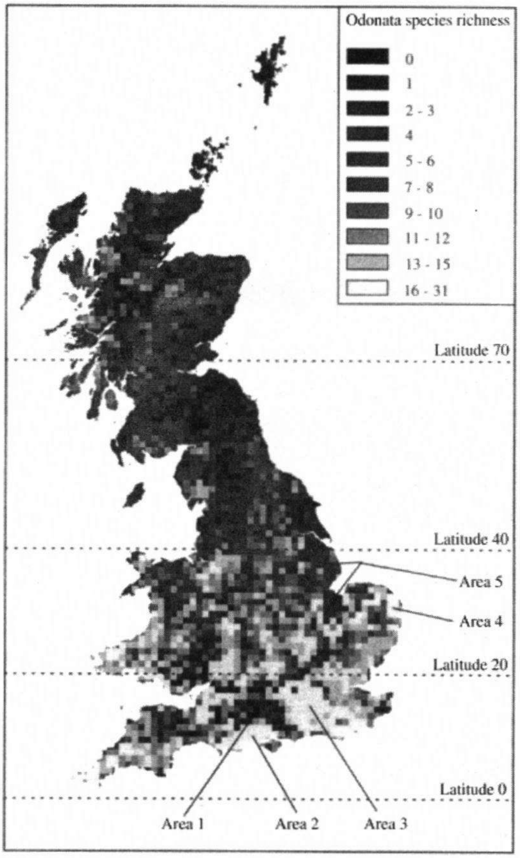

Fig. 1. Species-richness of dragonflies in Britain, shown as number of species in each 10×10 km square of the British National Grid. The lines of latitude shown are in National Grid units. Areas discussed in the text are: area 1= Salisbury Plain; area 2= Dorset heaths; area 3= Surrey heaths and New Forest; area 4= Norfolk Broad; area 5= intensive arable area of eastern England. Based on data in MERRITT et al. (1996).

Examination of maps of monthly mean temperatures suggested that certain months were much better correlated with dragonfly richness, but that this varied regionally. Table I shows the correlation between dragonfly richness and monthly mean temperatures, nationally and for the four latitude bands shown on Figure 1; these cor-

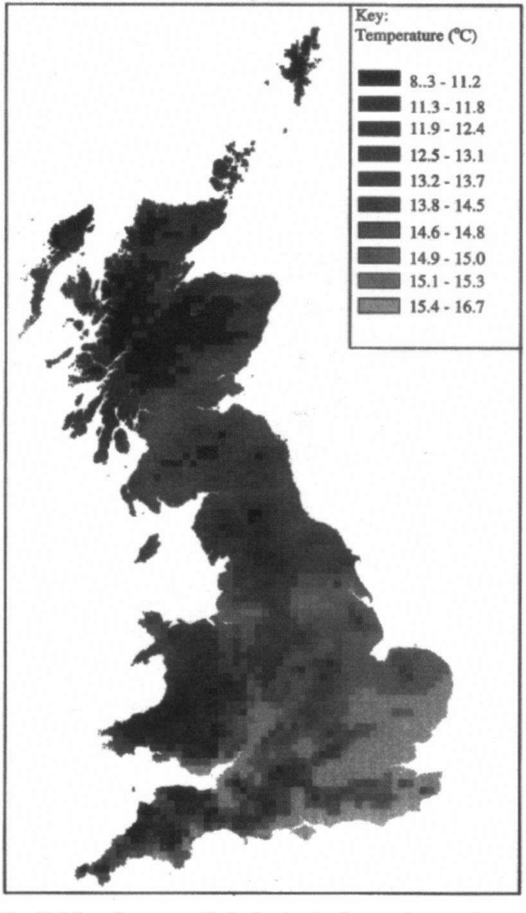

Fig. 2. Map of summer (July-September) mean temperature of 10×10 km national grid squares.

relations are plotted in Figure 4. Dragonfly richness and temperature are positively correlated at the national scale, and dragonfly richness varies much more closely with summer temperatures than with winter temperatures. Table II shows the correlations within the temperature data. The spatial patterns of most months are closely similar (coefficients mostly > 0.9), except when winter and summer are compared (coefficients of 0.6-0.7).

Summer temperatures are better predictors of dragonfly species-richness than winter, nationally and within each latitude band. In southern England and northern Scotland, the correlation with temperature in winter months is negative, albeit not significantly so. Although varying slightly with latitude, there is no clear tendency for the month of peak correlation to be later in the N than the S, as might hve been expected from trends in flight period, some species flying later in the N than the S (MERRITT et al., 1996). From Figure 4 it can be seen that dragonfly richness in the most northern latitude band (10 km squares N of 56°07'N) generally has the weakest correlations with mean monthly temperatures. However, these correlations are all non-significant, except May, June and July where $p < 0.01$ for each.

The weakness of correlation in northern Scotland was investigated further, by examining the faunal composition of the region. The dragonfly fauna of northern Scotland is more biogeographically divergent than elsewhere. At least four of the 20 resident species are boreo-montane (*Aeshna caerulea*) or more generally northern (*Coenagrion hastulatum, Somatochlora arctica, Leucorrhinia dubia*), and are rare or absent from southern Britain. A further two (*Aeshna juncea* and *Sympetrum* *danae*) are more frequent in the N than in the S in Britain and Europe (ASKEW, 1988; MERRITT et al., 1996) so are also likely to be to some degree cold-adapted, and their distributions might be expected to correlate negatively with temperature. (For convenience, this assemblage is referred to as 'boreal', although we recognise that most of the species also occur in mountains further south, and some have lowland southern populations). Conversely, most other species, such as *Coenagrion puella* and *Aeshna cyanea*, are more wide-ranging but generally southern in Britain, and probably require higher temperatures for development and activity. The two sets of species seldom co-occur in Scotland, so that total richness of dragonflies here is an amalgamation of separate subfaunas. To investigate this, the two groups were analysed separately. The correlations of these two groups with mean monthly temperatures are plotted in Figure 5. The southern group has a highly significant positive correlation with summer monthly temperatures (for each month May-August, $r > 0.12$, $n = 775$, $p < 0.01$), but no correlation with winter monthly temperatures (for each month November-March, $r < 0.03$, $n = 775$, $p > 0.5$). Conversely, the boreal group has a highly significant negative correlation with winter monthly temperatures (for each month November-March, $r < -0.17$, $n = 775$, $p < 0.01$), and no correlation with summer monthly temperatures, or a very weak negative correlation (for each month May-July, $r < 0.06$, $n = 775$, $p > 0.05$; August, $r = -0.09$, $n = 775$, $0.05 > p > 0.01$). Therefore, the species-richness of southern Odonata increases with increasing summer temperatures, and that of boreal spe-

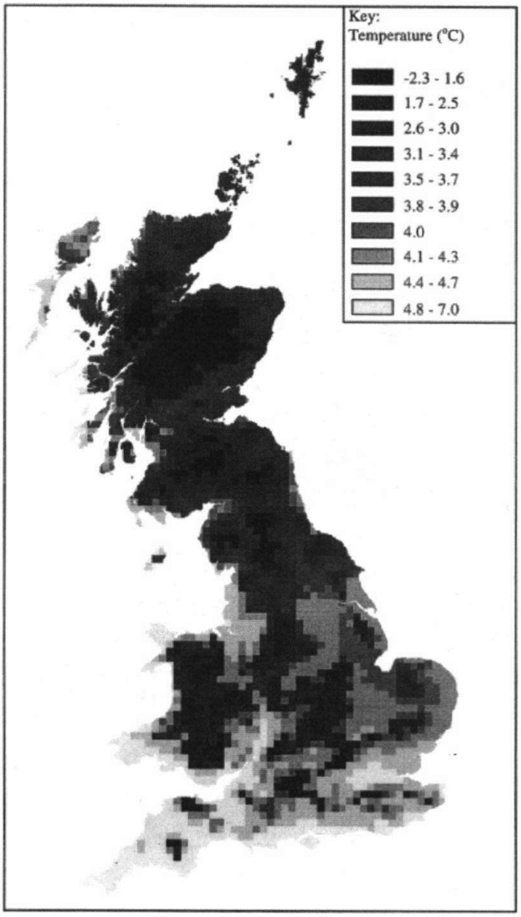

Fig. 3. Map of winter (January-March) mean temperature of 10×10 km national grid squares.

cies increases with decreasing winter temperatures. Overall, temperature is a strong predictor of dragonfly species-richness in Britain, explaining 34.1% of the variance (derived from the residuals of a log-linear regression fitted to the data using the least squares method in GENSTAT) in richness.

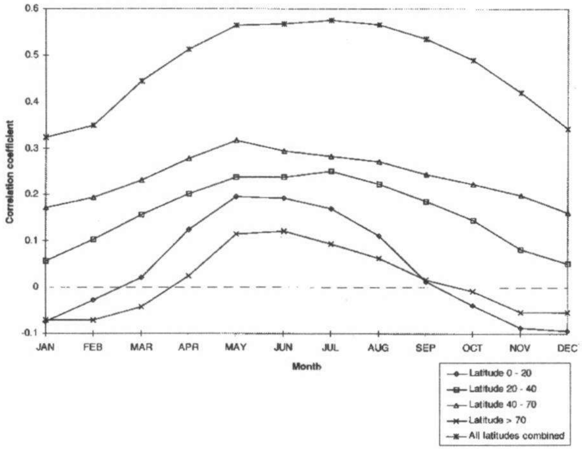

Fig. 4. Corelation between dragonfly richness and mean monthly daily temperatures for Britain as a whole and divided into four latitude bands based on the National Grid (cf. Fig. 1).

DISCUSSION

The lower absolute values of correlation coefficients in the latitude bands compared with the national dataset may be due simply to sample size and to the total climate range within each band. The seasonal effect is greatest in southern England, where a weak negative relationship with winter temperatures is probably due to the relatively low species-richness of dragonflies in the extreme SW, a region of mild winters but relatively cool summers.

The very weak correlations in all months of the northern Scottish latitude band is unlikely to be an artefact of lower recording effort (MERRITT et al., 1996). Rather, it arises from the combination of boreal and non-boreal species, which have increasing Odonata richness with decreasing winter and increasing summer temperatures respectively. TURNER et al., (1987), finding a negative relationship between mean winter temperature and

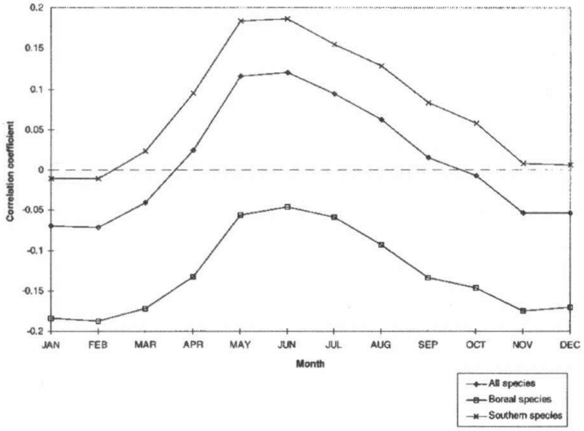

Fig. 5. Correlation between dragonfly richness and monthly mean daily temperatures N of the British National Grid latitude line 70 (cf. Fig. 1). — The boreal species are *Coenagrion hastulatum, Aeshna caerulea, Aeshna juncea, Somatochlora arctica, Sympetrum danae* and *Leucorrhinia dubia*. The southern species are all those not including the six boreal species.

Table I

Correlation between dragonfly richness and mean monthly temperature in 10 km squares for the whole of Britain and for four latitude bands based on the British National Grid. Correlations with summer (July-September) and winter (January-March) mean temperatures are also shown

Month	Latitude 0 - 20	Latitude 20 - 40	Latitude 40 - 70	Latitude > 70	All latitudes
January	-0.074	0.056	0.172	-0.070	0.324
February	-0.028	0.104	0.194	-0.071	0.349
March	0.022	0.157	0.231	-0.041	0.444
April	0.124	0.203	0.279	0.024	0.513
May	0.196	0.239	0.317	0.116	0.564
June	0.192	0.237	0.295	0.121	0.568
July	0.169	0.252	0.282	0.094	0.576
August	0.112	0.223	0.272	0.063	0.565
September	0.014	0.186	0.245	0.016	0.535
October	-0.039	0.145	0.223	-0.008	0.489
November	-0.087	0.082	0.198	-0.053	0.421
December	-0.093	0.052	0.161	-0.053	0.343
Summer (Jul-Sep)	0.105	0.225	0.268	0.060	0.563
Winter (Jan-Mar)	-0.034	0.110	0.202	-0.063	0.377

moth species-richness, suggested that mild winters were detrimental to diapausing moths because their energy reserves were depleted by a raised metabolic rate. The six boreal Odonata species, possibly being better adapted to lower temperatures, may become more active during mild winter weather than their non-boreal counterparts in northern latitudes. If food supplies are low in winter, activity would be detrimental to larval survival, and warmer winter temperatures may limit the distribution of boreal species. Conversely, the boreal species may be better adapted to low summer temperatures than the non-boreal species, resulting in a positive correlation between species-richness and summer temperature in the latter but not in the former. It is unfortunate that there appear to be no published data on the temperature thresholds for larval or adult activity in boreal dragonflies.

In other areas, the patchiness of dragonfly species-richness is not fully explained by temperature, and the effects of topography, geology, land use and habitat availability can be detected. For example, Salisbury Plain (area 1 in Fig. 1) is an extensive area of dry calcareous grassland, with very little standing or flowing water, and with very few dragonfly species as a result. The Dorset heaths and the New Forest (area 2 in Fig. 1) contain extensive acidic wetlands, as well as clean, base-rich rivers, supporting scarce species such as *Coenagrion mercuriale* and *Ceriagrion tenellum*. Area 3 comprises the heaths of Surrey, with *C. tenellum* and an outlying population of *Leucorrhinia dubia*, and the Weald, an area of clay and sand characterised by fast-flowing lowland rivers, abundant woodland, and rich lowland lakes and ponds, which form the British headquarters for *Cordulia aenea* and *Somatochlora metallica*. The Weald is bounded by the chalk hills of the North and South Downs, which support relatively few species of dragonfly. The Norfolk Broads and adjacent grazing marshes (area 4) comprise extensive fens derived from medieval peat digging, and rich lowland rivers and dykes, which support the only British populations of *Aeshna isosceles* and concentrations of *Libellula fulva* and *Brachytron pratense*. Much of the rest of eastern England (area 5) is very intensively farmed arable land, with few surviving wetlands.

It is not surprising that temperature is a strong predictor of dragonfly species-richness in Britain, in view of the gradient in species-richness at a European scale which may be deduced in broad terms from AGUILAR et al. (1986) and ASKEW (1988), both of which indicate far more Mediterranean than boreal species. It could also suggest that the paucity of the British fauna (40 spp., compared with 45 in Denmark, 64 in The Netherlands, 65 in Belgium and 81 in France [MERRITT et al., 1996]) is due as much to climatic factors as to Britain being an island (VINCENT, 1990; EVERSHAM & ARNOLD, 1992). If this were the case, then the predicted increase in British summer temperatures associated with global warming would be expected to permit the establishment in Britain of additional species from mainland Europe, if they are dispersive enough to arrive. Some, such as *Sympetrum fonscolombei* and *S. flaveolum*, have bred in the past (LONGFIELD, 1949), and arrived in large numbers in 1995, a year in which there were also large influxes of migrant Lepidoptera. Both species emerged from breeding sites in southern England in 1996, and it seems likely that this may be a permanent colonisation, at least until summer temperatures fall again.

Dragonfly species-richness is an important criterion in the selection of sites for conservation protection in Britain. Thresholds have been set for the number of species necessary if a site is to merit declaration as a Site of Special Scientific Interest on the grounds of its dragonfly fauna (NATURE CONSERVANCY COUNCIL, 1989). These are currently regional, based on political boundaries. This study suggests it should be possible to define such thresholds of importance based on local climate. For some purposes, it may be preferable to use a broader analysis of

Table II

Correlations between monthly mean daily temperatures of British 10×10 km National Grid squares

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan	1											
Feb	0.990	1										
Mar	0.931	0.963	1									
Apr	0.848	0.892	0.976	1								
May	0.735	0.790	0.917	0.978	1							
Jun	0.641	0.703	0.861	0.944	0.986	1						
Jul	0.610	0.672	0.837	0.923	0.973	0.995	1					
Aug	0.664	0.722	0.870	0.940	0.978	0.991	0.994	1				
Sep	0.759	0.806	0.920	0.962	0.975	0.969	0.968	0.987	1			
Oct	0.891	0.917	0.969	0.967	0.936	0.895	0.885	0.921	0.968	1		
Nov	0.969	0.971	0.963	0.919	0.845	0.776	0.759	0.807	0.882	0.97	1	
Dec	0.996	0.982	0.924	0.846	0.739	0.648	0.621	0.675	0.770	0.90	0.977	1

environmental factors (as in the definition of biogeographic zones, which are themselves based mainly on climatic factors [CAREY et al., 1995]), but this would be influenced by factors such as rainfall, which are of less significance to Odonata than to certain other taxa (EVERSHAM et al., in prep.).

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