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Factors influencing detection of density dependence in British birds

I. Population trends

Abstract We question why density dependence has remained elusive in series of annual abundances of British birds. In particular, an earlier study reported that significant temporal trends in abundances occur in up to 74% of time series from the Common Birds Census. Several studies showed that such trends can hinder detection of density dependence. Temporal trends do not preclude the presence of density dependence and two published tests for density dependence include temporal trends in the null hypothesis model. We explore the extent to which detection of density dependence was hindered by temporal trends in bird abundance data. We used a conservative method to test for trends, which found significant ($P < 0.05$) linear population trends in only 7 of 60 time series of abundances (of 17–31 years) compiled from the Common Birds Census data. However, both of the tests for density dependence that allow for trends and a third method gave P-values that were strongly influenced by the strength of trends, including trends that were not significant ($P > 0.05$). This shows that density dependence may be falsely rejected or detected when trends are present, even when these trends are weak and not statistically significant. To circumvent this problem we detrended the time-series prior to testing for the presence of density dependence. To minimize subjectivity we used simulated time series to check that this procedure did not increase the level of type I error (false rejection of density independence). Additionally, we confirmed that the method gave acceptable levels of type II error, where the test fails to reject density independence in series generated using a density dependent model. This showed that the detrending method was acceptable and represents a major improvement in our ability to detect density dependence in time series that contain temporal trends. Detrending the bird time series increased the number of series in which significant ($P < 0.05$) density dependence was found from 10 (17%), when trends are ignored, to 27 (45%) when series are detrended. However, this rate of 45% is still surprisingly low by comparison to other taxa, and we believe that other factors may contribute to this, which we explore in the second of this pair of papers.

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Introduction

The abundances of few animal groups have been recorded as thoroughly as those of British land birds. Each year for the past three decades, volunteer observers have contributed many thousands of hours of observations to the British Trust for Ornithology's census schemes (review Baillie 1990). The Common Birds Census (CBC) monitors population fluctuations of a large proportion of the British terrestrial avifauna at over 200 sites nationwide (Marchant et al. 1990). As well as being of unusually long duration and large spatial extent, the common bird census data are of uncommon accuracy, as each site is visited on about ten occasions each year, averaging a total of some 30 h of observations per plot. Despite the extent and accuracy of the CBC data, there is little evidence for density dependent feedback in population counts; only 21% of individual time series from woodland or farmland birds show statistically significant density dependence

(Greenwood and Baillie 1992). In contrast, in time series of similar lengths from moths and aphids, Woiwod and Hanski (1992) were able to demonstrate density dependence in up to 80% of moth series and 88% of aphid series, providing that time series were at least 20 generations long.

There are several reasons why British birds are expected to experience density dependence. Many of the species studied are territorial, which places upper limits on density. Bird abundances often appear unusually stable through time by comparison to other taxa, implying that an equilibrium abundance is present. Density dependence is a logical consequence of a species having an equilibrium abundance (Andrewartha 1958; Milne 1958). Finally, many detailed studies of within-generation dynamics in birds have demonstrated the presence of density dependence (reviewed by Sinclair 1989).

The scant evidence of density dependence in British birds led Murdoch (1994) to conclude that tests for temporal density dependence may be unreliable for statistical reasons. He surmised that temporal trends and sampling error reduce the efficacy of even the best tests available. In particular, Murdoch found significant ($P < 0.05$) temporal trends in 74% of the 92 CBC series that he analysed and these have been shown to hinder detection of density dependence (Bulmer 1975; Pollard et al. 1987; Woiwod and Hanski 1992). Without reliable tests, it is difficult to demonstrate that density dependence is acting and therefore whether it could regulate the populations being investigated. By coincidence, we tested the CBC series for density dependence before we became aware of Murdoch's concerns, but soon encountered similar difficulties. We attempted to use testing methods that include trends in the null hypothesis model (Pollard et al. 1987; Dennis and Taper 1994). However we also found problems with these methods. This led us to search for a more reliable way to deal with trends when testing for density dependence. We believe that the techniques developed will be useful in investigations of density dependence in time series of abundances, even if the series contain temporal trends.

The presence of temporal trends in abundances makes detection of density dependence less likely (Vickery and Nudds 1984; Pollard et al. 1987; Woiwod and Hanski 1992); in aphids, density dependence was detected from 87–91% of series without trends (depending on testing method) and 35–50% of series with trends (Woiwod and Hanski 1992). Equivalent figures for moths were 67–88% and 43–72% (all series ≥ 20 generations; Woiwod and Hanski 1992). The effect of temporal trends on detection of density dependence is of potential concern with the bird data (Murdoch 1994). The problems are both statistical and biological. Trends do not preclude the existence of density dependence; rather it is a logical necessity that detection of density dependence is affected by trends, since the relationship between abundance in successive years,

which is used in the tests, will be affected by trends. However, trends might arise when a population moves to a new equilibrium following a shift in levels of a key resource or a change in a major mortality factor, such as from pesticide poisoning or over-hunting. Under circumstances of this kind it is not clear that we should be able to detect density dependence.

A temporal trend can be viewed as a systematic change over time in the average density about which abundances fluctuate. Some statistical tests for density dependence, such as that of Pollard et al. (1987) and Dennis and Taper (1994) include trends in the density independent null model. We show that, even when these tests are used, detection of density dependence is biased by the presence of trends. As a result we tried to improve our ability to test for density dependence in series with trends by detrending time series prior to analysis for density dependence.

In preliminary work we explored several different methods for detrending time series. Here we report only the most successful of these. To avoid subjectivity, the detrending methods were tested using model data, before being applied to the bird time series. We need to know whether the process of detrending time series influences detection of density dependence when there are no changes in the mechanisms causing density dependence. A density independent random-walk model was used to test whether erroneous detection of density dependence increases in frequency when time series are detrended. A second model was used to test whether detrending abundance sequences enables us to detect the underlying density dependence. This was a density dependent model (modified from Ricker 1954; Cook 1965) which can be used to generate time series with or without temporal trends. The efficacy of the detrending method was tested using the two types of modelled data and then the method was applied to the CBC series.

Methods

A method for detrending time series

We quantified trends using the method of Dennis and Taper (1994). Depending on the values of a and b, Eq. 1 simplifies to give a number of different population models. The term used for drift, a, is equivalent to a linear trend in natural logarithms of abundance and b quantifies density dependence:

$$X_{t+1} = X_t + a + be^{X_t} + \sigma Z_t \qquad (1)$$

In Model 0 $a = 0$ and $b = 0$, which gives a density-independent random walk without drift. In Model 1 $a <> 0$ and $b = 0$ giving a random walk with drift. Finally in Model 2 $a <> 0$ and $b <> 0$, giving a density-dependent model with drift. However we only test the subset of cases with $b < 0$, which gives negative feedback density dependence. X_t is the natural logarithm of abundance at time t, σ is a positive constant and Z_t are normally distributed deviates with a mean of zero and variance of 1 and successive values of Z_t are uncorrelated. Hence, σZ_t represent random shocks to the population level. In Dennis and Taper's test for density dependence parametric bootstrapping is used to test for density dependence. The appropriate test for density dependence

to apply depends on whether or not trends are present, which is quantified by testing Model 0 against Model 1. If time series are of length $q + 1$, then maximum likelihood estimates of a (termed $\hat{a}_1$) and σ (termed $\hat{\sigma}_1^2$) are obtained using:

$$\hat{a}_1 = \bar{y} \tag{2}$$

In which $y_t = x_t - x_{t-1}$, where x_t-values are the measured values on ln(abundance) at time t, and $\bar{y}$ is the arithmetic mean of the first q values of y_t.

$$\hat{\sigma}_1^2 = \frac{1}{q} \sum_{t=1}^{q} (y_t - \bar{y})^2 \tag{3}$$

If $\hat{a}_1$ is not significant (as determined in a T-test, Eq. 5) then σ is approximated by $\hat{\sigma}_0^2$:

$$\hat{\sigma}_0^2 = \frac{1}{q} \sum_{t=1}^{q} y_t^2 \tag{4}$$

The significance of the difference between a random-walk and a random-walk with drift was determined using a Student's t-test, with $q-1$ degrees of freedom. Hence the probability of a trend comes from a standard t-table:

$$T_{01} = \sqrt{q}\hat{a}_1 / \sqrt{q\hat{\sigma}_1^2/(q-1)} \tag{5}$$

Equation 5 is a corrected form of Eq. 19 of Dennis and Taper (1994); the original contains a typographical error. At the time of conducting simulations we were not aware of the correct form of this equation and calculated T_{01} as $T_{01} = \sqrt{[(\hat{\sigma}_0^2/\hat{\sigma}_1^2)-1]} \cdot (q-1)$, which is equivalent to the correct form of Eq. 19. We used this expression to test for trends in all real and simulated time series, and $\hat{a}_1$ as a measure of the strength of any trends. Series were detrended by subtracting $\hat{a}_1 (t-1)$ from each of the t observed abundances.

Bird time series

Bird census data consisted of 60 time series of CBC index values. Species were included if they occurred at at least 30 sites in 1992 (Marchant and Balmer 1993) and survival rates were available from Dobson (1990) or Baillie and McCulloch (1993); survival rates were used in the analyses in the second of this pair of papers. The CBC data consist of an index of abundance for southern Britain, calculated using a chain method (Marchant et al. 1990). Indices were calculated by pairing data from each plot with those from the same plot in the previous year and summing counts across all pairs to produce an overall estimate of percentage change. This estimate was applied to the previous year's index value (Marchant et al. 1990). Indices were calculated for all sites in scarce species and separately for woodland and farmland sites in other species (Appendix 1). Over the years of the CBC there has been a substantial turnover of plots and sampling error may have accumulated to create drift in the index values resembling a random-walk. However, evaluations of CBC methodology have shown that these potential problems are not realised to any great extent (O'Connor and Fuller 1984; Moss 1985; Marchant et al. 1990). CBC index values were converted back to numbers of pairs using 1992 abundances (Marchant and Balmer 1993). Appendix 1 lists species used, lengths of series, and the magnitude of trends for each series.

The need to detrend time series

If temporal trends have been adequately dealt with by tests for density dependence we expect the p-values given by tests for density dependence to be uncorrelated with population trends. We applied three tests of density dependence:

1. That of Pollard et al. (1987), which is amongst the most reliable methods available (Holyoak 1993a).

2. The method of Dennis and Taper (1994; their test of Model 1 vs. 2) that tests a random-walk with drift against a model that includes negative-feedback density dependence and drift.
3. The method of Dennis and Taper (1994; their test of Model 0 vs. 2) that tests a drift-free random-walk against a drift-free density dependent model.

The form of Pollard et al's test used here is described in Holyoak (1993a). Both of the methods of Dennis and Taper (1994) are well described in their original article. In all three tests, density dependence was considered to be detected if $P \leq 0.05$ from 10000 randomizations.

Using the bird time series we looked at the correlation between the strength of trends $\hat{a}_1$ (from Eq. 2) and the P-values for trends (when logit-transformed to linearise them). We found that in all three of the tests there was a strong correlation, indicating that trends influence the P-values, and hence whether or not we accept or reject the presence of density dependence. From all 60 series, Spearman's rank correlations (r) for the three tests above were -0.507 ($P < 0.0001$), -0.514 ($P < 0.0001$) and -0.566 ($P < 0.00001$), respectively. These values were significant even if we excluded trends that were significant at $P < 0.05$; equivalent figures were -0.524 ($P < 0.0001$), -0.515 ($P < 0.0001$) and -0.525 ($P < 0.0001$). Hence both significant and non-significant trends influenced detection of density dependence in all three testing methods. In Dennis and Taper's methods the temporal trends that were non-significant in the density independent model (Models 0 vs. 1) were also non-significant in the density dependent models that contained trends (a test of Models 0 vs. 2). We are therefore left with non-significant ($P < 0.05$) trends that influenced the results of tests for density dependence in models lacking trends.

A logical progression in testing for density dependence in series that potentially contain trends is to test models of increasing complexity. Dennis and Taper (1994) suggest a progression from a random-walk to a random-walk with trend (exponential growth/decline), to density dependence with constant carrying capacity, and finally to density dependence with a trend in the carrying capacity. This progression from simple models to those with an increasing number of parameters is more elegant than the solution proposed here. However, it does not allow for non-significant trends that may still influence the P-values from tests for density dependence in trend-free models.

To circumvent this problem we detrended the bird time series prior to testing for density dependence using Pollard et al.'s test. This procedure removed the influence of trends on the detection of density dependence. Applying tests after detrending series gave a non-significant correlation between P and the strength of trends; $r = -0.223$, $P \approx 0.09$ for all series and $r = -0.203$, $P \approx 0.15$ for series lacking trends. Below we test the reliability of this method.

Density-independent time series

The frequency of erroneous detection of density dependence (when it is absent) was investigated by testing density-independent random-walk data for density dependence both before and after detrending time series. The random-walk model used was:

$$X_{t+1} = X_t + \sigma Z_t \tag{6}$$

where parameters are identical to those in Eq. 1. A total of 4000 random-walk series of 31 generations in length (the length of the longest CBC series) were generated using parameter values given in the legend to Table 1. Values of σ were chosen to yield population variabilities (standard deviation of X_t-values) similar to those in the bird series. Occasionally, series contained temporal trends (Table 1); the number of such series was similar to the 5% level expected by chance alone.

Table 1 The effect of detrending time series on detection of density dependence and rates of detection from bird time series. The table gives rates of erroneous detection from density independent random-walk data (from Eq. 6), rates of correct identification of density dependence from series generated using Eqs. 7 and 8, and rates of detection from 60 bird time series. The rate of detection of density dependence is the percentage of time series in which density dependence was detected at $P \leq 0.05$ using the test of Pollard et al. (1987); n is the number of series, and d is the strength of trends. In all simulations 1000 generations were discarded prior to generating series for analysis. In Eq. 2 values of X_1 were set to 3, 4.5, 6 or 7.5 and σ was 0.1, 0.2, 0.3 or 0.4 for each of these starting values in each of 250 replicates. In Eqs. 7 and 8, N_1 was set to the deterministic equilibrium, α_{1001} was 0.001, 0.003, 0.005, 0.01 or 0.05, r was 0.5, 1 or 1.5, ξ was 0.1..0.6 (6 values) and β was 0.9, 1.1, 1.25 or 1.4. Factorial combinations were carried out of all these values for Eq. 7 parameters for 100 replicates of each combination for $d = 0$ and 25 replicates for other d-values. There are fewer than 9000 series for the density dependent model with $d = 0$, because series containing significant trends ($P \leq 0.05$) were excluded; similarly, there are far fewer than 4500 series for $d <> 0$ because series which did not contain significant trends were excluded

Data source	n	Rate of detection of density dependence	
		Before detrending	Detrended series
Random-walk model:			
All series	4000	4.8%	5.0%
Series lacking trends	3799	4.9%	5.0%
Series with negative trends	99	1.0%	6.1%
Series with positive trends	102	2.9%	4.9%
Density dependent model:			
Series lacking trends ($d = 0$)	8994	95.8%	95.7%
Series with negative trends ($d = -0.02$ or -0.04)	410	0.0%	65.9%
Series with positive trends ($d = 0.04$ or 0.08)	479	1.0%	62.0%
Bird time series:			
All series	60	16.7%	45.0%
Series lacking trends	53	17.0%	41.5%
Series with negative trends	1	0.0%	0.0%
Series with positive trends	6	16.7%	83.3%

Density-dependent time series

To test whether detrending series is effective in allowing us to detect the underlying density dependence when it is present, we analysed series generated with a simple density-dependent population model. The model used is a modified version of the model of Ricker (1954) and Cook (1965):

$$N_{t+1} = N_t e^{r(1 - \alpha_t N_t) + \varepsilon_t} \qquad (7)$$

where N_t is the abundance in generation t, r is the intrinsic growth rate and α_t is the inverse of deterministic equilibrium density in generation t. The equilibrium density was made into a log-linear function of time, such that for $t > 1000$:

$$\alpha_t = e^{Ln(\alpha_{1001}) - dt} \qquad (8)$$

where α_{1001} is a constant and d is the strength of trend (for $t \leq 1000$, $\alpha_t = \alpha_{1001}$); the subscript 1001 arises because time series were constructed starting with this generation in order to avoid transient dynamics. Equation 8 reduces to Eq. 7 when $d = 0$. Stochasticity was added using ε_t, a normally distributed random variable with zero mean and variance ξ^2, which was a function of mean density; specifically $\xi = \gamma (1/\alpha_{1001})^\beta$, where γ and β are constants (Hanski and Woiwod 1993). This form of variability was chosen to give temporal abundance data with appropriate Taylor's (1961) power law plots (e.g. Hanski and Woiwod 1993).

A total of 9000 density-dependent series of 31 generations (the length of the longest CBC series) were simulated using Eqs. 7 and 8 with parameter values listed in the legend to Table 1. Values of α_{1001} were chosen to give realistic abundance levels; the intrinsic growth rate was set at values that are representative of bird populations; values of the strength of trends were typical of $\hat{a}_1$ and $\hat{a}_2$ values observed for the CBC series; and values of the stochasticity parameters β and ξ were selected to give series with similar Taylor's (1961) power law plots (from detrended series) to those observed for the CBC data, i.e. with a slope of ~0.90 (standard error: 0.06 from 60 series). The mean value of slopes of Taylor's power law plots was 1.04 ± 0.24 (SE) from 9000 series. Note that although Taylor's power law was formulated for spatial data, it is also appropriate for temporal data if temporal autocorrelation is not too strong.

The series from both the density dependent (Eqs. 7 and 8) and density independent models (Eq. 6) were detrended and tested for density dependence using Pollard et al.'s test.

Results

The rate of false detection of density dependence was acceptable ($\leq 5.0\%$) when density independent time series were detrended prior to analysis for density dependence with Pollard et al.'s test (Table 1). The only exception to this was that density dependence was detected (at $P < 0.05$) in 6.1% of density independent time series that contained significant temporal trends. However, this frequency of 6.1% is not significantly greater than the 5% rate of false detection expected by chance alone ($G = 2.31$ with 98 df, $0.1 < P < 0.5$).

When simulated time series contained density dependence and lacked temporal trends, density dependence was efficiently detected without detrending (from 95.8% of series; Table 1). Without detrending, density dependence was almost always masked in simulated series when significant ($P < 0.05$) trends were present (Table 1); density dependence was detected in no density-dependent series (out of 410) that contained negative trends and only 1% of 479 simulated density-dependent series with positive trends. When these series were detrended, detection rates increased to between 62.0% and 65.9%, compared to 95.7% for density-

dependent series that never contained trends. This shows that detrending time series does not completely overcome the reductions in levels of detection caused by trends.

In the bird time series, there were six positive trends and one negative trend. Detrending increased detection levels both in bird series that contained positive trends and those that lacked trends (Table 1). For time series with non-significant trends, detrending increased the rate of detection from 17% without detrending to 41.5% with detrending. This shows that even these weak trends hinder detection of density dependence; this was also suggested by the correlation of -0.524 between the strength of trends and the logit of P-values from Pollard et al.'s test for series that lacked significant trends discussed in the section entitled 'The need to detrend time series'. Furthermore, these increases in rates of detection are far greater than the rate of false detection of $\sim 5\%$ from analysis of detrended density- independent series that contained significant trends. When bird series were detrended, detection showed no residual effects of trends having been present, as there was no significant correlation $(r = 0.223, P \approx 0.09)$ between the P-value from the density dependence test (in detrended series) and the slope of the trend that was present, as discussed above. This is consistent with trends causing no change in the mechanism of density dependence in bird populations.

In all 60 of the bird series, density dependence was found in 45% (27) after all series were detrended. This figure is possibly misleading as 23 species are represented by two series (Appendix 1); limiting the analysis to one time series per species (the longest for each) gives 37 series. Density dependence was detected in 46% of these after detrending.

Discussion

We have shown that both of the available methods (Pollard et al. 1987; Dennis and Taper 1994) that attempt to compensate for the presence of temporal trends when testing for density dependence are liable to give false results. This is true even when weak and statistically non-significant $(P > 0.05)$ trends are present. When simulated time series were not corrected for the presence of temporal trends, the test of Pollard et al. (1987) detected density dependence (at $P \leq 0.05$) from only 1% of simulated density-dependent series that contained positive trends and no simulated series that contained negative trends (Table 1). These detection rates are extraordinarily low, compared to the 95.8% detection rate for simulated density-dependent time series which never contained trends. In order to correctly assess the presence of density dependence in time series containing trends (using Pollard et al.'s test), we must allow for the biasing effect of trends. In analyses of large numbers of time series for density depen-

dence, such as those conducted by Woiwod and Hanski (1992) or Holyoak (1993b), this was done by separately considering series with and without trends. With the CBC data, many of the series contain trends that are weak (Appendix 1) and which, although not statistically significant, may still affect detection of density dependence. Detrending time series prior to testing largely removes the effect of trends on detection of density dependence.

The detrending method developed here allows us to make a more accurate assessment of the frequency of density dependence in time series containing trends than when trends are ignored. The method preserves the 5% level of false detection that we expect from any statistical test. The detrending method does not however, fully overcome the reduction in the frequency of correct detection of density dependence caused by trends; 62–66% of detrended simulated series known to contain density dependence revealed evidence of density dependence, compared to 96% for equivalent (density-dependent) series which never contained trends. This type II error rate is, however not very different from other tests of density dependence (Holyoak 1993a).

We found density dependence (at $P \leq 0.05$) in 17% of the bird time series prior to detrending and in 45% of series after detrending. Although temporal trends are frequently responsible for masking density dependence in the bird time series, taking account of trends lead to detection of density dependence in only 45% of series (46% of species). This frequency of detection, when trends are allowed for, is still low by comparison to moths and aphids (Woiwod and Hanski 1992). Given the small number of bird time series with significant trends, allowing for the type II error rate would not greatly increase the rate of detection of density dependence. In the second of this pair of papers we show that the way in which abundances are sampled annually from species that live for >1 year may mask density dependence.

We found temporal trends in far fewer of the CBC series than Murdoch (1994). This is because we used a more conservative detrending method. The detrending method used by Murdoch [regression of ln(abundance) against year number] identified significant trends in 82% of the bird series used here. Additionally, this detrending method identified trends (at $P < 0.05$) from 78% of random-walk time series, where we would expect only 5% of series to contain significant trends by chance alone. The method for quantifying trends proposed by Dennis and Taper (1994) shows no such problems. The two methods give measures of the strength of trends that are highly correlated in the bird series (Pearson's correlation = 0.90. $P < 0.00001$).

Sampling error was expected to be a problem in census data because it increases the frequency of erroneous detection of density dependence (Kuno 1971; Itô 1972; Bulmer 1975; Pollard et al. 1987; Murdoch 1994).

However, Dennis and Taper (1994) showed using simulations that the increase in false detection caused by sampling error is small; even large amounts of sampling error caused changes in the probability of erroneous detection of density dependence (when none is present) of <0.02 and of correct detection (when density dependence present) of <0.06 (for series of ten generations). These rates of false detection due to sampling error are small by comparison to the detection rate of 45% seen in the bird series.

In conclusion, it is necessary to consider population trends in analyses which try to detect density dependence from time series of abundances. The effects of trends on detection of density dependence using the test of Pollard et al. (1987) can largely be corrected for by detrending time series if the method of Dennis and Taper (1994) is used to quantify trends.

Appendix 1 Details of Common Birds Census series used. Here n is the length of each series (in years) and $\hat{a}_1$ is the strength of trends; *indicates that the trend was significant at the 5% probability level in an t-test; P is the probability of detection of density dependence from the test of Pollard et al. (1987) test carried out on detrended time series

	Farmland			Woodland			All		
	n	$\hat{a}_1$	P	n	$\hat{a}_1$	P	n	$\hat{a}_1$	P
Accipiter nisus, sparrowhawk	–			–			19	0.5147	0.0175
Falco tinnunculus, kestrel	–			–			28	0.0087	0.0047
Gallinula chloropus, moorhen	31	−0.0070	0.0646	–			–		
Columba palumbus, wood pigeon	17	0.0662*	0.0416	17	0.0694*	0.4820	–		
Streptopelia decaocto, collared dove	22	0.1234*	0.0207	–					
Strix aluco, tawny owl	–			–			30	0.0030	0.0037
Hirundo rustica, swallow	31	−0.0083	0.1229	–			–		
Anthus pratensis, meadow pipit	–			–			30	0.0041	0.0369
Motacilla alba, pied wagtail	31	−0.0065	0.0080	–			–		
Troglodytes troglodytes, wren	31	0.0158	0.0713	29	0.0417	0.0254	–		
Prunella modularis, dunnock	31	0.0029	0.1080	29	−0.0020	0.0190	–		
Erithacus rubecula, robin	31	0.0132	0.0528	29	0.0035	0.0587	–		
Turdus merula, blackbird	31	−0.0071	0.0651	29	−0.0028	0.0009	–		
T. philomelos, song thrush	31	−0.0428	0.1748	29	−0.0145	0.0042	–		
T. viscivorus, mistle thrush	31	−0.0277	0.0011	29	0.0190	0.1050	–		
Sylvia communis, whitethroat	31	−0.0370	0.4865	–			–		
S. atricapilla, blackcap	30	0.0544	0.0022	29	0.0166	0.0093	–		
Phylloscopus collybita, chiffchaff	30	0.0242	0.2780	29	0.0021	0.3159	–		
P. trochilus, willow warbler	31	0.0076	0.3271	29	−0.0188	0.6977	–		
Regulus regulus, goldcrest	–			28	0.0142	0.3510	–		
Panurus biarmicus, long-tailed tit	29	0.0503	0.0047	28	0.0404	0.0609	–		
Parus ater, coal tit	28	0.0188	0.0961	29	0.0446	0.2476	–		
P. caeruleus, blue tit	31	0.0183	0.0157	29	0.0091	0.0037	–		
P. major, great tit	31	0.0214	0.2751	29	0.0076	0.0975	–		
Garrulus glandarius, jay	29	0.0170	0.0015	29	0.0066	0.0205	–		
Pica pica, magpie	31	0.0421*	0.0259	28	0.0473	0.0702	–		
Corvus monedula, jackdaw	30	0.0318	0.2125	17	0.0378	0.0368	–		
C. corone, crow	31	0.0408*	0.0362	29	0.0536*	0.0184	–		
Passer domesticus, house sparrow	–			–			17	−0.0247	0.3517
Sturnus vulgaris, starling	31	−0.0004	0.0229	28	−0.0562*	0.4275	–		
Fringilla coelebs, chaffinch	31	0.0141	0.0173	29	0.0073	0.2723	–		
Carduelis chloris, greenfinch	31	0.0212	0.1356	28	0.0116	0.0018	–		
C. carduelis, goldfinch	30	0.0174	0.0725	–			–		
Acanthis cannabina, linnet	31	−0.0236	0.1376	–			–		
Pyrrhula pyrrhula, bullfinch	31	−0.0172	0.0483	29	−0.0036	0.1275	–		
Emberiza citrinella, yellowhammer	31	−0.0067	0.2158	28	−0.0155	0.4305	–		
E. schoeniclus, reed bunting	31	−0.0062	0.3510	–			–		

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