A long-term study of temporal variation in wing feather mite (Acari: Astigmata) infestations on robins, *Erithacus rubecula,* in Nottinghamshire, U.K.

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Keywords

Astigmata, Analgoid mites, Wing feather mites, *Proctophyllodes*, *Trouessartia*, European robins, *Erithacus rubecula,* seasonal variation, age-related variation, annual cycles.

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Abstract

European robins (*Erithacus rubecula*) were mist netted and assessed for wing feather mite infestations in north-east Nottinghamshire, England from June 1998 until March 2014. We analysed records of 899 first capture birds using three measures of infestation: prevalence of mites (% showing evidence of infestation), number of wing feathers infested with mites on one wing (NIWF), and the total mite infestation score (TOTMIS). The latter is the sum of scores (range 0-4) allocated to each of the 19 flight feathers on the assessed wing. The overall prevalence of infestation was 90.9% (95% confidence limits=88.19-93.02), and average NIWFs and TOTMIS (± SEM) were 6.0 ± 0.15 and 6.5 ± 0.23, respectively. All three measures varied significantly between age classes of birds, but not between the sexes, and varied markedly between months of the year. TOTMIS values were highest in late winter/early spring months and then dropped markedly in May to a low in summer months (usually by August), the dip in abundance of mites coinciding with the breeding season of robins. The best mixed-effects generalized statistical model was one that comprised month of capture and age of birds but there was also a highly significant negative correlation between TOTMIS values of individual birds and the mean monthly ambient temperature in the month of capture as well as that of the preceding month. The most parsimonious interpretation of our data is that the highly consistent dip in mite abundance on adult robins from spring to summer months reflects vertical transmission of mites to their nestlings / fledgelings. These results are discussed in the context of the biology of both hosts and mites.

Introduction

The European robin (*Erithacus rubecula)* is one of the most common and best-known birds in British urban gardens. Its biology, ecology and behavioural characteristics are all well-known having been documented in considerable detail in the seminal work by Lack (1953). Perhaps surprisingly, little is known about the diseases that affect robins, notably the parasites that they carry and their consequences for the birds.

Although, overall wing feather mite infestations on robins are poorly studied (but see Jovani & Serrano, 2001; Campos *et al*., 2011; Diaz-Real *et al*., 2014; Doña *et al*., 2015), robins are known to be infested by feather mites of the genera *Proctophyllodes* and *Trouessartia* (Santana, 1976), both of the super family Analgoidea (Astigmata, Acariformes;

Dabert & Mironov, 1999; Proctor, 2003). Mites of both genera live predominantly on the flight and tail feathers of their hosts, and rarely on other types of plumage such as the soft downy body feathers (vane mites and down mites of Dabert & Mironov, 1999). The robin specific species are *Proctophyllodes rubeculinus (Koch, 1941)* and *Trouessartia rubecula* (Jablonska, 1968) (Atyeo & Braasch, 1966; Santana 1976, respectively). Species of both genera have been recorded in Spain, coexisting on migratory robins (Campos *et al*., 2011) and on overwintering blackcaps, *Sylvia atricapilla* (Fernández-González *et al.,* 2013, 2018).

Whilst historically feather mites were regarded as parasitic (Atyeo & Gaud, 1979; Harper, 1999; Thompson *et al*., 1997), evidence is currently largely in favour of analgoid feather mites being innocuous (Blanco *et al*., 1997; Galván *et al*., 2012), with little impact on host survival (Brown *et al*., 2006). They feed on secretions from the skin, including oils from the uropygial glands, algae, fungi and pollen trapped on feathers and generally cause little damage to their hosts (Blanco & Frias, 2001; Galván & Sanz, 2006; Doña *et al*., 2019). Feather mites may even have beneficial consequences for infested birds in feeding on microflora on feathers and thereby controlling potentially threatening pathogens (Blanco *et al*., 2001; Pap *et al*., 2005; Galván *et al*., 2008; Campos *et al*., 2011). Analgoid feather mites cannot live independently off their hosts, other than for very brief periods, and are therefore best regarded as obligatory ecto-symbionts/ecto-mutualists. Transmission between hosts is most likely via contact when birds roost together (Jovani & Blanco, 2000) or during courtship and mating (horizontal transmission), and in the nesting period when mites can transfer to the nestlings once the latter have started growing flight feathers (vertical transmission; Blanco *et al*., 1997; Doña *et al*., 2017). Insect mediated transmission, via hippoboscid flies, has also been considered, but now thought to be highly unlikely (Jovani *et al*., 2001).

Transmission of mites to nestlings should be reflected in quantitative changes in feather mites on both parents and their offspring in the breeding season. Consistent with this hypothesis, reductions in mite burdens on parents, with concomitant increases in burdens on nestlings, have been demonstrated in some species (Mironov & Malyshev, 2002; Pap *et al*. 2010), however, the robustness/repeatability of the associated trends over successive years have not been thoroughly tested. In this paper we provide an analysis of the annual cycle of prevalence and abundance of wing feather mites on locally resident robins over a period of 14 years, and since seasonal, sex and age effects on mite infestations have been reported previously, these are taken into account when relevant and their contribution to annual cycles is evaluated.

Materials and methods

Study site and choice of bird species

The study was conducted in Treswell Wood (53°81′ N, 0°85′ W) in NE Nottinghamshire, where a long-term constant effort mist-netting scheme has been based since the late 1970s. The wood is composed of 47 ha of mature broad-leaved trees, mainly ash (*Fraxinus excelsior*) with some oak (*Quercus robur*), and predominantly hazel (*Corylus avellana*) understorey (du Feu and McMeeking 1991). Robins were selected for this study because they are present throughout the year in appropriate numbers, represent a locally resident population in our study site (Supporting information 1 (Appendix S1); Wernham *et al*., 2002) and are robust enough to allow handling of the sort required for this study. The methods used in netting birds, extraction, ringing and recording standard biometric measures are all well documented in previous publications (Redfern & Clark, 2001; Yom-Tov *et al*., 2006).

Assessment of age and sex of the robins

Age was assessed by plumage based on conventional indicators (Svensson, 1992). In the field, we used the European Union for Bird Ringing (EURING, 2010) codes for age. These were later converted to age classes 1 to 4, reflecting an ageing sequence from the youngest to the oldest birds. Age class 1 corresponds to birds hatched in the current year and still in juvenile plumage (code=3J), age class 2 to full-grown bird hatched in the current calendar year after the moult from juvenile plumage (code=3), age class 3 to birds hatched in the previous calendar year, now in their second calendar year but before full adult moult (code =5) and age class 4 to older birds which have undergone at least one full adult moult (code 6). Thirteen birds of uncertain age were omitted from relevant analyses.

Since robins are essentially monomorphic and the sexes cannot be distinguished on plumage, they could only be sexed confidently in the breeding season based on brood patches in females (*n*=86) and cloacal protuberances in males (*n*=59). In our experience, sexing robins on any biometric measure is unreliable. In analyses that included the sex of birds, we excluded all birds that could not be sexed accurately.

Assessment of feather mite infestations on robins

While both immature and adult feather mites are motile at times, they generally appear quiescent when wings are inspected for their presence (Blanco *et al*., 2001). Infestations were assessed by the semi-quantitative method of Behnke *et al*. (1995, 1999), a modified version of the method originally devised by McClure (1989), and used effectively by others (Harper, 1999). Once experience has been gained, scoring is easy to implement in the field, minimising the handling time of birds and hence consistent with the spirit of the 3 Rs in animal handling (Reduction, Refinement and Replacement; British, Animals (Scientific Procedures) Act 1968), as it can be carried out extremely rapidly by trained ringers, minimising the time that birds are kept captive and handled, before their release. Rapid processing of birds is of particular importance in the breeding season. Briefly, feather mite burdens were assessed by eye on each of the ten primary, six secondary and three tertial wing feathers of one wing, using a scoring system where zero = no mites evident, and 4 = heavy infestation. The scores from the 19 flight feathers were then summed to derive the total mite infestation score (TOTMIS), the values of which can range from 0 to 76 for each bird. The number of feathers with evident mites (NIWF, range 0 to 19) was also recorded. Prevalence of infestation was the percentage of birds with a TOTMIS >0. Thus, three related but distinct measures were used as indicative of feather mite infestation. Behnke *et al*. (1999 showed that scores on individual feathers correlated very closely to the actual number of mites detected on plucked feathers inspected by microscopy and that mite burdens and scores were very similar on both wings.

Meteorological data

We used data from the meteorological station in Gringley-on-the-Hill, the nearest meteorological station to Treswell Wood, located 12.5 km north of our study site, comprising minimum and maximum temperatures recorded at 9 am each day. From these data we calculated the average daily temperature as the mean of the minimum and maximum temperatures. These daily averages were then used to calculate the mean monthly and mean annual values, and also the mean monthly value for each of the months in each year of the study.

Feather mite data

We used the first capture records of robins (*n*= 899) in the period 1998 to 2014 inclusive (Data set of the Treswell Wood Ringing Group), but where only the year of capture was a variable under consideration, we excluded birds assessed in 1998 (*n*=21; incomplete year, data available only from September for first capture birds) and in 2013 (*n*=2) and 2014 (*n*=3) when very few birds were assessed.

Statistical analysis

Summary statistics are given in the text as mean values ± standard error of the mean (SEM) and as prevalence (% of birds infested in data subsets) with 95% confidence limits (CL_{95}). Figures show 95% confidence intervals, calculated in bespoke software based on the tables of Rohlf & Sokal (1995).

Following the recommendations of Zuur *et al*. (2009) we first explored the data, assessing each explanatory factor in turn for its effect on the three measures of infestation. For this we applied non-parametric tests (Kruskal-Wallis, Mann-Whitney *U* test, Chi squared and Spearman's test of correlation) and in each case we provide the value of the relevant test statistic (H, U, χ^2, and r_s, respectively) as well as the probability (P) for rejecting the null hypothesis ($\alpha = 0.05$).

TOTMIS and temperatures form a time series of 168 monthly values and time series analysis was initially used to explore them, to decide on the most appropriate predictor variables. The fitted observed values for TOTMIS (Fig. S1A) were decomposed into their additive components generating a smoothed trend (Fig S1B), a seasonal (Fig. S1C) and a remaining 'random' component (Fig. S1D), using the decompose() command in R version 2.2.1 , base code (R Core Development Team). The seasonal component was removed by differencing from the original series (Fig. S1E). Then the same series of operations was carried out on the matching (monthly) mean daily temperature series, and a cross-correlation analysis carried out using the ccf() command of R on the seasonally adjusted values of TOTMIS and mean daily temperature. There was only one significant correlation: the temperature of the previous month (i.e. a time lag of one month before in the temperature series). Thus, we decided to use the mean daily temperature of the previous month in addition to that of the current month as predictors.

We then fitted 33 different mixed-effects models in R (vers 4.1.0, R Core Development Team) with year as a random factor, covering all possible permutations of available explanatory factors, using glmer from the lme4 package in R for analysis of prevalence (binomial data) and lme in the nlme package for TOTMIS (quantitative data).. Model selection was carried by comparing all the models with different combinations of variables by the corrected Akaike Information Criterion (AICc; Burnham & Anderson, 2002), using the AICcmodavg package. We present the top 10 models and the bottom 5 for each of prevalence and TOTMIS (All models are given in Table, S1). As an additional aid to comparison between models we also give the evidence ratio (ER; Symonds & Moussalli, 2011). Finally, we fitted the best models, and explored these by using the deletion procedure in R, removing explanatory factors in turn and comparing models with or without relevant factors. Values of χ^2 are given for models based on binomial errors, while for models based on Gaussian errors, we give the likelihood ratio (LR). The percentage of deviance accounted for by each significant factor was calculated as recommended by Xu (2003).

Results

Overall quantitative measures of mite infestations

The prevalence of wing feather mites was 90.9% (88.19-93.02%). An average of 6.0 ± 0.15 (range=0-19) flight feathers were infested with evident mites and mean TOTMIS was 6.5 ± 0.23 (range=0-44). The frequency distribution of TOTMIS is given in Fig. S2.

Age-related variation in feather mite infestations

Reliable age estimates were available for 886 birds. Prevalence of mites was lowest in birds with juvenile plumage (Table 1; age class 1 ; χ^2_3=33.4, P<0.001), which also had fewer infested wing primary flight feathers (H_3=258.3, P<0.001) and the lowest mean TOTMIS (H_3=276.8, P<0.001), compared with other age classes. Values for all three measures were highest in age class 3 birds, but lower for age class 4 birds, perhaps suggesting some decline in measures of infestation in the oldest birds. However, since feather mite burdens peaked in late winter/early spring, by which time all birds were in age classes 2, 3 or 4, we repeated this analysis on all birds caught in the months when age class 1 birds were still around (May to September, inclusive) The outcome was much the same, although the values were lower in all cases (Table 1; for prevalence, χ^2_3=10.8, P=0.013 ; NIWF, H_3=56.28, P<0.001: TOTMIS, H_3=62.02, P<0.001).

Sex-related variation in feather mite infestations

Only 145 birds (Table 1; males n=86, females n=59) could be confidently sexed. There was no significant difference between the sexes in prevalence of mites (χ^2_1=0.145, P=0.7), NIWF ($U_{59,86}$=2489.5, P=0.85) or TOTMIS ($U_{59,86}$=2357, P=0.47).

Between-year variation in feather mite infestations

Annual prevalence of feather mites was over 80% throughout and despite some perturbation did not vary significantly across this period of 14 years (χ^2_{13}=18.2, P=0.149; Fig. 1A). However, there was significant between-year variation in both NIWF (H_{13}=41.58, P<0.001; Fig. 1B) and TOTMIS (H_{13}=43.93, P<0.001; Fig. 1C).

Monthly variation in feather mite infestations

Over the course of a year, the prevalence of mite infestation fell from April to August and then increased to reach more than 95% in October. This pattern was significant (i.e. for month as an explanatory factor, χ^2_{11}=70.9, P<0.001, Fig. 2A). NIWF followed a similar trajectory of a fall from April to August (H_{11}=383.05, P<0.001, Fig. 2B), as did also TOTMIS (H_{11}=410.9, P<0.001, Fig. 2C).

Within-year variation in feather mite infestations; effects of age and sex

In May, when the youngest birds (age class 1) were first ringed, prevalence was 100% (Fig. 3A), however, the sample size was very small (just 12 birds and 95% confidence limits ranged from 24.26 to 100%). Prevalence then fell over the following 4 months until September, by which time they had all moulted to adult plumage. In age class 2 birds (first year birds in adult plumage, first seen in July) prevalence rose in each successive month from 55.6% in July. Adult birds (age classes 3 and 4), clearly showed a marked dip in prevalence between June and September.

As above in the combined data, mean TOTMIS values in adult birds (age classes 3 and 4) were remarkably constant from January until April, and then dipped sharply to a low in August, before rising again in each successive month thereafter. Mean TOTMIS values in age class 1 and 2 birds (Fig. 3B) merged by September after which all the birds had moulted to adult plumage but TOTMIS values were still mostly lower than those in age class 3 (one year old birds) and 4 (two-year old and older) birds, although the subsequent pattern of change over successive months was similar.

In each of March and August only one female bird was sexed. Nevertheless, it is apparent from the data (Fig. 3C) that TOTMIS values followed the same declining trajectory in both male and female birds between April and July.

Between-year monthly variation in feather mite infestations

Despite the small sample sizes in some months, the annual pattern of feather mite infestations was clearly discernible and very similar in each year (Fig. 4). Prevalence was 100% in most months, but dipped mostly in July (in 10/14 years) and in the months immediately preceding and following July (Fig. 4A). In the 14 years for which we had records from January until December (Fig. 4B; 1999 – 2012, inclusive), maximum TOTMIS was recorded 13 times in the late winter/spring period (January, n=1, February, n=7; March, n=2; April, n=3). The exception was a single instance of a maximum in November (in 2001). The lowest TOTMIS was recorded 12 times in summer months (June, n=2; July, n=5; August, n=5). The exceptions were a single case in May (2012) and another in September (1999).

Between-year and monthly variation in feather mite infestations in relation to local ambient weather conditions

There was no correlation between the mean annual TOTMIS and mean annual average daily temperature, when data for both parameters were averaged by year and confined to the period 1999 to 2012, inclusive (r_s= -0.011, n=14 P=0.97). However, much as expected, given the data illustrated in Fig. 4C, there was a highly significant negative correlation between mean monthly TOTMIS and mean monthly average daily temperature (both parameters averaged by month; r_s=-0.811, n=12 P=0.001). This was also the case when data for TOTMIS and average daily temperature were averaged separately for each month of the 14 years of the study (r_s=-0.674, n=152 P<0.001), but was marginally better when we fitted the average daily temperature for the previous month, rather than for the month of capture (r_s=-0.766, n=152 P<0.001). Correlation between TOTMIS records for individual birds and the average daily temperature in the month of capture was also highly significant (r_s= -0.595, n=899 P<0.001), and almost identical when the average monthly temperature was that of the preceding month (r_s= -0.596, n=899 P<0.001).

Time-series analysis

These data (Fig. S1) are essentially stationary, showing no trend in the adjusted TOTMIS values over time (r=0.021, $F_{1,166}$=0.072, P=0.78).

Models that best account for variation in prevalence of mites and TOTMIS

For prevalence (Table 2 and Table S1), there was little difference between the four top models, each of which comprised two explanatory factors, comprising different permutations of the temperature in the month of capture (AvDailyYrMnthT), temperature in the preceding month (AvDailyYrMnthmin1T; Fig. 5A) and squares of these variables. The predictive power of each of these top four models ranged between 11 and 13% of the total predictive power provided by the full set of models. All the remaining models were weaker with the first model approximately 2.52 times more likely to be the best approximating model than model 5, and by greater amounts for all remaining models. The possibility of collinearity between the two covariates (AvDailyYrMnthT and AvDailyYrMnthmin1T) was excluded (VIF=3.176), and the deletion approach showed that both were significant (χ^2_1 = 12.732, P=0.0004 and χ^2_1 = 3.87, P=0.049), respectively, although AvDailyYrMnthmin1T was only marginally so.

For TOTMIS, there was only one acceptable model, comprising age and month of capture. This model accounted for 99% of the predictive power provided by the full set of models, and was 140 times more likely to be the best approximating model than the second model which comprised only month of capture. Both main effects were highly significant (for age, $LR_{3,833}$=16.115, P=0.0011, variance explained = 0.31% and for month, $LR_{11,833}$=272.9, P<0.0001, variance explained = 5.06%).

Although models with AvDailyYrMnthT and AvDailyYrMnthmin1T, were considerably weaker, it was nevertheless of interest to examine how these factors varied with TOTMIS. Regression analysis of AvDailyYrMnthT on TOTMIS, gave a negative linear gradient ($ß = -0.943 \pm 0.0426$, t=-22.13, P<0.0001). The best fit for AvDailyYrMnthmin1T was a shallow negative second order polynomial curve ($ß1= -1.963 \pm 0.218$, t=-8.98, P<0.0001; $ß2= 0.0440 \pm 0.0098$, t= 4.502, P<0.0001). These indicated in both cases that as monthly temperature increased, TOTMIS fell (Fig. 5).

Discussion

Analysis of wing feather mite infestations on adult robins revealed that a steep decline in infestations occurred consistently from April until August, in each of 14 successive years, during the months when the birds were brooding. Each year's young birds experienced a corresponding increase in mite infestations from July, while mite abundance on the adults also increased from August, stabilizing by January. This dip in mite infestations in the late spring/ summer months occurred in both sexes of robins. In mixed-effects GLMs, variation in mite abundance was best explained by month of capture of birds, and age. Moreover, TOTMIS correlated negatively with the average ambient temperature in the month of capture of birds when analysed independently of other factors, but marginally better with that of the preceding month. Prevalence of mites, was mostly close to 100% and only dipped in the breeding season, but in mixed-effects GLMs variation in prevalence of mites was best accounted for by the average ambient temperature in the month of capture of birds and that of the preceding month.

The longest previous temporal study of feather mite infestations was by McClure (1989), who monitored 90 species of birds in California over a period of 12 years, reporting peaks of mite infestation on the most abundant resident species, house finches and white-crowned sparrows, in summer months, between March and October. Other temporal studies have mostly monitored wing feather mite infestations on birds for part of, for a complete single, or 2-3 calendar years (Blanco *et al*., 1997; Mironov, 2000; Pap *et al*., 2010). Campos *et al*. (2011) reported a twofold increase in the abundance of feather mites on migratory robins in Spain as the winter progressed from November until February, after which robins migrated northwards for the summer months. Figuerola (2000) found that prevalence of feather mites was higher in winter months in a range of winter flocking species of passerine birds, but not in colony breeding or solitary species. Studies on summer visitors in Europe such as barn swallows have reported increasing prevalence and abundance of feather mites from early July, after the breeding season, until mid-September before departure for Africa, but not the full annual picture for obvious reasons (Blanco & Frias, 2001). Blanco *et al*. (1997) reported a steep increase in the abundance of the feather mite *Gabucinia delibata* on red-billed choughs in Spain between autumn and winter, and on second and third year birds from spring through to winter, but also noted a dip on breeding birds between spring and summer-autumn. However, the most comprehensive studies to-date of temporal changes in feather mite infestations are those by Mironov (2000) and Pap *et al*. (2010). The former studied feather mites (*Monojobertia microphylla*) on chaffinches from their arrival in April until their departure in October in NW Russia. Here, in contrast to our findings, feather mite burdens increased from April to May on adult birds, and then dropped markedly from May, continuing to fall until July on female birds. Concurrently, in summer months, feather mite burdens increased on fledgelings, just as we found on robins, but subsequently decreased in the autumn. Interestingly, feather mite burdens on male chaffinches continued to increase in June, rather than to fall as in females, and only began to decline in abundance a month later in July, during the post-breeding moult. This is consistent with male chaffinches playing no role in brooding although they provide food for the nestlings. Pap *et al*. (2010) found a pattern of change in mite infestations (*Proctophyllodes troncatus*) on house sparrows that was very similar to our results, mite infestations decreasing in both sexes in the breeding period, although in contrast to robins, male house sparrows share brooding (Cramp and Perrins, 1994). The highly repeatable finding in our data of a dip in feather mite burdens on adult robins in early summer therefore complements these earlier studies, and highlights the almost exact coincidence of the dip in mite abundance with the period when the first broods of young robins will have acquired flight feathers (see also Mironov, 2000).

The earliest nests are usually built by robins in mid-March. Eggs are laid in late March and early April, followed by a two-week incubation period, so that the young hatch in the 2nd/3rd weeks of April, when caterpillar populations are high. Flight feathers are acquired a week later (Lack, 1953). The period from the start of nest building until independence of the young is 58 days (Lack, 1953), so the first fledgelings are seen in late May. However, since nest building is asynchronous, some pairs initiating nest building as late as early June, and because robins have multiple broods, the year’s final fledgelings are seen often in July and occasionally even very early August (C. du Feu *pers com*). Since robins lead solitary lives throughout most of the year, opportunities for transmission for feather mites are essentially restricted to the breeding season, as with many other contact-transmitted agents (Tinsley, 1990). At this time, transfer between the pairs becomes possible (during copulation and when the cocks feed incubating hens) and from the parents to their young during brooding and feeding in the nest (Doña *et al*., 2017), once the latter have acquired flight feathers in the limited nestling period.

The possibility that feather mites may transfer from robin parents to their offspring during nesting has been considered previously (Campos *et al*., 2011) but demonstrated convincingly earlier in chaffinches (*Fringilla coelebs*) by Mironov & Malyshev (2002), who monitored 65 nestlings in 15 nests from the day of hatching until the 11th day. These authors concluded that feather mites were acquired by nestlings from female chaffinches during brooding at night time, in the process the females losing about three quarters of their mite burden. In turn, the mites appeared on the nestlings on days 7-9 after hatching, depending on species, and their burdens increased steadily until fledging on the 11th day. Doña *et al*. (2017) treated adult European flycatchers, *Ficedula hypoleuca* with an acaricide during the nesting period and showed that the nestlings of treated parents did not acquire feather mites, in contrast to those of untreated controls. Concurrently, a reduction in feather mites was observed on non-treated parent birds between when assessed first during egg incubation and then subsequently when rearing nestlings. Our results are therefore consistent with these studies, indicating that the most parsimonious explanation of the annual dip in mite burdens on adult birds between April and August is the transfer of a proportion of mites from adults to their young, i.e. that this is largely a case of vertical transmission (Clayton & Tompkins, 1994; Doña, *et al*., 2017).

While our data are largely consistent with this hypothesis, i.e. vertical transfer of mites, there is one anomalous data point among our results that is incongruent with this idea; we found that mite burdens in age class 1 birds in May were higher than those recorded in June and July. However, the sample size of this age class in May was very small (n= 12) and this may have been just an unfortunate consequence of having caught a small number of exceptionally heavily infested fledgelings in May. Thereafter, mite burdens increased in all age groups to reach the maximum intensities by January.

Feather mites are known to take up water from the surrounding atmosphere, and do so particularly efficiently under humid conditions (Gaede & Knülle, 1987), so the possibility that some loss of feather mites may have been attributable also to the drier months, typically associated with late spring and early summer in the British Isles, cannot be dismissed. Given that feather mites have been shown to be capable of redistribution in response to environmental conditions (Wiles *et al*., 2000), it is equally possible that the mites were less conspicuous on the flight feathers when TOTMIS values dipped, through having dispersed to coverts for shelter from the drier, warmer surrounding air (Dubinin,1951). It could be argued that to some extent our results may have arisen through variation in the proportion of migratory and sedentary robins netted in different periods of the year, but the robin population in our study site is known to be a locally resident population with little evidence for distant dispersal or influx from other sites (See supporting information 1, Appendix S1) .

In the British Isles, robins moult their feathers in July and August, so the low abundance values recorded in these months may have been attributable additionally to loss of feathers during the annual moult, as suggested for mite burdens on chaffinches (Mironov, 2000). However, it has been shown since that feather mites are less abundant on feathers that are about to fall out (Jovani & Serrano, 2001), responding to the vibration and loosening of the attachment of flight feathers to the wing prior to detaching completely (Pap *et al*., 2006), by moving onto adjoining feathers, thereby avoiding loss from their host, so there may not be as severe a loss of feather mites during moulting as perhaps originally anticipated.

We conclude with the key take-home message from our study that the prevalence and abundance of feather mites on robins show very clear seasonal cycles that are highly predictable and repeatable in successive years. Our data are consistent with Mironov (2000) and Pap *et al*. (2010), but extended over a tenfold longer period of monitoring. It is clear from all three studies that assessment of feather mite burdens in specific months of the year, rather than throughout complete years, and without knowledge of when peak and low mite burdens are most likely, may generate an incomplete picture of the extent to which a given bird species is affected by feather mites. Whilst we cannot discount entirely alternative explanations (see above), on the basis of our results we hypothesise that the most likely explanation for the seasonal cycles in feather mite abundance on robins is vertical transmission of mites from parents to their offspring during the breeding season, particularly during brooding and subsequent feeding of nestlings/fledgelings. Transfer of a proportion of the mites from parents to offspring would necessarily result in lower mite burdens on the adults and would be followed on both parents and offspring by increasing burdens as the remaining/transferred mites reproduce in subsequent months. This hypothesis is supported by the results of Mironov & Malyshev (2001), Pap *et al*. (2010) and more recently by Doña *et al*. (2017), is eminently testable and requires further substantiation by careful monitoring of both parents and their broods.

Acknowledgements

We are grateful to Chris du Feu, John Clark, the late John McMeeking, and their team of ringers from the Treswell ringing group for their fieldwork and for providing their data on mite infestations in robins. We thank Gill Albones, Regional Network Manager at the Meteorological Office in Derby and Mike Stewart from the Quality Control Team for the provision of the meteorological data for this study. The contributions of undergraduate students at the University Nottingham who conducted preliminary analyses on this and earlier datasets are gratefully appreciated. We thank Peter McGregor, Chris du Feu, Francis Gilbert and Tom Reader for their advice on earlier drafts of the manuscript and statistical analysis.

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Table 1 Variation in measures of infestation with feather mites by host sex and age

Factor	level	*n*	Prevalence		NIWF*		TOTMIS**	
			%	95% CL	Mean ± SEM		Mean ± SEM	
Sex	Males	86	97.7	89.84-99.70	8.4	0.45	9.5	0.74
	Females	59	96.6	90.37-99.05	8.2	0.62	8.9	0.94
Age based on all birds throughout the year								
	Class 1	299	84.6	80.45-88.07	3.6	0.17	2.9	0.16
	Class 2	249	90.8	87.54-93.22	4.7	0.22	4.0	0.25
	Class 3	239	97.9	96.04-98.92	9.8	0.28	12.6	0.53
	Class 4	99	93.9	83.33-98.29	7.4	0.47	8.7	0.77
Age based on birds examined in May to September, inclusive								
	Class 1	299	84.6	80.45-88.07	3.6	0.17	2.9	0.16
	Class 2	128	83.6	77.00-88.69	3.4	0.28	2.6	0.24
	Class 3	89	95.5	86.41-98.89	7.3	0.46	7.5	0.61
	Class 4	46	91.3	76.54-97.62	4.8	0.56	4.8	0.68

*Number of infested wing feathers
**Total mite infestation score

Table 2. Model selection of mixed-effects models based on corrected Akaike's Information Criterion (AICc) for testing the effects of the individual variables age, month of capture (month), average daily temperature in month of capture (AvDailyYrMnthT) and average daily temperature in the month preceding that of capture (AvDailyYrMnthmin1T) on prevalence of feather mites and on feather mite infestation scores (TOTMIS) on robins gland.

Model	K	AICc	ΔAICc	w_i	ER
Prevalence					
1. AvDailyYrMnthT+AvDailyYrMnthmin1T	**4**	**483.05**	**0.00**	**0.13**	
2. AvDailyYrMnthT+AvDailyYrMnthmin1T^2	4	483.05	0.01	0.13	1.01
3. AvDailyYrMnthmin1T+AvDailyYrMnthT^2	4	483.15	0.10	0.13	1.05
4.AvDailyYrMnthT^2+AvDailyYrMnthmin1T^2	4	483.43	0.38	0.11	1.21
5. AvDailyYrMnthT	3	484.90	1.85	0.05	2.52
6.AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthT^2	5	485.01	1.96	0.05	2.66
7. AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthmin1T^2	5	485.04	1.99	0.05	2.70
8. AvDailyYrMnthT+AvDailyYrMnthT^2+ AvDailyYrMnthmin1T^2	5	485.07	2.02	0.05	2.75
9.AvDailyYrMnthmin1T+AvDailyYrMnthT^2+ AvDailyYrMnthmin1T^2	5	485.16	2.12	0.05	2.89
10. age+AvDailyYrMnthT	6	486.06	3.01	0.03	4.50
29. age+AvDailyYrMnthmin1T^2	6	495.66	12.61	<0.01	546.94
30. age+month	16	495.90	12.85	<0.01	616.67
31. AvDailyYrMnthmin1T^2	3	497.17	14.12	<0.01	>1000
32. age+month+month:age	32	506.65	23.60	<0.01	>1000

33. age	5	509.60	26.55	<0.01	>1000

	K	AICc	ΔAICc	w_i	ER
TOTMIS					
1. age+month	**17**	**5151.77**	**0.00**	**0.99**	
2. month	14	5161.65	9.89	0.01	140.40
3. age+AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthmin1T^2	9	5213.09	61.33	<0.01	>1000
4. age+AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthT^2+AvDailyYrMnthmin1T^2	10	5213.84	62.07	<0.01	>1000
5. age+AvDailyYrMnthT+AvDailyYrMnthmin1T	8	5218.18	66.42	<0.01	>1000
6. age+AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthT^2	9	5220.22	68.46	<0.01	>1000
7. age+AvDailyYrMnthmin1T+AvDailyYrMnthT^2	8	5221.57	69.81	<0.01	>1000
8. age+AvDailyYrMnthT+AvDailyYrMnthmin1T^2	8	5223.43	71.66	<0.01	>1000
9. age+AvDailyYrMnthT	7	5224.55	72.78	<0.01	>1000
10. age+AvDailyYrMnthT+AvDailyYrMnthT^2+ AvDailyYrMnthmin1T^2	9	5225.36	73.59	<0.01	>1000
28. AvDailyYrMnthmin1T^2	4	5358.86	207.10	<0.01	>1000
29. AvDailyYrMnthT	4	5384.06	232.29	<0.01	>1000
30. AvDailyYrMnthT+AvDailyYrMnthT^2	5	5385.58	233.82	<0.01	>1000
31. AvDailyYrMnthT^2	4	5401.84	250.08	<0.01	>1000
32. age	6	5402.04	250.27	<0.01	>1000

- All models included year as a random factor. The table shows the top 10 and the bottom five models.

- K= degrees of freedom (no. of parameters in model +2), ΔAICc =change in AICc from the top model above, w_i:=AICc weight, proportion of the total predictive power provided by the full set of models in each of the assessed models. ER=evidence ratio (Symonds & Moussalli, 2011. For prevalence, models are with binary errors and for TOTMIS, with Gaussian errors.

Legends for figures

Fig. 1. Annual variation in feather mite infestations. Percentage of birds with mites (A), mean number of primary flight feathers with mites (B) and mean TOTMIS (C). Twenty-one birds in 1998, two in 2013 and three birds assessed in 2014 were omitted from these analyses. The sample sizes from 1999 to 2012, inclusive were 72, 43, 38, 31, 99, 71, 53, 84, 81, 90, 77, 69, 29, and 36, respectively (total =873).

Fig. 2. Monthly variation in feather mite infestations. Percentage of birds with mites (A), mean number of primary flight feathers with mites (B) and mean TOTMIS (C). The sample sizes from January to December, inclusive were 27, 35, 71, 58, 60, 108, 154, 144, 100, 78, 30, and 34, respectively (total =899).

Fig. 3. Monthly variation in feather mite infestations as reflected in (A) prevalence, (B) TOTMIS in birds of different age and (C) TOTMIS in both sexes. For female robins the sample sizes in March to August were 1, 16, 18, 16, 7, and 1, respectively, and for male birds in April to July the numbers were 25, 27, 25, and 9, respectively.

Fig. 4. Variation in feather mite infestations on robins, by year and month of the study, and mean ambient temperature.

A; Prevalence of feather mite infestation in successive months over a period of 14 years. Data are shown for 156 months in the period from September 1998, until October 2012, inclusive, spanning 14.5 years. In this period values in all 12 months of the year were available in three years (1999, 2004, and 2007), for eleven months in eight years (2000, 2002, 2003, 2005, 2006, 2008, 2009, 2011), ten months in two years (2001, 2012) and eight in one year (2011). In 1998, data were available for only four months from September (when the project was initiated) to December, inclusive.

B; TOTMIS values in successive months over a period of 14 years.

C; Relationship of mean monthly TOTMIS values to mean monthly average temperatures (°C). Error bars are not shown in C, so as not to obscure the relationship between temperature and TOTMIS.

Fig. 5. Correlations between prevalence (A) and individual TOTMIS values (B and C) in each month of the study, and the mean of average daily temperatures in the month of capture (AvDailyYrMnthT; A and B)) and the preceding month (AvDailyYrMnthmin1T; A and C). The linear regression equation for B is TOTMIS = 18.486 - (0.943 x AvDailyYrMnthT) and the second order polynomial equation for C, TOTMIS = 22.999 - (1.963 x AvDailyYrMnthmin1T) + (0.044 x [AvDailyYrMnthmin1T]^2). R^2 values are 0.363 and 0.435, respectively. For additional statistical analyses, see text.

Fig. 1.

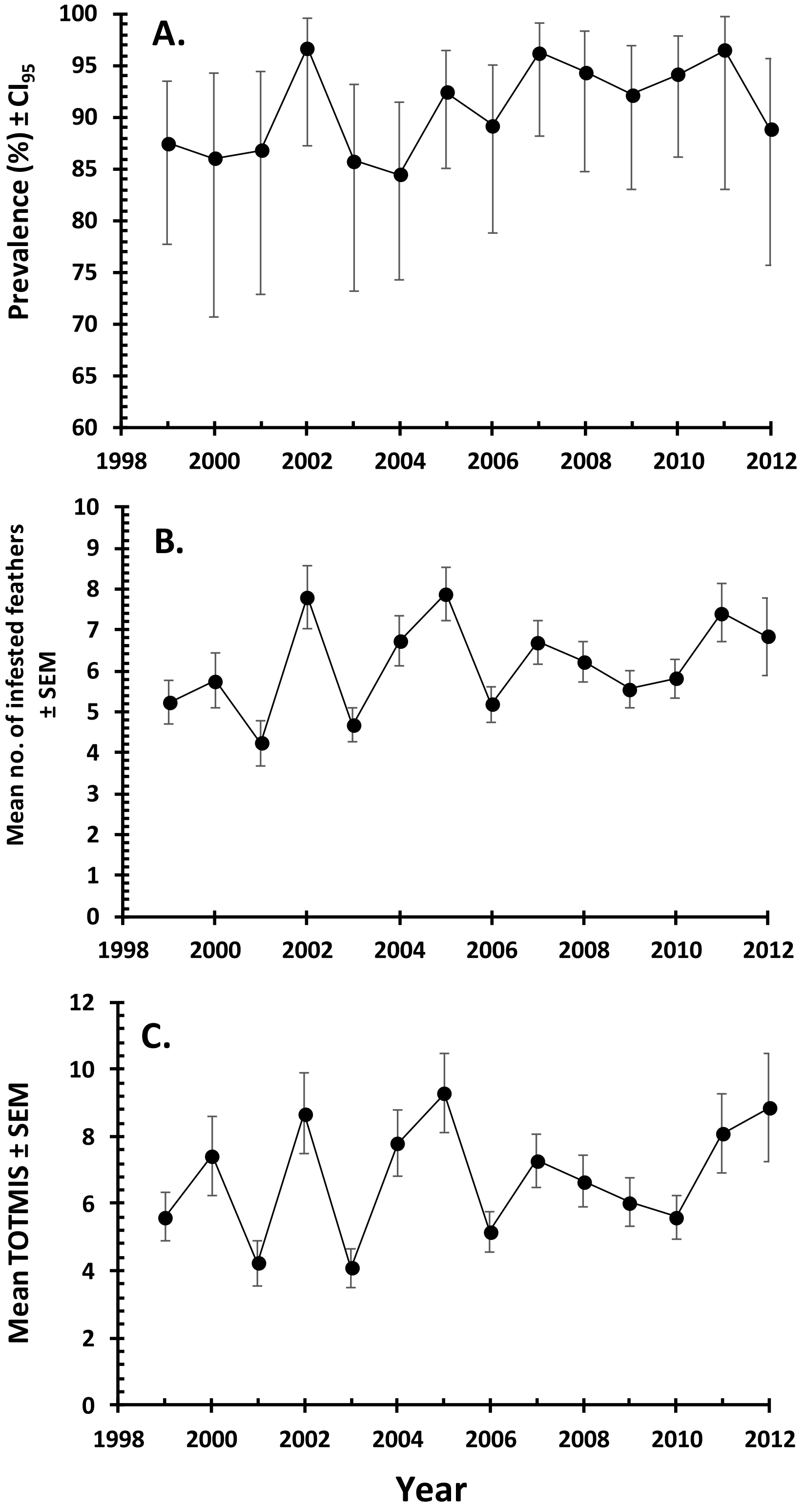

A.
Prevalence (%) ± CI_{95}
100
95
90
85
80
75
70
65
60
B.
Mean no. of infested feathers ± SEM
10
9
8
7
6
5
4
3
2
1
0
C.
Mean TOTMIS ± SEM
12
10
8
6
4
2
0
1998
2000
2002
2004
2006
2008
2010
2012
Year

Fig. 2.

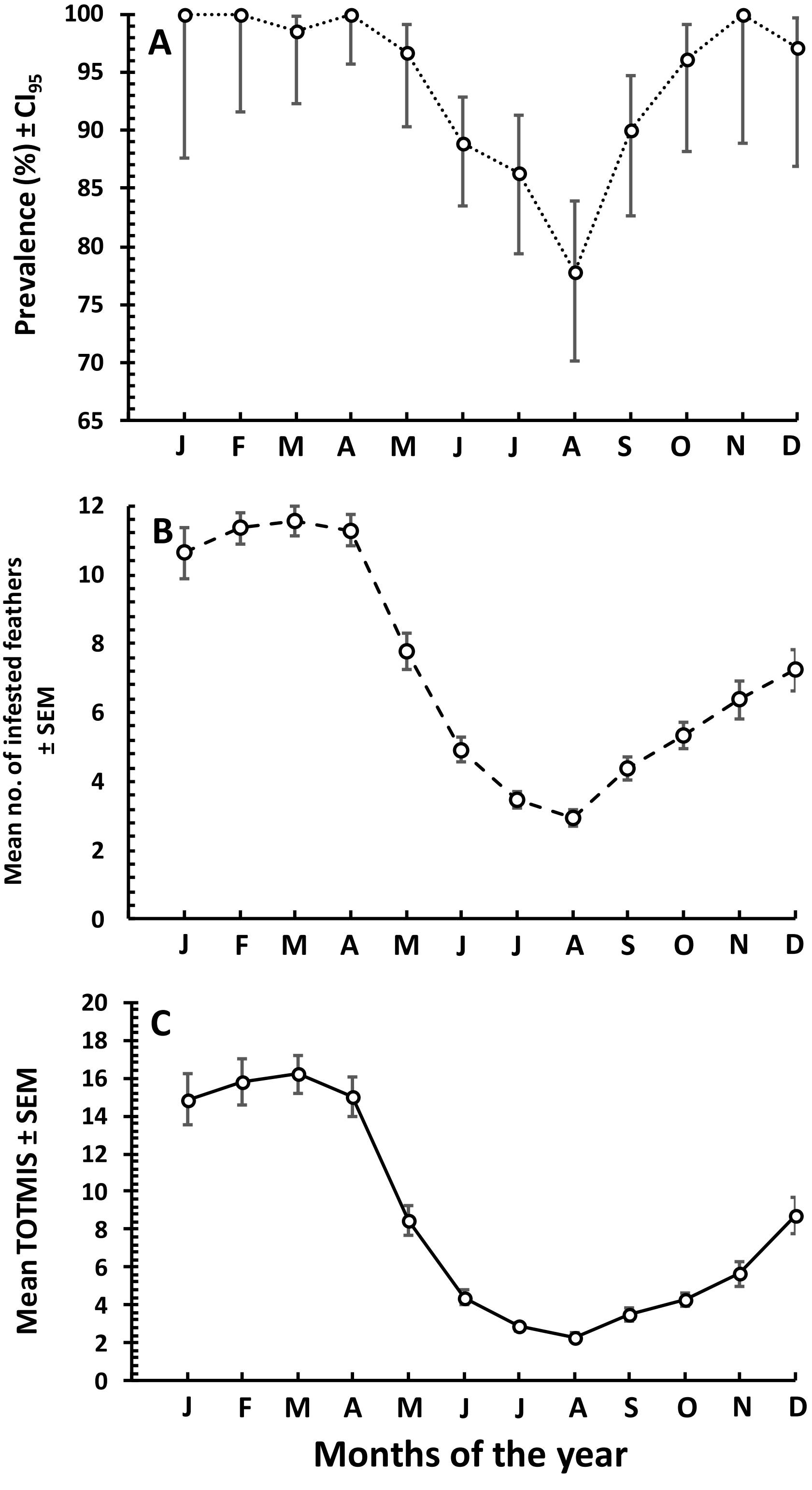

A
Prevalence (%) ± CI95
100
95
90
85
80
75
70
65
J F M A M J J A S O N D
B
Mean no. of infested feathers ± SEM
12
10
8
6
4
2
0
J F M A M J J A S O N D
C
Mean TOTMIS ± SEM
20
18
16
14
12
10
8
6
4
2
0
J F M A M J J A S O N D
Months of the year

Fig. 3

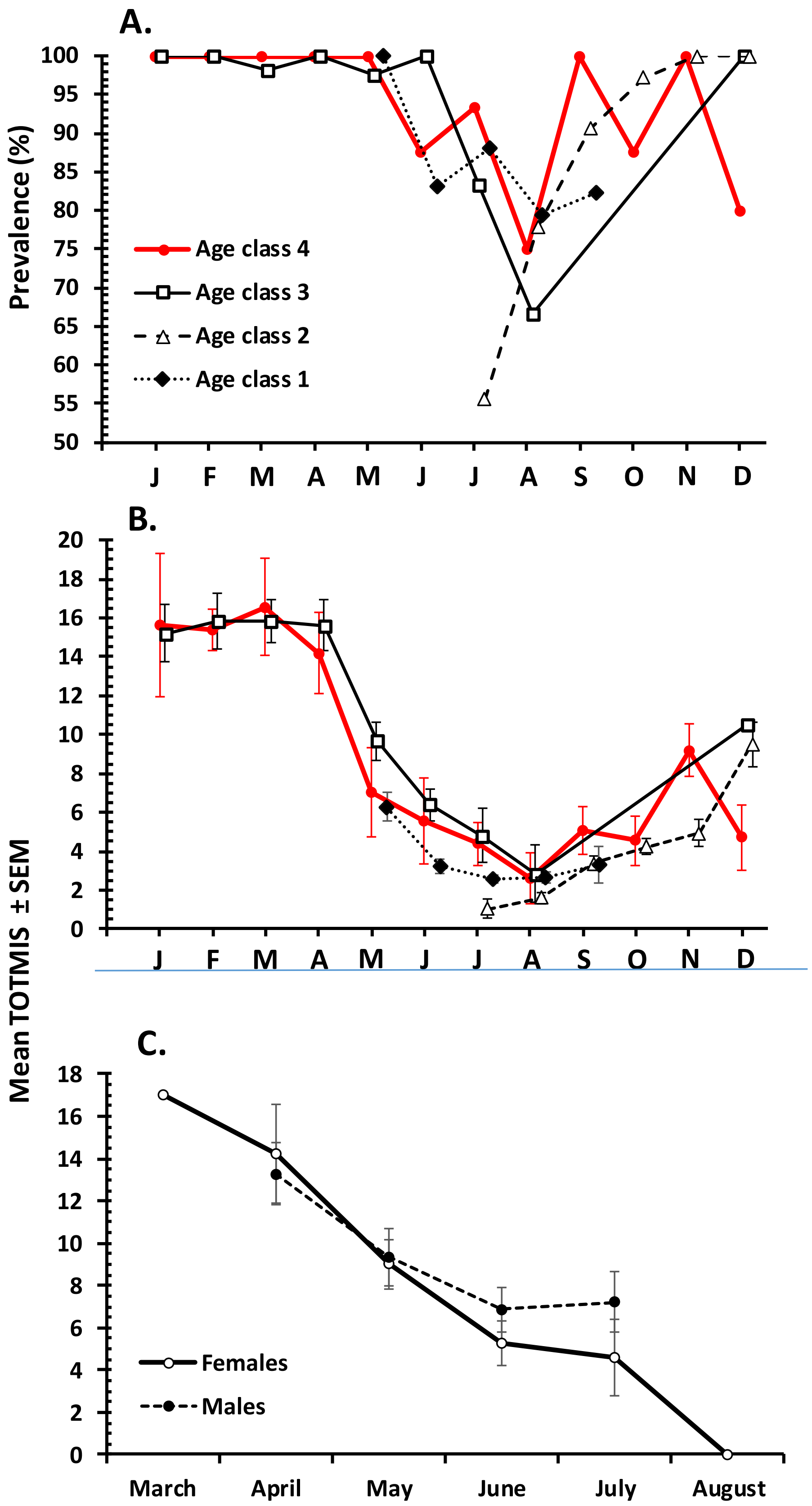

A.
Prevalence (%)
100
95
90
85
80
75
70
65
60
55
50
Age class 4
Age class 3
Age class 2
Age class 1
J
F
M
A
M
J
J
A
S
O
N
D
B.
20
18
16
14
12
10
8
6
4
2
0
J
F
M
A
M
J
J
A
S
O
N
D
Mean TOTMIS ± SEM
C.
18
16
14
12
10
8
6
4
2
0
Females
Males
March
April
May
June
July
August

Fig. 4

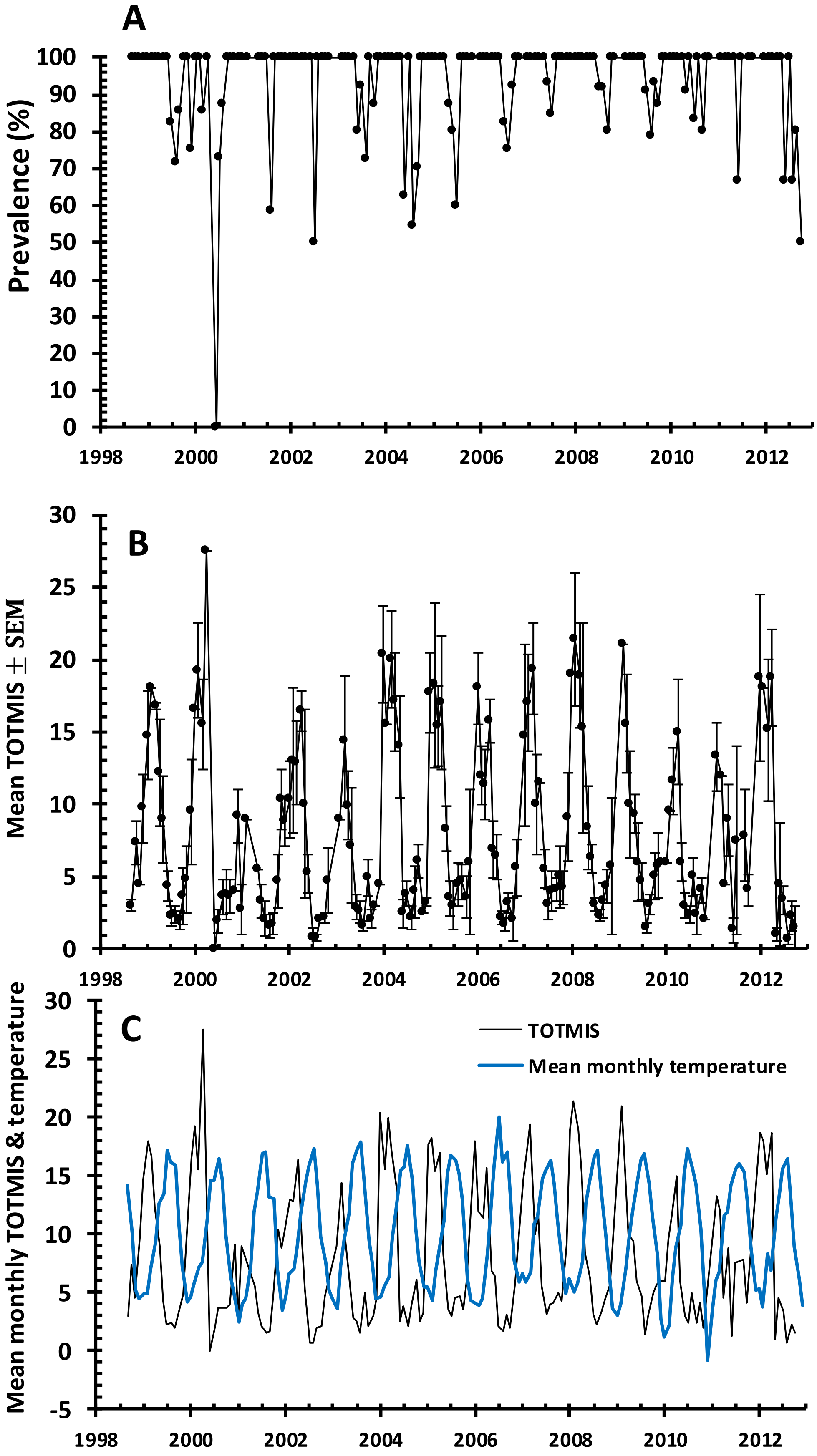
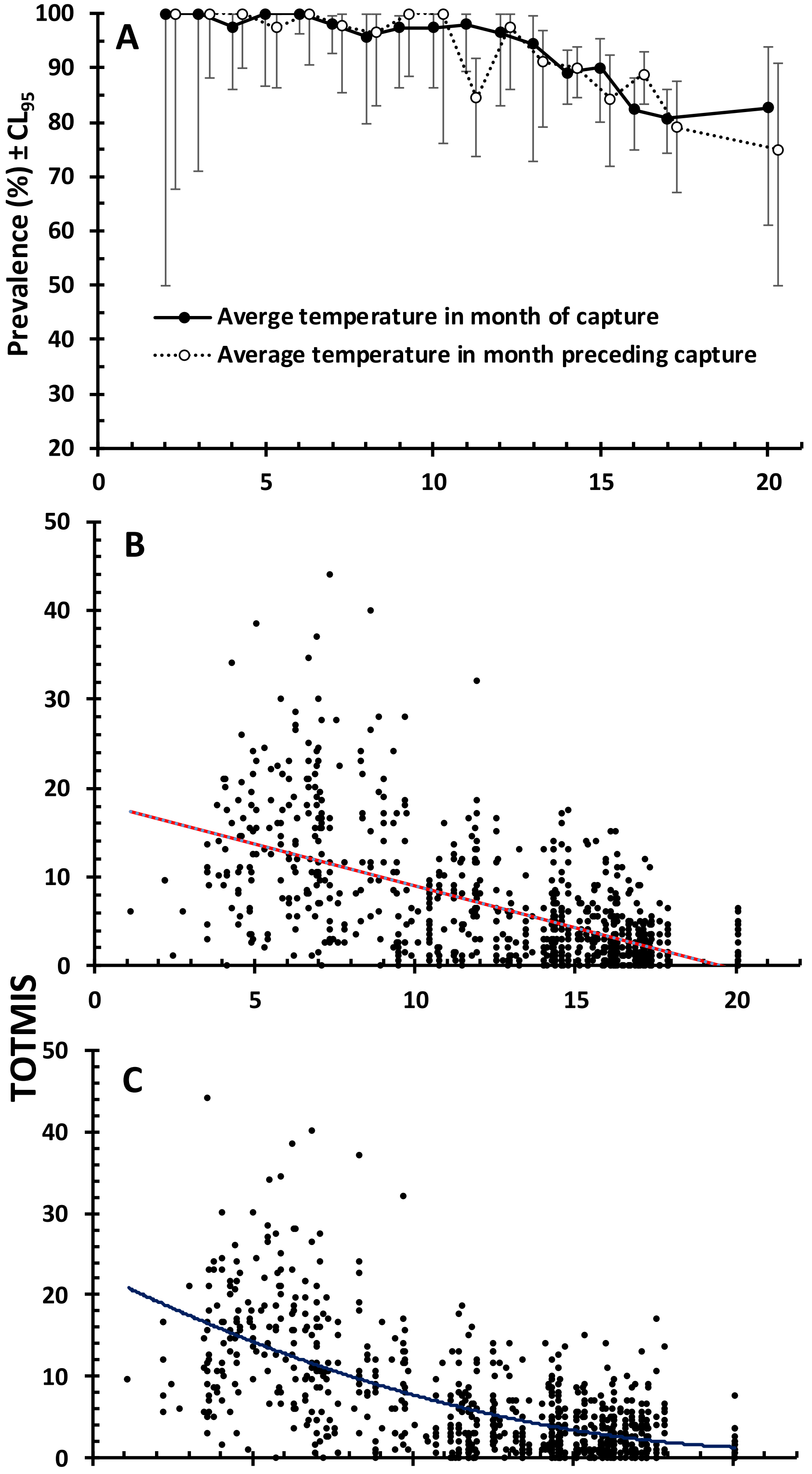

A
Prevalence (%)
100
90
80
70
60
50
40
30
20
10
0
1998
2000
2002
2004
2006
2008
2010
2012
B
Mean TOTMIS ± SEM
30
25
20
15
10
5
0
1998
2000
2002
2004
2006
2008
2010
2012
C
Mean monthly TOTMIS & temperature
TOTMIS
Mean monthly temperature
30
25
20
15
10
5
0
-5
1998
2000
2002
2004
2006
2008
2010
2012

Fig. 5


A
Prevalence (%) ± CL_{95}
100
90
80
70
60
50
40
30
20
0
5
10
15
20
Averge temperature in month of capture
Average temperature in month preceding capture
B
50
40
30
20
10
0
0
5
10
15
20
TOTMIS
C
50
40
30
20
10
0
0
5
10
15
20
Mean monthy temperature (°C)

Supporting information (Appendix I)

Evidence in support of the robins in Treswell wood constituting an essentially resident population.

As far as we have been able to ascertain the robin population in Treswell Wood is essentially a resident population, with movement of birds mostly confined to the woods and to the immediate vicinity and only vary rarely further afield.

Overall, we have encountered 4,569 robins from December 1972 onwards, of which only 18 have been encountered elsewhere. These break down as follows:

- 11 ringed as juvenile, found locally (i.e. within local villages or towns in the north of the county of Nottinghamshire, furthest being in Worksop). These are essentially juvenile birds that have moved, often several kilometres, to or from the wood as part of post-natal dispersal.
- 4 ringed as adults in the breeding season and found in a subsequent breeding season elsewhere (same localities as juveniles)
- 1 ringed as an adult in the breeding season and found in a local village in a subsequent winter.
- 1 juvenile found in Worthing the following spring.
- 1 adult ringed at Gibraltar Point in March and found in the wood two weeks later. This was a most odd movement. Gibraltar Point is where migrants may land in autumn but in spring they can use it as a location from which to set off before crossing the North Sea. However, this was quite the wrong time of year for a migrating bird to be caught there.

Therefore, overall these observations point to very little long-distance movement.

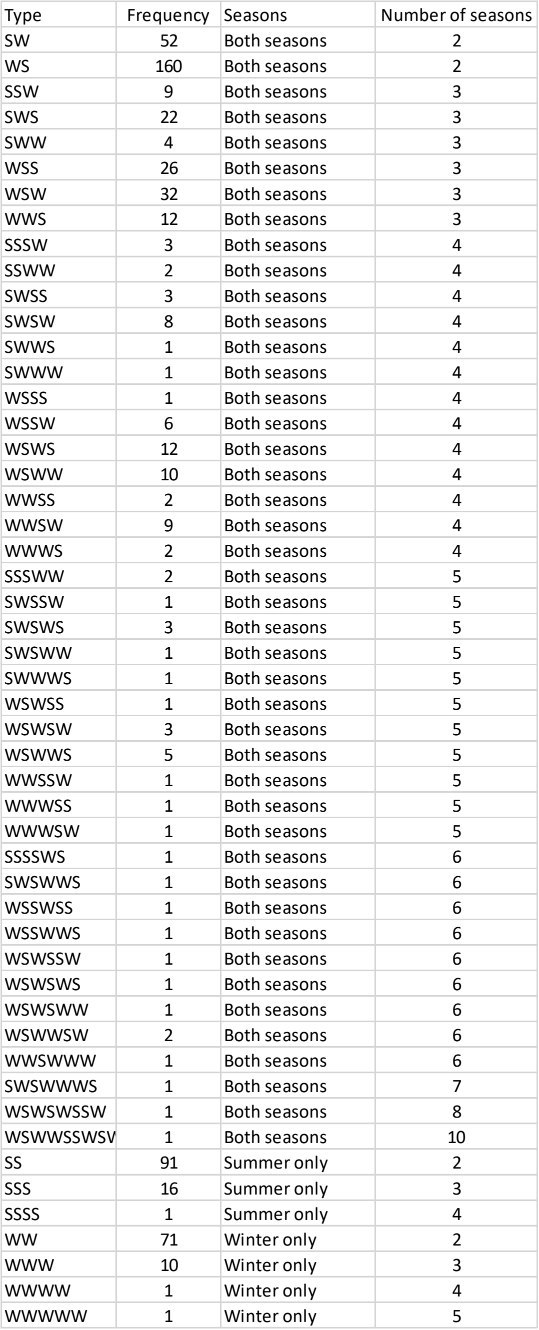
Next, all the juvenile captures were eliminated because they are potentially the birds that will disperse and we focused only on birds caught in the winter (October to February) and the breeding season (March to June). Each bird record was considered and it was noted whether it has been caught in a breeding season, or in a winter, or both.

The numbers in the table below demonstrate that the population is essentially sedentary.

Period	Multiple captures	Captured only once	Totals
Both seasons	410	-	410
Summer only	108	1139	1247
Winter only	83	732	815
Total	601	1871	2472

Data for records up to June 2021

The table below shows the seasons in which we re-examined the 601 birds that were trapped more than once, and for each category, the number of seasons involved. From the top downwards, 52 birds were seen twice, first re-trapped in the summer and then winter. Next, 160 birds were first re-trapped in the winter and then were seen also in a summer. Nine birds were re-trapped three times, the first two occasions being in the summer and then once in the winter, and so on.



Type	Frequency	Seasons	Number of seasons
SW	52	Both seasons	2
WS	160	Both seasons	2
SSW	9	Both seasons	3
SWS	22	Both seasons	3
SWW	4	Both seasons	3
WSS	26	Both seasons	3
WSW	32	Both seasons	3
WWS	12	Both seasons	3
SSSW	3	Both seasons	4
SSWW	2	Both seasons	4
SWSS	3	Both seasons	4
SWSW	8	Both seasons	4
SWWS	1	Both seasons	4
SWWW	1	Both seasons	4
WSSS	1	Both seasons	4
WSSW	6	Both seasons	4
WSWS	12	Both seasons	4
WSWW	10	Both seasons	4
WWSS	2	Both seasons	4
WWSW	9	Both seasons	4
WWWS	2	Both seasons	4
SSSWW	2	Both seasons	5
SWSSW	1	Both seasons	5
SWSWS	3	Both seasons	5
SWSWW	1	Both seasons	5
SWWWS	1	Both seasons	5
WSWSS	1	Both seasons	5
WSWSW	3	Both seasons	5
WSWWS	5	Both seasons	5
WWSSW	1	Both seasons	5
WWWSS	1	Both seasons	5
WWWSW	1	Both seasons	5
SSSSWS	1	Both seasons	6
SWSWWS	1	Both seasons	6
WSSWSS	1	Both seasons	6
WSSWWS	1	Both seasons	6
WSWSSW	1	Both seasons	6
WSWSWS	1	Both seasons	6
WSWSWW	1	Both seasons	6
WSWWSW	2	Both seasons	6
WWSWWW	1	Both seasons	6
SWSWWWS	1	Both seasons	7
WSWSWSSW	1	Both seasons	8
WSWWSSWSV	1	Both seasons	10
SS	91	Summer only	2
SSS	16	Summer only	3
SSSS	1	Summer only	4
WW	71	Winter only	2
WWW	10	Winter only	3
WWWW	1	Winter only	4
WWWWW	1	Winter only	5

W= winter, non-breeding season and S= summer breeding season

The numbers for birds caught only in the breeding season or only in the winter appear high and a pertinent question is where have they gone? Could these be birds from afar which bring different mite loads into the Treswell Wood population? We believe that the answer is No. These are birds just caught in one season and not again in subsequent years. Where do they go? Probably not far at all and likely to have died or fallen victims to predators. Very many small birds do not live to see a second winter or second breeding season.

Whether a bird is re-trapped in a subsequent season depends on two things - its survival and its probability of recapture. Of the birds caught in at least one of the seasons, about 75% (1871/2472) are not found in a subsequent season. That suggests the probability of recapture in a subsequent season is about 25% so we can expect a good number of birds which are in the wood in the next season not to be re-trapped, but some of those could be re-trapped in the season after that (making them an apparent WW or SS bird). In fact 68% of the birds found in more than one season have captures in at least one winter and one summer. These observations are also compatible with our view that the adult robins are generally resident, while juveniles disperse.

With our netting regime (nets are rotated around the wood netting sites, with a different location in successive weeks) we may set nets in the same place perhaps twice in each season. Even if the nets run right through a bird's territory there is no guarantee that we will catch it on that occasion - to be caught it needs to fly into the net. The net 'catching area' is very small compared to the total in the Robin's territory - trees are perhaps 30m tall and the nets only reach about 2.5 m. The Robin might see the net and avoid it. It might not even fly near the net at all, especially if sitting on a nest. We consider that the 601 captures in subsequent seasons really is quite a high recapture rate when these things are considered. Thus, the fact that we have 'only' found 601 out of 2472 in at least one subsequent season does not suggest, in the least, any great mobility of the species.

Supporting information (SI)

Fig. S1. Time series analysis of TOTMIS values, showing (A) the fitted observed values, (B) the smoothed trend, (C) the seasonal component, (D) the remaining random variation, and (E) the adjusted data after removal of the seasonal component.

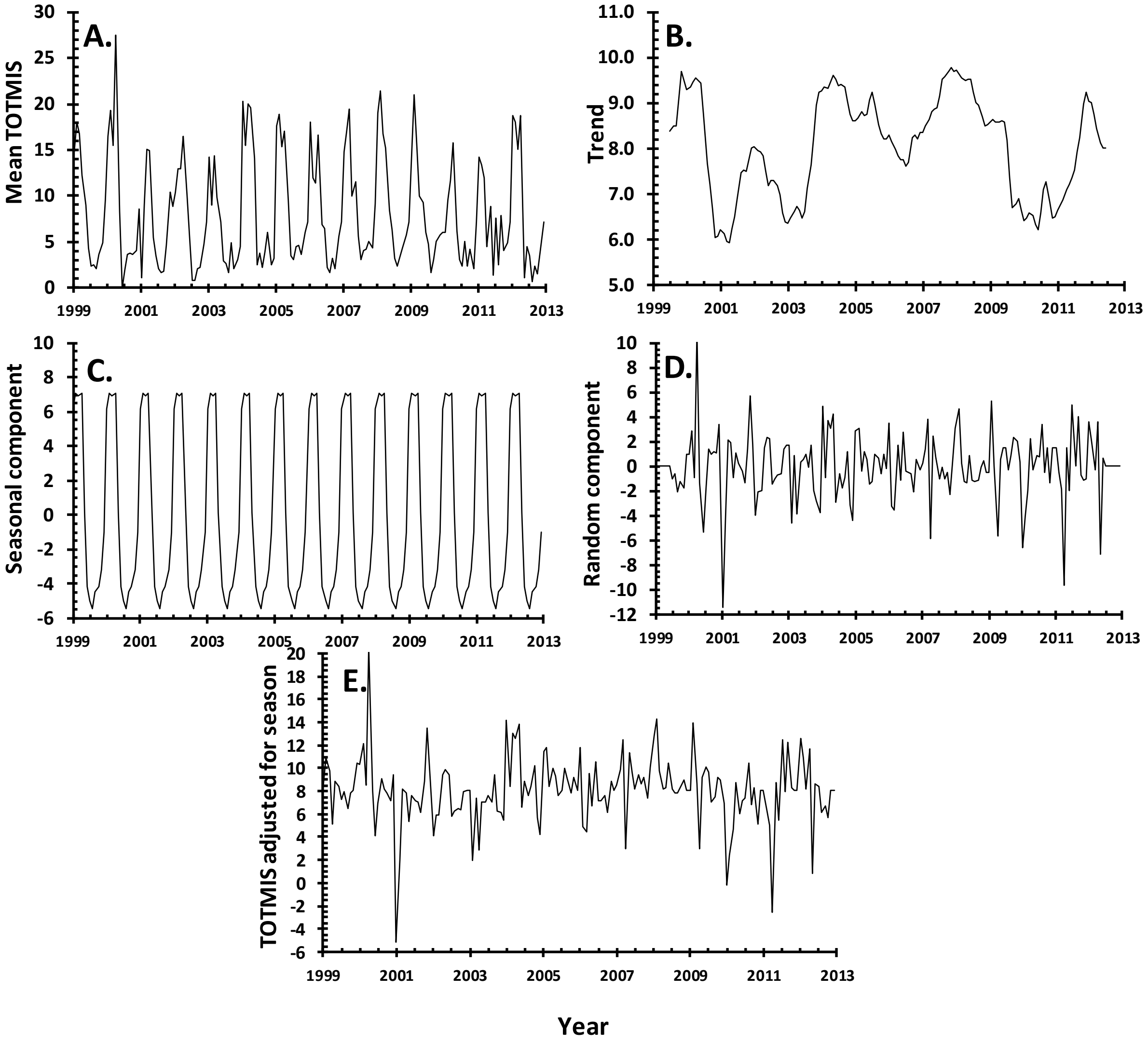
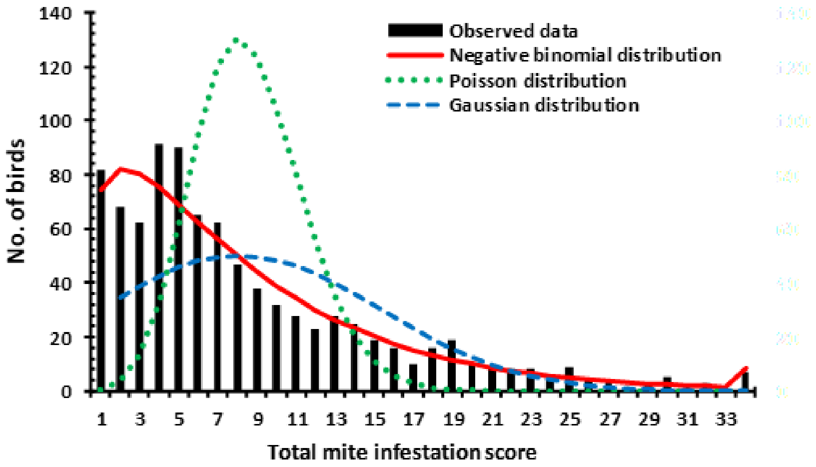


Fig. S2 . Frequency distribution of total mite infestation scores and negative binomial, Poisson and Gaussian distributions fitted to the data. I=7.443 and D=0.486.

The degree of aggregation in the data was assessed by the index of discrepancy (D) as described by Poulin (1993) and the index of dispersion (I, variance to mean ratio). Frequency distributions were tested for goodness of fit to Gaussian, negative binomial, positive binomial and Poisson models by χ^2 in bespoke software based on Elliott (1977) and the negative binomial exponent k is given as appropriate.

The distribution of TOTMIS was a good fit to the negative binomial distribution (Fig. S2; χ^2_{24}=31.1, P=0.151; k=1.292 ± 0.0053; I=7.452 and D=0.487). Whilst the distribution of NIWF differed significantly from a negative binomial distribution (not illustrated; χ^2_{19}=64.7, P<0.001; k=1.892 ± 0.016; I=3.362 and D=0.422), nevertheless, it was a better fit to this distribution than to Poisson (χ^2_{12}=2604.5, P<0.001) or Gaussian (χ^2_{17}=107.2, P<0.001) distributions.



Elliott, J.M. (1977). *Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates.* Freshwater Biological Association, Cumbria, UK.

Poulin, R. (1993) The disparity between observed and uniform distributions: a new look at parasite aggregation. *Int. J. Parasitol.* **23**, 937-944.

Table S1. Model selection of mixed-effects models based on corrected Akaike's Information Criterion (AICc) for testing the effects of the individual variables age, month of capture (month), average daily temperature in month of capture (AvDailyYrMnthT) and average daily temperature in the month preceding that of capture (AvDailyYrMnthmin1T) on prevalence of feather mites and feather mite infestation scores (TOTMIS) on robins in Nottinghamshire, England.

Model	JMBno	K	AICc	ΔAICc	AICcWt	Cum.Wt	.LL
Prevalence							
1. AvDailyYrMnthT+AvDailyYrMnthmin1T	**10**	**4**	**483.05**	**0.00**	**0.13**	**0.13**	**-237.50**
2. AvDailyYrMnthT+AvDailyYrMnthmin1T^2	12	4	483.05	0.01	0.13	0.27	-237.50
3. AvDailyYrMnthmin1T+AvDailyYrMnthT^2	13	4	483.15	0.10	0.13	0.40	-237.55
4.AvDailyYrMnthT^2+AvDailyYrMnthmin1T^2	15	4	483.43	0.38	0.11	0.51	-237.69
5. AvDailyYrMnthT	2	3	484.90	1.85	0.05	0.56	-239.43
6.AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthT^2	22	5	485.01	1.96	0.05	0.61	-237.47
7. AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthmin1T^2	24	5	485.04	1.99	0.05	0.66	-237.49
8. AvDailyYrMnthT+AvDailyYrMnthT^2+ AvDailyYrMnthmin1T^2	23	5	485.07	2.02	0.05	0.71	-237.50
9.AvDailyYrMnthmin1T+AvDailyYrMnthT^2+ AvDailyYrMnthmin1T^2	25	5	485.16	2.12	0.05	0.76	-237.55
10. age+AvDailyYrMnthT	6	6	486.06	3.01	0.03	0.79	-236.98
11. age+AvDailyYrMnthT+ AvDailyYrMnthmin1T^2	18	7	486.53	3.48	0.02	0.81	-236.20
12.AvDailyYrMnthT^2	4	3	486.56	3.51	0.02	0.83	-240.27
13. age+AvDailyYrMnthT+AvDailyYrMnthmin1T	16	7	486.70	3.65	0.02	0.85	-236.29
14. age+AvDailyYrMnthT^2+ AvDailyYrMnthmin1T^2	21	7	486.71	3.66	0.02	0.88	-236.29

15. age+AvDailyYrMnthmin1T+ AvDailyYrMnthT^2	19	7	486.73	3.68	0.02	0.90	-236.30
16. AvDailyYrMnthT+AvDailyYrMnthT^2	11	4	486.82	3.78	0.02	0.92	-239.39
17. age+AvDailyYrMnthT^2	8	6	486.86	3.81	0.02	0.94	-237.38
18. AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthT^2+AvDailyYrMnthmin1T^2	29	6	487.03	3.98	0.02	0.96	-237.46
19. age+AvDailyYrMnthT+AvDailyYrMnthT^2	17	7	488.09	5.04	0.01	0.97	-236.98
20. age+AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthmin1T^2	27	8	488.52	5.47	0.01	0.98	-236.18
21. age+AvDailyYrMnthT+AvDailyYrMnthT^2+ AvDailyYrMnthmin1T^2	28	8	488.53	5.48	0.01	0.98	-236.18
22. age+AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthT^2	26	8	488.65	5.61	0.01	0.99	-236.24
23. age+AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthT^2 +AvDailyYrMnthmin1T^2	30	9	490.55	7.50	<0.01	1.00	-236.17
24. month	31	13	491.36	8.31	<0.01	1.00	-232.47
25. age+AvDailyYrMnthmin1T	7	6	493.74	10.69	<0.01	1.00	-240.82
26. AvDailyYrMnthmin1T	3	3	493.76	10.71	<0.01	1.00	-243.87
27. AvDailyYrMnthmin1T+ AvDailyYrMnthmin1T^2	14	4	494.42	11.37	<0.01	1.00	-243.19
28. age+AvDailyYrMnthmin1T+ AvDailyYrMnthmin1T^2	20	7	495.07	12.02	<0.01	1.00	-240.47
29. age+AvDailyYrMnthmin1T^2	9	6	495.66	12.61	<0.01	1.00	-241.78
30. age+month	32	16	495.90	12.85	<0.01	1.00	-231.63
31. AvDailyYrMnthmin1T^2	5	3	497.17	14.12	<0.01	1.00	-245.57
32. age+month+month:age	33	32	506.65	23.60	<0.01	1.00	-220.05
33. age	1	5	509.60	26.55	<0.01	1.00	-249.76

	No	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
TOTMIS							
1. age+month	**32**	**17**	**5151.77**	**0.00**	**0.99**	**0.99**	**-2558.52**
2. month	31	14	5161.65	9.89	0.01	1.00	-2566.58
3. age+AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthmin1T^2	27	9	5213.09	61.33	<0.01	1.00	-2597.44
4. age+AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthT^2+AvDailyYrMnthmin1T^2	30	10	5213.84	62.07	<0.01	1.00	-2596.79
5. age+AvDailyYrMnthT+AvDailyYrMnthmin1T	16	8	5218.18	66.42	<0.01	1.00	-2601.01
6. age+AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthT^2	26	9	5220.22	68.46	<0.01	1.00	-2601.00
7. age+AvDailyYrMnthmin1T+AvDailyYrMnthT^2	19	8	5221.57	69.81	<0.01	1.00	-2602.70
8. age+AvDailyYrMnthT+AvDailyYrMnthmin1T^2	18	8	5223.43	71.66	<0.01	1.00	-2603.63
9. age+AvDailyYrMnthT	6	7	5224.55	72.78	<0.01	1.00	-2605.21
10. age+AvDailyYrMnthT+AvDailyYrMnthT^2+ AvDailyYrMnthmin1T^2	28	9	5225.36	73.59	<0.01	1.00	-2603.57
11. age+AvDailyYrMnthT +AvDailyYrMnthT^2	17	8	5226.45	74.69	<0.01	1.00	-2605.14
12. age+AvDailyYrMnthT^2+AvDailyYrMnthmin1T^2	21	8	5230.88	79.12	<0.01	1.00	-2607.36
13. age+AvDailyYrMnthT^2	8	7	5235.07	83.30	<0.01	1.00	-2610.47
14. age+AvDailyYrMnthmin1T+ AvDailyYrMnthmin1T^2	20	8	5235.95	84.19	<0.01	1.00	-2609.89
15. age+AvDailyYrMnthmin1T	7	7	5250.88	99.11	<0.01	1.00	-2618.37
16. AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthT^2+AvDailyYrMnthmin1T^2	29	7	5265.30	113.54	<0.01	1.00	-2625.59
17. AvDailyYrMnthmin1T+AvDailyYrMnthT^2+ AvDailyYrMnthmin1T^2	25	6	5265.39	113.63	<0.01	1.00	-2626.65
18. AvDailyYrMnthT+AvDailyYrMnthmin1T+							

AvDailyYrMnthmin1T^2	24	6	5269.18	117.41	<0.01	1.00	-2628.54
19. AvDailyYrMnthmin1T+AvDailyYrMnthmin1T^2	14	5	5279.33	127.56	<0.01	1.00	-2634.63
20. AvDailyYrMnthmin1T+AvDailyYrMnthT^2	13	5	5281.14	129.38	<0.01	1.00	-2635.54
21. AvDailyYrMnthT+AvDailyYrMnthmin1T	10	5	5281.95	130.19	<0.01	1.00	-2635.94
22. AvDailyYrMnthT+AvDailyYrMnthmin1T+ AvDailyYrMnthT^2	22	6	5283.07	131.31	<0.01	1.00	-2635.49
23. age+AvDailyYrMnthmin1T^2	9	7	5283.86	132.10	<0.01	1.00	-2634.87
24. AvDailyYrMnthmin1T	3	4	5300.51	148.74	<0.01	1.00	-2646.23
25. AvDailyYrMnthT+AvDailyYrMnthmin1T^2	12	5	5310.48	158.71	<0.01	1.00	-2650.20
26. AvDailyYrMnthT+AvDailyYrMnthT^2+ AvDailyYrMnthmin1T^2	23	6	5312.46	160.70	<0.01	1.00	-2650.18
27. AvDailyYrMnthT^2+AvDailyYrMnthmin1T^2	15	5	5314.64	162.88	<0.01	1.00	-2652.29
28. AvDailyYrMnthmin1T^2	5	4	5358.86	207.10	<0.01	1.00	-2675.41
29. AvDailyYrMnthT	2	4	5384.06	232.29	<0.01	1.00	-2688.00
30. AvDailyYrMnthT+AvDailyYrMnthT^2	11	5	5385.58	233.82	<0.01	1.00	-2687.76
31. AvDailyYrMnthT^2	4	4	5401.84	250.08	<0.01	1.00	-2696.90
32. age	1	6	5402.04	250.27	<0.01	1.00	-2694.97

K= degrees of freedom (no. of parameters in model +2), ΔAICc =change in AICc from the top model above. All models included year of capture as a random factor. For prevalence models are with binary errors and for TOTMIS with Gaussian errors.