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Comparison of trends in butterfly populations between monitoring schemes

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Abstract

Butterflies are an important indicator of the impacts of environmental change. Butterfly Monitoring Schemes have provided national and Europe-wide trends in their abundance and been widely used for research. Most schemes sample sites that are self-selected by contributors and therefore tend to cover locations that are rich in butterflies. To provide a more representative assessment of butterfly populations, the Wider Countryside Butterfly Survey (WCBS) was developed with a stratified-random sample of survey sites across the UK. We compare butterfly trends from the WCBS locations against those measured from traditional butterfly transects which are typically located in areas of good quality semi-natural habitats. Across the 26 species analysed, there was a significant positive relationship between trends measured from the two schemes between 2009 and 2013, the period when both schemes were operating fully. There was a tendency (17 out of 26 species analysed) for these changes to be greater within WCBS compared to traditional BMS transects, although this effect was not consistent across comparisons between pairs of consecutive years. When assessing these individual year-to-year changes, there was however a significant correlation between the two schemes in all cases. Over relatively short time periods, weather patterns are likely to dominate butterfly population fluctuations and lead to comparable trends across monitoring schemes. Over longer time periods, differences in land management may affect habitat condition differently for protected areas versus the wider countryside and it is therefore important to maintain comprehensive butterfly monitoring programmes to detect and interpret such effects.

Introduction

Parties to the United Nations (UN) Convention on Biological Diversity (CBD) recognise the need to reduce the rate of biodiversity loss (CBD 2010). Monitoring of species' populations is one of the key biodiversity variables for measuring progress against national goals and targets for conserving biodiversity (Pereira et al. 2013), as well as providing the additional benefits of being a rich resource for fundamental research (Fisher et al. 2010), policy and conservation management (Pereira et al. 2012).

Monitoring by standardised counts has been successful for a limited set of taxa but remains severely geographically restricted, with most programmes operating in developed countries (Pereira et al. 2010). Insect populations pose particular problems for monitoring as they are species-rich (representing an estimated 50-60% of all known species on earth) and require specialist skills for many families (Brereton et al. 2011a; Thomas 2005). The role of insect monitoring for measuring biodiversity change is recognised by the growing body of literature about the processes driving change in insect populations (Dempster and McLean 1998) and evidence that well-studied groups of insects are representative of obscure ones (Thomas and Clarke 2004). Insects play a key role in many ecosystem functions and key links in food webs, including as a major food resource for insectivorous animals (Strong et al. 1984).

Butterflies are the insect group for which monitoring of trends has proved most tractable, at least in some parts of the world. Butterflies have been advocated as indicator taxa due to their rapid and sensitive responses to habitat and climate change, and their potential to represent change in other wildlife, especially insects (e.g. Thomas 2005). Several butterfly species which reach their northern range margin in Britain have expanded their range in the past four decades, in common with other insects (Chen et al. 2011; Hickling et al. 2006), linked to improved climatic conditions (Warren et al. 2001). However, butterfly species with more specialised habitat requirements have decline over a similar period through the loss of habitat. As a group, butterflies are contracting more rapidly than either birds or plants in Great Britain (Thomas et al. 2004), emphasising their potential importance for assessing the status of biodiversity beyond more charismatic groups.

Schemes to measure relative change in the abundance of butterflies were established in the 1970s (Pollard 1977) and have expanded to more than 20 countries around the world, although predominantly within Europe and North America. Sampling is predominantly undertaken by volunteer contributors, continuing the rich tradition of citizen involvement (especially by amateur experts) in monitoring (Miller-Rushing and Primack 2008). Citizen science, including participatory schemes for monitoring butterflies, is increasingly being recognised as the only practical way of gathering the biodiversity data required to identify and address large-scale, long-term changes in biodiversity (Hochachka et al. 2012).

One of the disadvantages of volunteer-based monitoring schemes, and citizen science more generally, is potential bias, particularly if contributors are given a free choice in where to survey, leading to geographic bias in results (Gregory et al. 2005). For most butterfly monitoring schemes, volunteer recorders undertake sampling at locations they select which leads to a tendency to monitor areas rich in butterflies. Such a bias has provided good coverage of sites with environmental protection and semi-natural habitats that support butterfly diversity, but may not provide representative trends in species that are common elsewhere. In the heavily-modified landscape of the United Kingdom, evidence suggests that declines in many butterflies away from sites protected for nature conservation were largely undetected by monitoring and mapping schemes (Cowley et al. 1999).

Intensively farmed areas dominate the UK landscape yet are typically under-represented by butterfly monitoring schemes, mainly because they support a relatively depauperate butterfly fauna. Voluntary recorders are often reluctant to sample in areas where they see only a few individuals of a few common species, particularly when a high level of within-season repeat sampling is required; long-established butterfly monitoring schemes advocate weekly sampling throughout the main season of butterfly activity (26 weeks in the United Kingdom). Increasingly, the need for surveys to cover all regions and habitats appropriately is being recognised by conservationists; for example the (intensive, self-selected) Common Birds Census was replaced by the less intensive, but more representative, BTO/JNCC/RSPB Breeding Bird Survey (BBS) based on randomly selected sites (Freeman et al 2007). To address the limitations of traditional butterfly monitoring schemes, a stratified-random sampling schemes with less within-year sampling has therefore been designed (Roy et al. 2007) and implemented within the United Kingdom as the Wider Countryside Butterfly Survey, WCBS (Brereton et al. 2011b). The design of the survey closely matches that of the BBS, and indeed many of the sites are common to both.

This paper compares year-to-year growth rates in butterfly populations between 2007 and 2013 from the WCBS and traditional transects, hereafter termed traditional Butterfly Monitoring Scheme transects (also referred to as Pollard Walks). The WCBS was launched in 2009 following two pilot years and we compare year-to-year and overall population growth rates (2007-2013) for the scheme with those of the traditional BMS at the same time of the year. This comparison is undertaken to assess whether differences are apparent in butterfly trends between the two networks of sites, and to provide a basis for producing representative assessments of butterfly population trends in the UK by combining data from both surveys (Dennis et al. 2013).

Methods

Traditional Butterfly Monitoring Scheme (tBMS)

The first national scheme to monitor butterflies was initiated in the United Kingdom in 1976. The scheme is based on a standardized method, described in detail elsewhere (Pollard & Yates 1993). A fixed transect route is walked at least once a week from 1 April to 29 September, under defined weather conditions and at specified times of the day when adult butterflies are active. Every sighting of each species made in an imaginary, fixed 5-m box around the recorder is counted. Transect routes are 1.9km long on average (median) and therefore cover multiple 1km grid squares; we use the central 1km grid reference to characterise the coverage of the network. Traditional BMS transect routes are established by recorders, with only general guidance provided by the scheme co-ordinators. In this paper, we label the traditional BMS transects using the acronym tBMS.

Wider Countryside Butterfly Monitoring Scheme (WCBS)

The key difference between the Wider Countryside Butterfly Survey (WCBS) and traditional BMS is that volunteer surveyors are allocated a randomly selected 1 km^2 square within their local region (Brereton et al. 2011b). WCBS locations are selected at random, with a larger number of 1km grid squares surveyed in regions with a higher density of recorders (the strata for selection). A total of 755 grid squares were surveyed in 2009 (Figure 1), the launch year for the scheme; the scheme had two pilot years in 2007 and 2008, with reduced sampling. Within each grid square, two parallel, 1 km long, fixed transects were established. Volunteers walked these transects twice within July and August (additional visits are also permitted outside these months) with most other aspects of the survey the same as for traditional transect, i.e. weather and time of day criteria and line sampling criteria (Brereton et al. 2011b). A further difference of the WCBS is the strip-width of the linear transect is 10m (5m each side of the recorder) as opposed to 5m (2.5m each side of the recorder) for the tradition BMS.

Data selection

Other than selection of sites and line transect length, the two surveys of the UKBMS are equivalent and therefore the data arising are similar in form. Analysis of seasonal insect population abundance requires account to be taken of pronounced variation in numbers across the season, commonly via the estimation of a seasonal correction factor (Dennis et al. 2013; Matechou et al. 2014; Rothery and Roy 2001). For this reason, and as the WCBS is nominally restricted to two visits in the months of July and August (though there are limited additional data from beyond this period), data in this analysis are restricted to these months only. The WCBS dataset therefore comprises 1 or 2 visits per year whereas the traditional BMS dataset comprises between 1 and 8 weekly visits. We restrict analysis to the years covered so far by the scheme (2007-2012, including 'pilot' years for which a reasonable amount of data are available). Due to differences in protocol (weekly visits for the traditional BMS, compared to monthly for the WCBS), more data is available for the traditional BMS although the number of sites within each species is similar (~750-1000 sites sampled each year for both schemes). We restrict analysis to species occurring in more than 25 sites in each network.

In order to explore regional differences in habitat coverage, we assign all UKBMS (WCBS and tBMS) 1km sites to seven Environmental Zones defined for the UK (Carey et al. 2008). In order to characterise the habitat coverage of the two schemes, we summarise the land cover of all 1km grid cells covered by the UKBMS surveys (WCBS and tBMS) using the Centre for Ecology & Hydrology Land Cover Map (Morton et al. 2011).

Statistical model

We adopt a simple Poisson-based model for the data of each survey. The expected total counts of a species made in a total of $v_{i,t}$ visits in year *t* to site *i* are defined as $\mu_{i,t}$. We further assume that annual proportional changes in abundance over consecutive years are identical at all sites in a survey. They are however permitted to vary over time, such that the ratio of expected counts, per visit made, in years *t* and *t*+1 can be written as follows:

$$\log\left(\frac{\mu_{i,t+1}/V_{i,t+1}}{\mu_{i,t}/V_{i,t}}\right) = R_t$$

We require therefore the estimates of annual growth R_t. In the form of equation (1), the model is impractical to fit; the ratios of consecutive counts observed are undefined wherever the count in year *t* is zero or (as is often the case) the site was not visited during that year. Merely to omit such cases from the analysis would lead to the discarding of a considerable amount of useful data. However, if we further define $\mu'_{i,t} = \mu_{i,t} / v_{i,t}$ then $\log(\mu_{i,1}) = \log(\mu'_{i,1}) + \log(v_{i,1})$ and, after some algebra we have a more tractable expression of the same model for any t as follows:

$$\log(\mu_{i,t}) = \sum_{j=1}^{t-1} R_j + \log(\mu'_{i,1}) + \log(v_{i,t})$$

Equation (2) expresses any log-transformed expected count in year t as a simple linear combination of unknown parameters, with the similarly transformed number of visits $v_{i,t}$ (which may vary between sites and years) as a standardising offset (*cf*. Freeman and Newson, 2008). These parameters, and most usefully the annual growth rates R_t, are thus readily estimated and compared across surveys by fitting to observed counts for all sites and years via any of the many standard Generalized Linear Model (GLM) software packages. Specifically, 'unknown' counts in years lacking visits can thus be safely ignored.

Butterfly counts are highly variable in their nature and the goodness-of-fit of such models, in which annual trends are constrained to be identical at all sites, is in formal terms rarely good. We therefore adjust standard errors and hypothesis tests rescaling by the Pearson Chi-squared statistic in the standard, 'quasiPoisson' fashion, to compensate for overdispersion.

Maximum likelihood estimates $\hat{R}_t$ of the growth rates under the two surveys in a given year t can be compared, using confidence limits based upon their associated estimates of asymptotic standard error, also available from the standard GLM software. We use these to estimate the difference in growth between the two surveys, log-transformed, defined as $d_t = R_t(\mathrm{WCBS}) - R_t(\mathrm{tBMS})$ along with its 95% Confidence Limits. Where the confidence limits of the difference between the two surveys d_t include zero, we conclude that there is no significant difference between their population change estimates for the year in question.

We also have a ready comparison of the net change *N* over the five years 2009-2013 under the two surveys, since, for either survey:

$$\hat{N} = \sum_{t=1}^{4} \hat{R}_t \; ; \qquad \mathrm{var}\left(\hat{N}\right) = \sum_{t=1}^{4} \mathrm{var}\left(\hat{R}_t\right) + 2\sum_{t=1}^{4}\sum_{k=1}^{t-1}\left[\mathrm{cov}\left(\hat{R}_t, \hat{R}_k\right)\right]$$

and as the annual estimates of growth are independent between surveys confidence limits for the difference in *N* between the two can be examined and found to include zero or otherwise, giving a test of equality between surveys as above.

Results

Within lowland England and Wales (Environmental Zones 1 & 2), traditional BMS transects are predominantly located within areas of relatively high cover of broadleaved woodland and sub-urban land cover, with typically correspondingly lower cover of arable land (Figure 1; Table 1). In contrast, WCBS samples in lowland areas are similar to the average values for the region, as would be expected from a random sample of locations. Within upland regions, 1km grid squares sampled by traditional BMS transects and the WCBS are both characterised by relatively low cover of montane habitats. Within upland regions, sampling locations for the WCBS tends to have relatively high cover of arable land and coniferous woodland (Table 1).

Of the butterfly species included in the analysis, there was no overall clear tendency for mean counts (per km of line transect per visit) during the survey period (July and August) to be higher on one survey versus the other, in spite of the minor difference in protocol; 14 out of 26 species had higher counts for WCBS versus traditional BMS transects. Species with notably higher mean counts within WCBS survey squares included the three *Pieris* species: *P. brassicae, P. napi* and *P. rapae*. In contrast, *Nymphalidae* tended to have higher counts within traditional BMS survey locations, i.e. *Maniola jurtina, Aphantopus hyperantus* and *Erebia aethiops* (Table 2). It should be noted, however, that abundance estimates between the two schemes may not be directly comparable. The Wider

Countryside Survey typically samples public rights of way due to the practical difficulties of accessing land within randomly-located 1km grid squares; traditional transect routes are likely to be more representative of habitat parcels. Difference in the visibility of butterfly species between habitats can also affect their detectability (Dennis et al. 2006) and ideally is taken into account when comparing population abundance between schemes. Analysis of differences in growth rates between the two schemes, the primary aim of this manuscript, is not affected by these factors.

For all but one species (*Erebia aethiops,* the only predominantly Northern species considered), the number of sites where species were recorded was markedly higher for the traditional BMS survey; mean number of sites per species of 601 for WCBS and 951 for the traditional BMS. The number of samples (visits) was approximately ten times higher for the BMS survey than the WCBS survey with mean number of samples per species of 24,485 and 2306 respectively (Table 2).

Over the period since the WCBS became fully operational following its full launch in 2009, 12 species had a significantly positive and 5 had a significantly negative change in abundance (Table 2) for this scheme. More species had significant growth rates over this period when sampled by traditional BMS transects, suggesting higher power for this scheme for detecting trends; 15 and 8 species showed a significant positive or negative change respectively over this period. For most species, change was similar between the two schemes, being negative or positive for both surveys over the 2009 to 2013 period. For only 2 species were changes significantly different from zero and in opposite directions for the two schemes. *Polyommatus icarus* declined within WCBS sites yet increased within traditional BMS transects over this period. In contrast, *Pyronia tithonus* had positive population growth within WCBS sites over the period yet negative growth rate within traditional BMS transects (Table 2).

There was a significant overall correlation ($\rho = 0.75$, $p < 0.001$) between the population change from the two sampling schemes over the period 2009-2013 (Figure 2). The confidence intervals of the growth rate estimates are larger for the WCBS compared to the traditional BMS (mean CIs: WCBS = 0.43; tBMS = 0.14), likely to be caused by fewer sampling visits per year for this scheme.

When assessing individual year-to-year changes, there was also a significant correlation between the two schemes (Figure 3), and similarly between 2007/2008 and 2008/2009 when the WCBS was being piloted and therefore relatively few locations were sampled. *Vanessa cardui* is a notable outlier when comparing growth rates between 2008 and 2010 (Figure 3). The significant correlation between population change from the two schemes remains when this species is excluded. *V. cardui* is migratory in the UK, arriving each spring from populations that emerge in North Africa or Southern Europe. Numbers arriving in the UK fluctuate markedly from year to year, depending on conditions in natal areas. Vast numbers arrive in some years, with recent migrant events occurring in 1996 and 2009. Growth in numbers of *V. cardui* during the invasion event of 2009 was higher on traditional BMS sites than Wider Countryside Survey transects.

For the period 2009-2013, there was a slight tendency for change to be greater within WCBS than for traditional BMS transects with for 17 (65%) of the 26 species analysed showing this difference (Table 3). Of the 15 species with a significant difference between the two surveys, 12 had a significantly higher growth rate within WCBS survey locations. However, there was no species where the difference in growth rates was in the same direction for all individual year-to-year comparisons (Table 3) showing a lack of consistency in this result. When restricted to significant growth rates, there was some consistency in effects with *Polyommatus icarus* and *Celestrina argiolus* having significantly lower growth rates for the WCBS. The three species with a significantly higher growth rates 2009-2013 within traditional BMS transects over 2009-2013 were *Pieris rapae*, *Polyommatus icarus* and *Erebia aethiops* (Table 3).

When assessing year-to-year growth, for most years there is a relatively even split between higher growth rates for species on one scheme or the other (Table 3). For three year-to-year comparisons (2009/10, 2010/11 and 2011/12), the majority of species had higher growth rates greater on WCBS sites compared to traditional BMS transects. Notably, between 2011 and 2012, growth rate was higher on WCBS transects for 17 out of the 26 species analyses, 11 significantly so.

In contrast, growth rates were higher on traditional BMS transect sites between 2008 and 2009 for 19 out of 26 species, with this difference statistically significant for 8 species.

Discussion

There is no strong evidence from this analysis that there is a systematic difference in butterfly population trends between locations sampled by the two UKBMS schemes – the Wider Countryside Butterfly Survey and traditional BMS transects. Comparing species' trends over the main period for comparison (2009-2013), when both schemes were operating fully, there was a strong positive relationship in butterfly population trends between the two schemes. There were only two (out of 26) species where significant trends 2009-2013 for the two schemes were in opposite directions, i.e. a significant decline for one scheme and a significant increase for the other. However, there were no species for which growth rates differences were consistent for all comparisons over consecutive years; all species performed better on either scheme at some time during the period of analysis.

The relative consistency in trends between the two UKBMS schemes suggests that previous results based solely on analysis of the traditional BMS sites are likely to be validated (for most species) by the Wider Countryside Butterfly Survey. Monitoring data has been a rich resource for assessing the impacts of climate change (e.g. Oliver et al. 2013; Roy and Thomas 2003), habitat management (Woodcock et al. 2012) and conservation policies (Brereton et al. 2008) for example. However, there is considerable scope for using the combined UKBMS surveys to understand further the impact of environmental change on butterfly populations using a more representative sample of the UK. A particular advantage of the combined UKBMS datasets is good coverage of both protected areas and the wider countryside. Although protected areas have been shown to facilitate range expansion (Thomas et al. 2012) and support higher population sizes than non-protected areas (Gillingham et al. 2014), there is a lack of evidence of the influence of site protection on population dynamics (i.e. improved population trends or stability of populations). Similarly, data from the combined datasets enables future studies to investigate the effects of habitat composition and configuration (i.e. fragmentation) and land management on butterfly population trends; previous studies addressing these questions have been limited to the traditional UKBMS sites which predominantly sample semi-natural habitats.

Although trends between the two surveys are broadly similar, it should be noted that the traditional BMS enables trends to be reported for a wider set of species, particularly those with smaller ranges and/or tending to occur in rarer habitats which are not sampled sufficiently by the stratified-random set of WCBS locations. The traditional BMS enables trends to be estimated for 56 species for example, compared to the 26 species reported in this paper. The WCBS also has lower power for detecting trends in populations due to fewer visits within the season and therefore greater error in estimates of annual growth rates (Roy et al. 2007). Therefore, a comprehensive UKBMS is ideally composed of both surveys, realising the beneficial features of each. Combined data from the two schemes is also invaluable for assessing the spatial distribution and abundance of butterfly populations (Oliver et al. 2012a), particularly when combined with opportunistic recording data (Pagel et al. 2014). The improved coverage of habitats achieved by combining the WCBS and the traditional BMS transect scheme offers potential for estimation of population abundance on a regional basis. However, although the WCBS improves sampling of previously under-represented habitats such as arable farmland and urban areas, the transect route typically follows public rights of way through sample 1km grid squares. Random location of transect routes within a larger 1km grid square was shown to not impractical during the design of the scheme (Brereton et al. 2011b). Models to upscale UKBMS data for population estimates therefore need to account for habitat coverage, as well as differences in the detectability of species (Dennis et al. 2006).

Butterflies population size and annual fluctuations are known to be strongly affected by climate and weather (Oliver et al. 2012b; Powney et al. 2010; Roy et al. 2001); over the relatively short time periods available for comparison here, weather effects are therefore likely to dominate year-to-year population changes. Given summer temperatures typically show a high degree of similarity between locations (i.e. high spatial autocorrelation), we expect UKBMS sites for both schemes (WCBS and traditional BMS) to experience similar conditions within a year. Annual changes in butterfly population size are therefore likely to be broadly similar between the two schemes over short time-periods, as demonstrated here. Such a result is particularly likely for relatively mobile species which can disperse across the UK landscape. Such 'wider countryside' species are those predominantly sampled by the WCBS (Brereton et al. 2011b) and therefore form the basis of the analyses presented here.

Habitat availability and quality are also known to strongly affect butterfly populations (Warren et al. 2001). Habitat associations of butterflies have been shown to vary across geographic ranges (Oliver et al. 2009) with several species restricted to a narrower set of habitats towards the northern edge of their distribution in Britain. Monitoring data have also shown that the range of habitats used by butterflies in Britain has reduced over the last 40 years, despite predicted expansions in associations through recent climate warming (Oliver et al. 2012c).

Effects of habitat change and associated interactions with climate (Oliver and Morecroft 2014) are typically subtle and have the greatest effects on species which are specialised to localised habitat conditions – species that were not analysed here as they do not occur frequently within WCBS samples. For widespread butterfly species, populations are likely to be sensitive to management of habitats that are common in the landscape, such as farmland. Within the European Union, considerable financial resource is allocated to enhancement of the farmed environment through the Common Agricultural Policy, although the effectiveness of these measures for biodiversity have come into question (Pe'er et al. 2014) unless they are well-designed and implemented effectively (Pywell et al. 2012). Evidence is lacking as to whether such schemes are having a positive effect on butterfly populations. If effective, we would predict butterfly population trends in the wider countryside (where agri-environment schemes are implemented) to be better than within other habitats. Although from this initial assessment we find no evidence of improved trends in the wider countryside versus semi-natural habitats that might be evident if management of the farmed environment agri-environment was effective, it is important that monitoring schemes are in place to undertake robust assessments.

Butterfly populations have declined in the UK, markedly since the turn of the 20th Century but also within the more recent period since standardised monitoring began in 1976 (Fox et al. 2006). The decline in the distribution of butterflies has been more marked than for other well monitored taxa, birds and vascular plants (Thomas et al. 2004), stressing the importance of effective monitoring of insects to provide a more representative assessment of the status of biodiversity. The two component sampling schemes of the UKBMS estimate similar population trends for relatively common and widespread species. Together, these schemes provide a strong framework for future assessments of butterfly populations.

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Figure 1. Location of UKBMS survey squares for two surveys in 2009. Environmental Zones as defined in Carey *et al.* (2008). Solid symbols represent locations of traditional BMS sites; open circles are locations of Wider Countryside Butterfly Survey sites.

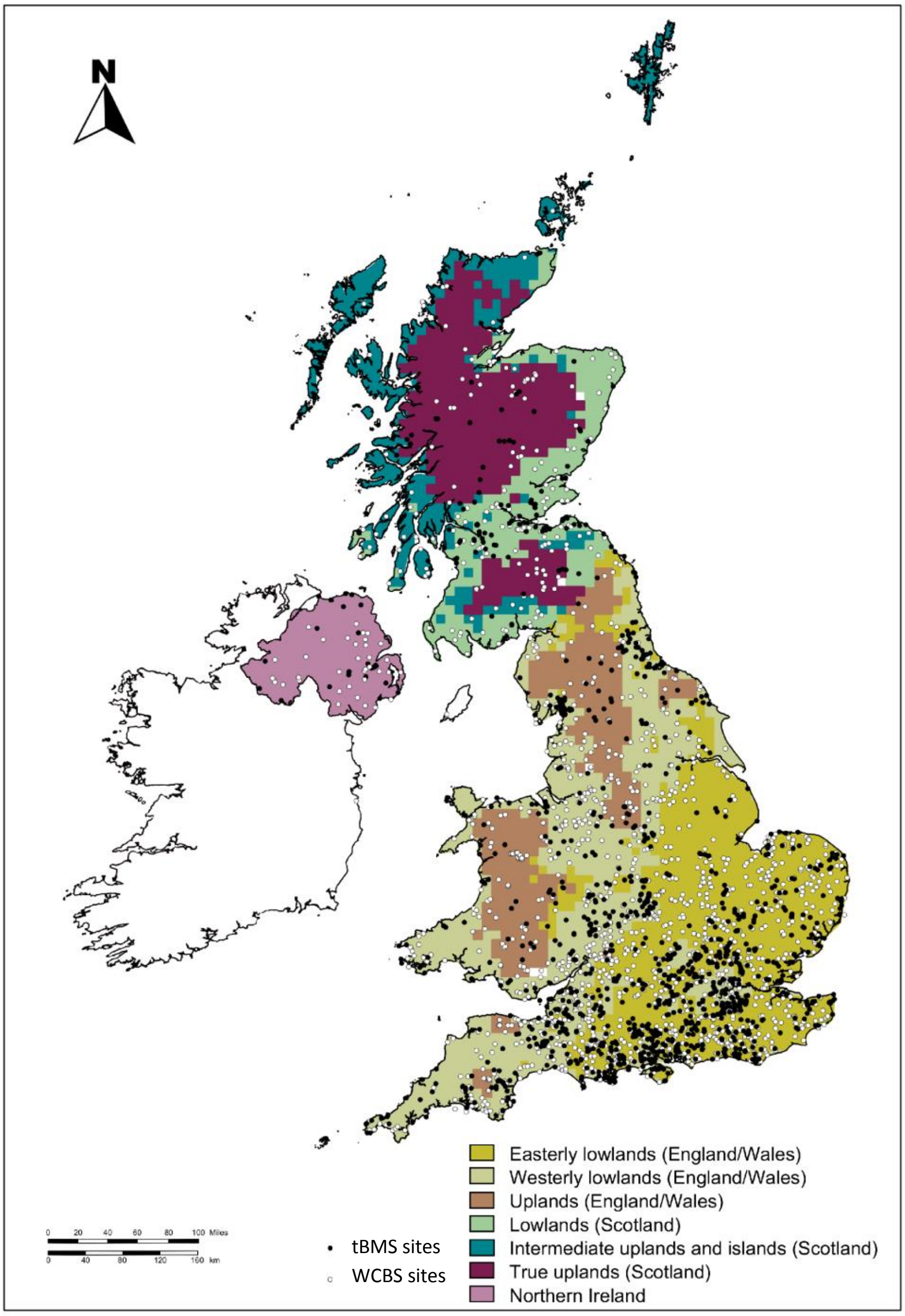

Figure 2. Comparison of log (growth rates) from 2009 to 2013 of the two surveys for 26 species analysed. Solid lines to indicate zero growth for the WCBS (vertical) and tBMS (horizontal) are shown; the dashed line indicates the line of unity where growth rates are equal for the two schemes. Bars represent 1 standard error.

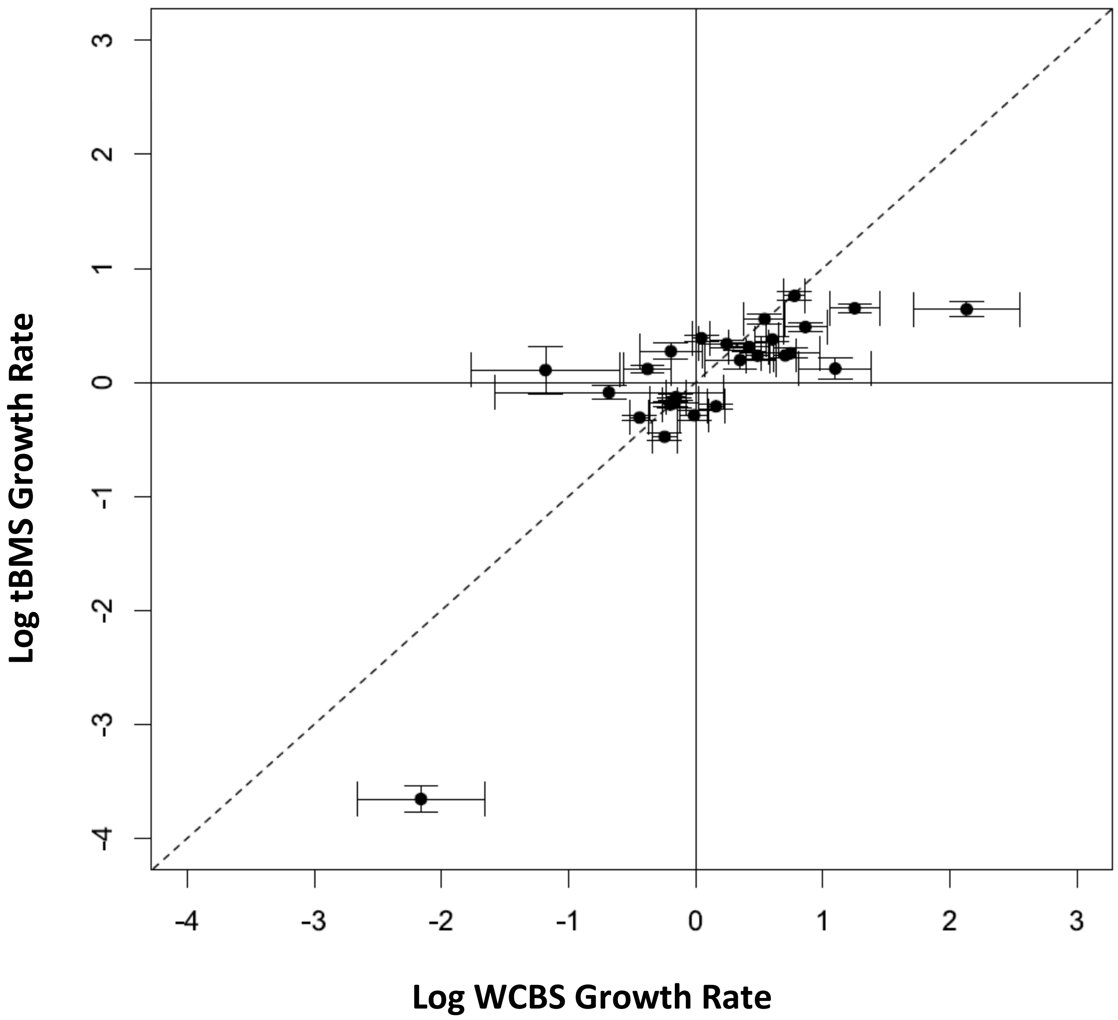

Figure 3. Comparison of year-to-year growth rates from 2007 and 2013 of the two surveys for 26 species analysed. ; the dashed line indicates the line of unity where growth rates are equal for the two schemes. Bars represent 1 standard error.

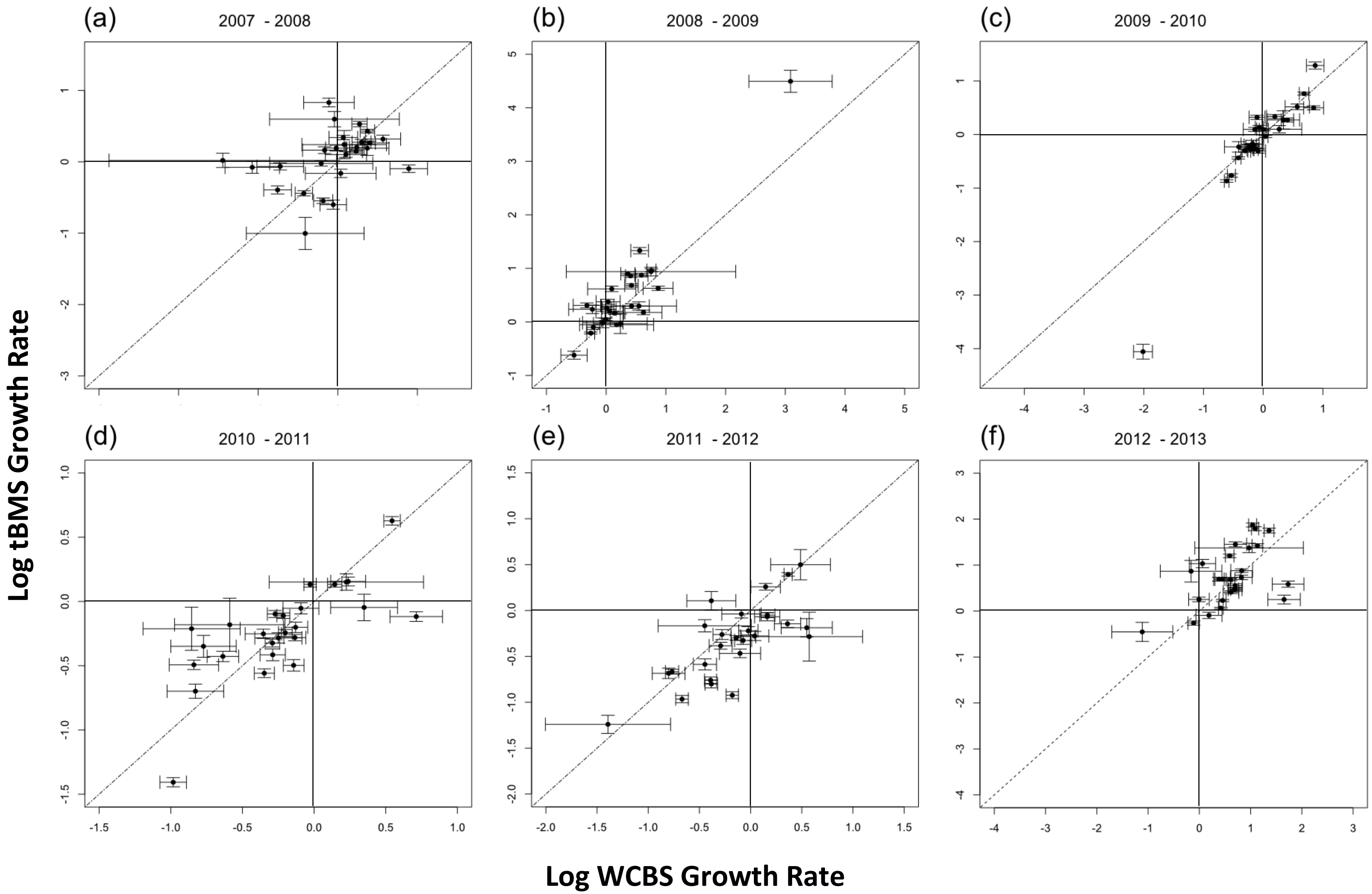

Table 1. Mean (SE) cover of habitat types (%) for 1km squares sampled by the traditional BMS transects (n=1220) and WCBS survey squares (n=1408) during the period 2007-2013. Mean cover for all 1km squares in the UK are included for comparison (n=264002). Habitat data from the CEH Land Cover Map 2007 (Morton et al. 2011).

(table overleaf to fit on a single page)

[a] Fen, Marsh and Swamp & Bogs

[b] Salt water and freshwater

[c] Littoral and supra-littoral rocks and sediments (sand dunes, saltmarsh)

Zone Scheme	Broadleaved woodland	Coniferous woodland	Arable and horticulture	Improved grassland	Natural grassland	Wetland[b]	Heath	Montane habitats	Inland rock	Water[c]	Coastal habitats[d]	Urban - Suburban
Zone 1. Easterly lowlands (England/Wales)												
tBMS	20.16 (0.86)	3.30 (0.41)	28.82 (1.06)	26.21 (0.87)	7.00 (0.40)	0.78 (0.30)	2.01 (0.37)	0.00 (0.00)	0.43 (0.09)	1.33 (0.25)	0.31 (0.14)	9.52 (0.70)
WCBS	10.02 (0.56)	2.93 (0.45)	48.95 (1.20)	26.35 (0.82)	4.23 (0.29)	0.03 (0.01)	0.54 (0.16)	0.00 (0.00)	0.37 (0.09)	0.58 (0.12)	0.18 (0.10)	5.92 (0.54)
all zone	7.87	1.68	53.37	24.06	4.90	0.13	0.56	0.00	0.26	0.75	0.37	5.94
Zone 2. Westerly lowlands (England/Wales)												
tBMS	18.27 (0.88)	3.48 (0.43)	21.34 (0.96)	28.50 (0.96)	7.08 (0.47)	0.98 (0.32)	1.52 (0.27)	0.00 (0.00)	0.62 (0.14)	1.78 (0.26)	4.62 (0.67)	9.22 (0.76)
WCBS	9.01 (0.63)	2.35 (0.32)	33.44 (1.27)	34.82 (1.10)	7.55 (0.43)	0.19 (0.16)	0.74 (0.20)	0.00 (0.00)	0.35 (0.11)	1.20 (0.24)	1.52 (0.36)	7.97 (0.84)
all zone	7.24	2.09	33.2	35.33	7.18	0.17	0.90	0.00	0.33	1.36	2.43	7.56
Zone 3. Uplands (England/Wales)												
BMS	9.88 (1.53)	7.37 (2.33)	8.43 (2.06)	31.22 (3.91)	24.24 (2.78)	3.45 (2.31)	8.96 (1.77)	0.00 (0.00)	2.39 (1.58)	1.29 (0.71)	0.00 (0.00)	3.06 (1.38)
WCBS	4.86 (0.70)	8.80 (1.61)	3.91 (0.73)	31.53 (2.65)	28.16 (2.24)	9.19 (2.23)	10.52 (1.68)	0.00 (0.00)	0.15 (0.06)	0.93 (0.42)	0.00 (0.00)	2.02 (0.63)
all zone	4.27	8.27	4.17	27.56	28.30	8.77	14.82	1.48	0.58	0.67	0.00	1.30
Zone 4. Lowlands (Scotland)												
BMS	13.42 (1.54)	13.29 (2.31)	11.28 (2.06)	21.25 (2.38)	9.88 (1.43)	1.07 (0.74)	3.08 (0.87)	0.00 (0.00)	0.76 (0.35)	5.97 (1.69)	5.60 (2.05)	13.07 (2.41)
WCBS	7.10 (0.97)	8.23 (1.68)	30.58 (3.28)	31.27 (2.46)	9.77 (1.19)	3.63 (1.59)	2.29 (0.53)	0.00 (0.00)	0.33 (0.12)	1.18 (0.46)	0.20 (0.11)	4.73 (1.49)
all zone	5.82	10.85	26.13	30.04	10.79	2.72	4.56	0.00	0.48	1.96	1.16	3.90
Zone 5. Intermediate uplands and islands (Scotland)												
BMS	9.68 (3.02)	13.88 (4.34)	2.36 (0.97)	16.68 (3.96)	16.12 (4.41)	1.12 (1.00)	9.60 (2.95)	0.00 (0.00)	0.48 (0.25)	7.28 (3.26)	6.64 (2.42)	4.16 (1.79)
WCBS	4.38 (1.30)	20.83 (4.79)	5.29 (1.79)	14.69 (2.93)	17.85 (2.75)	6.75 (2.81)	22.00 (4.22)	0.00 (0.00)	0.44 (0.20)	1.73 (0.76)	2.23 (1.70)	1.48 (0.89)
all zone	2.62	11.22	2.91	10.67	17.20	14.24	18.91	0.15	0.91	3.52	2.67	0.59
Zone 6. True Uplands (Scotland)												
BMS	1.32 (0.45)	17.89 (6.73)	1.11 (0.67)	4.11 (1.93)	34.05 (6.77)	5.32 (3.15)	25.74 (5.78)	6.47 (4.99)	0.26 (0.21)	3.68 (2.35)	0.00 (0.00)	0.16 (0.12)
WCBS	2.29 (0.70)	32.92 (4.92)	2.94 (1.65)	4.54 (1.60)	21.02 (3.85)	3.63 (1.14)	27.67 (4.54)	2.29 (2.09)	0.54 (0.28)	2.15 (1.36)	0.00 (0.00)	0.21 (0.11)
all zone	1.69	13.04	0.84	3.66	26.51	9.04	28.29	14.00	1.03	1.91	0.01	0.09
Zone 7. Northern Ireland												
BMS	8.81 (1.83)	9.28 (2.77)	3.47 (1.00)	24.76 (4.79)	14.77 (3.53)	3.74 (2.94)	5.79 (1.92)	0.00 (0.00)	0.16 (0.11)	7.16 (3.03)	7.98 (3.97)	8.92 (3.05)
WCBS	3.01 (0.90)	2.42 (0.99)	6.49 (1.02)	58.18 (4.26)	13.50 (2.03)	1.83 (1.46)	5.59 (2.78)	0.00 (0.00)	0.90 (0.26)	1.96 (1.41)	0.12 (0.12)	5.96 (2.00)
all zone	1.79	2.16	2.87	23.47	6.52	3.06	2.42	0.02	0.32	2.50	0.30	2.13
UK (all zones)												
BMS	17.84 (0.55)	4.73 (0.35)	22.51 (0.67)	26.41 (0.61)	8.71 (0.36)	1.13 (0.23)	2.79 (0.27)	0.10 (0.08)	0.60 (0.10)	2.07 (0.21)	2.56 (0.31)	9.08 (0.47)
WCBS	8.45 (0.34)	5.25 (0.41)	35.09 (0.83)	29.27 (0.63)	8.92 (0.38)	1.49 (0.26)	3.40 (0.34)	0.08 (0.07)	0.36 (0.05)	0.96 (0.12)	0.63 (0.13)	5.76 (0.38)
all UK	5.17	5.71	23.84	23.43	12.41	4.20	8.01	1.86	0.50	1.64	1.07	3.93

Table 2. Sample size, mean count and estimated population change 2009-2013 for the two schemes. The number of sites for the two schemes are: WCBS – 1366 sites; tBMS – 1446 sites. Mean counts are standardised to number of individuals per 1km linear transect during July and August. A log (growth rate) of zero is a stable population, i.e. no change.

Species	Common name	WCBS			BMS		
		Sites (visits)	Mean Count (se)	Log (growth rate)	Sites (visits)	Mean Count (se)	Log (growth rate)
Thymelicus sylvestris	Small Skipper	415 (1490)	2.05 (0.32)	0.42**	891 (20717)	1.87 (0.04)	0.31***
Thymelicus lineola	Essex Skipper	168 (550)	1.06 (0.10)	1.10***	376 (6893)	0.71 (0.06)	0.12
Ochlodes sylvanus	Large Skipper	390 (1404)	0.88 (0.04)	0.86***	1056 (28583)	0.77 (0.02)	0.49***
Gonepteryx rhamni	Brimstone	319 (982)	0.55 (0.04)	0.24	952 (26728)	0.58 (0.01)	0.34***
Pieris brassicae	Large White	1140 (5020)	3.91 (0.10)	-0.20***	1305 (36332)	2.21 (0.04)	-0.19***
Pieris napi	Green-veined White	1061 (4373)	3.63 (0.10)	-0.15	1281 (34479)	2.28 (0.03)	-0.13***
Pieris rapae	Small White	1134 (4995)	5.18 (0.13)	0.05	1292 (36107)	2.62 (0.05)	0.39***
Lycaena phlaeas	Small Copper	482 (1449)	0.70 (0.03)	-0.16	1105 (26436)	0.59 (0.01)	-0.18***
Aricia agestis	Brown Argus	174 (504)	1.00 (0.10)	-0.68	576 (13304)	0.94 (0.03)	-0.09
Polyommatus icarus	Common Blue	643 (2192)	1.78 (0.08)	-0.38*	1192 (31653)	3.16 (0.06)	0.12***
Celastrina argiolus	Holly Blue	442 (1412)	0.60 (0.03)	0.35	982 (22790)	0.25 (0.01)	0.20*
Aglais urticae	Small Tortoiseshell	931 (3423)	1.60 (0.06)	0.78***	1221 (29640)	0.58 (0.02)	0.76***
Aglais io	Peacock	968 (3587)	1.33 (0.05)	0.49***	1306 (36509)	1.35 (0.04)	0.23***
Polygonia c-album	Comma	700 (2631)	0.66 (0.02)	-0.24*	1114 (30120)	0.49 (0.01)	-0.48***
Argynnis aglaja	Dark Green Fritillary	74 (185)	0.84 (0.11)	2.13***	383 (8205)	1.52 (0.06)	0.64***
Argynnis paphia	Silver-washed	126 (479)	1.26 (0.13)	0.75**	485 (11344)	1.98 (0.05)	0.26***
Pararge aegeria	Speckled Wood	955 (4079)	1.99 (0.05)	-0.44***	1196 (34147)	2.32 (0.03)	-0.31***
Lasiommata megera	Wall Brown	174 (530)	1.21 (0.13)	-0.19	418 (7978)	0.51 (0.02)	0.27***
Melanargia galathea	Marbled White	222 (743)	2.07 (0.20)	1.25***	657 (18392)	4.81 (0.11)	0.65***
Pyronia tithonus	Gatekeeper	991 (4656)	5.17 (0.13)	0.16*	1092 (32166)	8.02 (0.09)	-0.21***
Maniola jurtina	Meadow Brown	1213 (5462)	7.55 (0.17)	0.60***	1332 (37969)	17.42 (0.17)	0.38***
Aphantopus hyperantus	Ringlet	853 (3413)	5.06 (0.20)	0.71***	1164 (31277)	8.05 (0.14)	0.24***
Coenonympha	Small Heath	363 (1116)	1.60 (0.10)	0.54***	914 (21016)	1.92 (0.04)	0.56***
Erebia aethiops	Scotch Argus	63 (182)	10.88 (1.54)	-1.18	28 (674)	16.56 (1.39)	0.11
Vanessa atalanta	Red Admiral	944 (3490)	0.88 (0.02)	-0.01	1288 (34259)	0.57 (0.01)	-0.29***
Vanessa cardui	Painted Lady	675 (1607)	2.76 (0.24)	-2.16***	1121 (18887)	1.70 (0.09)	-3.66***

Table 3. Differences in (log) annual growth rates per year, R_t(WCBS)- R_t(tBMS), and in (log) total growth 2009-2013 with 95% Confidence Limits. Species with asterisks indicate a statistically significant difference ($p<0.05$).

Species	2007/08	2008/09	2009/10	2010/11	2011/12	2012/13	2009-2013
Thymelicus sylvestris	-0.33 (-0.89, 0.23)	0.44 (-0.17, 1.05)	0.22 (-0.03, 0.47)	-0.04 (-0.29, 0.21)	0.15 (-0.10, 0.40)	-0.24 (-0.54, 0.06)	0.11(-0.22,0.40)
Thymelicus lineola	0.18 (-0.38, 0.74)	-0.04 (-0.73, 0.65)	-0.12 (-0.67, 0.43)	0.18 (-0.37, 0.73)	-0.47 (-1.02, 0.08)	1.40 (0.74, 2.06)*	0.98(0.40,1.58)*
Ochlodes sylvanus	-0.65 (-1.23, -0.07)*	0.12 (-0.47, 0.71)	-0.23 (-0.52, 0.06)	-0.10 (-0.37, 0.17)	0.56 (0.29, 0.83)*	0.15 (-0.14, 0.44)	0.38(0.02,0.74)*
Gonepteryx rhamni	0.00 (-0.52, 0.52)	-0.15 (-0.61, 0.31)	-0.01 (-0.26, 0.24)	0.07 (-0.25, 0.39)	-0.09 (-0.48, 0.30)	-0.05 (-0.47, 0.37)	-0.09(-0.51,0.35)
Pieris brassicae	-0.26 (-0.47, -0.05)*	-0.20 (-0.37, -0.03)*	0.24 (0.14, 0.34)*	0.03 (-0.08, 0.14)	0.42 (0.27, 0.57)*	-0.70 (-0.86, -0.54)*	0.00(-0.13,0.11)
Pieris napi	0.03 (-0.22, 0.28)	-0.28 (-0.50, -0.06)*	0.00 (-0.11, 0.11)	-0.18 (-0.29, -0.07)*	0.76 (0.62, 0.90)*	-0.61 (-0.79, -0.43)*	-0.03(-0.19,0.13)
Pieris rapae	0.04 (-0.15, 0.23)	-0.45 (-0.62, -0.28)*	0.17 (0.07, 0.27)*	0.06 (-0.05, 0.17)	0.26 (0.11, 0.41)*	-0.83 (-1.01, -0.65)*	-0.34(-0.48,-0.20)*
Lycaena phlaeas	0.20 (-0.67, 1.07)	-0.53 (-1.32, 0.26)	0.15 (-0.08, 0.38)	-0.17 (-0.4, 0.06)	0.30 (0.01, 0.59)*	-0.26 (-0.66, 0.14)	0.02(-0.36,0.40)
Aricia agestis	-1.46 (-4.27, 1.35)	-0.19 (-2.98, 2.60)	0.05 (-0.35, 0.45)	-0.11 (-0.5, 0.28)	-0.13 (-1.34, 1.08)	-0.40 (-2.49, 1.69)	-0.59(-2.36,1.18)
Polyommatus icarus	-0.94 (-1.58, -0.3)*	0.24 (-0.26, 0.74)	-0.09 (-0.26, 0.08)	0.46 (0.27, 0.65)	-0.11 (-0.44, 0.22)	-0.75 (-1.19, -0.31)*	-0.50(-0.86,-0.12)*
Celastrina argiolus	-0.37 (-0.72, -0.02)*	0.08 (-0.37, 0.53)	-0.40 (-0.72, -0.08)*	0.18 (-0.02, 0.38)	0.08 (-0.18, 0.34)	0.28 (-0.23, 0.79)	0.15(-0.43,0.71)
Aglais urticae	0.54 (0.19, 0.89)*	-0.77 (-1.09, -0.45)*	0.02 (-0.14, 0.18)	0.35 (0.18, 0.52)*	0.05 (-0.16, 0.26)	-0.39 (-0.61, -0.17)*	0.02(-0.16,0.22)
Aglais io	0.37 (0.12, 0.62)*	-0.54 (-0.79, -0.29)*	0.29 (0.13, 0.45)*	0.06 (-0.14, 0.26)	0.20 (0.00, 0.40)	-0.29 (-0.5, -0.08)*	0.25(0.06,0.46)*
Polygonia c-album	-0.21 (-0.48, 0.06)	-0.26 (-0.48, -0.04)*	0.06 (-0.07, 0.19)	0.21 (0.05, 0.37)*	0.26 (0.08, 0.44)*	-0.31 (-0.52, -0.1)*	0.23(0.03,0.41)*
Argynnis aglaja	-0.99 (-1.67, -0.31)*	-0.46 (-1.26, 0.34)	0.38 (-0.47, 1.23)	0.19 (-0.86, 1.24)	-0.22 (-1.15, 0.71)	1.15 (0.53, 1.77)*	1.49(0.67,2.33)*
Argynnis paphia	0.99 (0.50, 1.47)*	-0.34 (-0.74, 0.06)	0.2 (-0.14, 0.54)	-0.24 (-0.56, 0.08)	0.45 (0.06, 0.84)*	0.09 (-0.33, 0.51)	0.49(0.05,0.95)*
Pararge aegeria	-0.06 (-0.24, 0.12)	-0.25 (-0.41, -0.09)*	0.01 (-0.08, 0.10)	0.02 (-0.09, 0.13)	-0.09 (-0.22, 0.04)	-0.08 (-0.25, 0.09)	-0.13(-0.29,0.01)
Lasiommata megera	-0.64 (-2.24, 0.96)	0.25 (-0.99, 1.49)	0.00 (-0.40, 0.40)	-0.38 (-0.86, 0.1)	0.89 (0.36, 1.42)*	-0.97 (-1.51, -0.43)	-0.47(-0.97,0.05)
Melanargia galathea	-0.19 (-1.47, 1.09)	0.22 (-1.00, 1.44)	-0.29 (-0.67, 0.09)	0.80 (0.44, 1.16)*	-0.12 (-0.41, 0.17)	0.21 (-0.09, 0.51)	0.60(0.21,0.99)*
Pyronia tithonus	0.08 (-0.08, 0.24)	-0.06 (-0.20, 0.08)	0.07 (-0.02, 0.16)	-0.09 (-0.20, 0.02)	0.17 (0.06, 0.28)*	0.22 (0.08, 0.36)*	0.37(0.23,0.51)*
Maniola jurtina	0.14 (0.00, 0.28)	-0.05 (-0.19, 0.09)	0.02 (-0.07. 0.11)	-0.15 (-0.24, -0.06)*	-0.00 (-0.09, 0.09)	0.36 (0.25, 0.47)*	0.23(0.13,0.33)*
Aphantopus hyperantus	-0.27 (-0.63, 0.09)	-0.03 (-0.35, 0.29)	-0.09 (-0.25, 0.07)	0.16 (-0.01, 0.33)	0.18 (0.03, 0.33)*	0.22 (0.05, 0.39)*	0.47(0.28,0.66)*
Coenonympha pamphilus	0.25 (-0.20, 0.70)	-0.63 (-1.09, -0.17)*	-0.43 (-0.72, -0.14)*	0.03 (-0.24, 0.30)	0.16 (-0.09, 0.41)	0.23 (-0.04, 0.50)	-0.01(-0.31,0.29)
Erebia aethiops	-0.16 (-1.27, 0.95)	0.27(-0.68, 1.22)	0.10 (-0.55.0.75)	-0.65(-1.41,0.11)	-0.07(-0.75,0.61)	-0.66 (-1.89, 0.57)	-1.29(-2.50,-0.06)*
Vanessa atalanta	0.01 (-0.22, 0.24)	-0.12 (-0.35, 0.11)	-0.17 (-0.33, -0.01)*	-0.09 (-0.22, 0.04)	0.38 (0.24, 0.52)*	0.15 (-0.08, 0.38)	0.28(0.02,0.52)*
Vanessa cardui	0.59 (-0.92, 2.10)	-1.4 (-2.83, 0.03)	2.05 (1.63, 2.47)*	-0.36 (-1.20, 0.48)	0.83 (-0.29, 1.95)	-1.03 (-2.3, 0.24)	1.49(0.49,2.49)*
N. species with WCBS growth higher (N sign.)	13 (3)	6 (0)	17 (4)	14 (3)	17 (11)	11 (5)	17 (12)
N. species with tBMS growth higher (N sign.)	13 (5)	19 (8)	9 (3)	12 (2)	9 (0)	15 (7)	9 (3)