Season and ambient air temperature influence the distribution of mites (*Proctophyllodes stylifer*) across the wings of blue tits (*Parus caeruleus*)

P.R. Wiles, J. Cameron, J.M. Behnke, I.R. Hartley, F.S. Gilbert, and P.K. McGregor

Abstract: Changes in the distribution of the wing-feather mite *Proctophyllodes stylifer* (Buckholz 1869) on the flight feathers of blue tits (*Parus caeruleus*) were studied throughout the seasons and in relation to ambient air temperature at three combinations of study sites (Lancashire, West Midlands, and South Midlands). We tested the hypotheses that the distribution of mites is influenced in part by season and ambient air temperature. In the winter months mites clustered predominantly on the tertiary feathers, whereas in late spring, summer, and autumn, mite-infestation scores were higher on the proximal primary and secondary feathers. Three approaches were employed to determine whether this seasonal redistribution of mites arose as a response to changes in microclimate, probably ambient air temperature, rather than to season per se. Firstly, meteorological data for the Lancashire study sites, and our own monitoring of the precise air temperature at the time of handling and inspection at the West Midlands study sites, enabled us to establish a link between distribution pattern and ambient temperature. Secondly, limited observations on the distribution of mites on birds recaptured when ambient air temperatures differed by 5°C or more between first and second nettings, one temperature being below 10°C and the other above, supported the idea that the change in distribution was associated with air temperature. Finally, the results of a small experiment in which heavily infested birds caught on a day when air temperatures ranged from 9 to 11°C were taken indoors and temporarily subjected to a higher ambient air temperature (20 min) prior to re-inspection and release also confirmed that mite movement was associated with the temperature of their environment. We conclude that the seasonal changes in distribution were driven by microclimatic changes, in part by temperature.

Résumé : Les changements dans la répartition des acariens parasites des plumes, *Proctophyllodes stylifer* (Buckholz 1869) sur les rémiges de la Mésange bleue (*Parus caeruleus*) ont été étudiés pendant toutes les saisons et en fonction de la température ambiante de l'air à trois combinaisons de sites (Lancashire, et les Midlands ouest et sud). Nous avons vérifié l'hypothèse suivante : la répartition des acariens est influencée en partie par la saison et par la température de l'air ambiant. Au cours des mois d'hiver, les acariens se regroupaient surtout sur les rémiges tertiaires, alors qu'à la fin du printemps, en été et en automne, ils étaient plus nombreux sur les rémiges primaires et secondaires proximales. Trois approches ont été utilisées pour déterminer si cette nouvelle répartition saisonnière des acariens est le résultat d'un ajustement au microclimat en changement, probablement à la température de l'air ambiant, plutôt qu'une réaction à la saison elle-même. D'abord, les données météorologiques des sites de Lancashire et nos propres mesures de la température précise au moment de la manipulation et de l'inspection aux sites des Midlands nous ont permis d'établir un lien entre les patterns de répartition et les températures ambiantes. En second lieu, les résultats d'observations limitées sur la répartition des acariens chez des oiseaux recapturés quand la température ambiante différait par 5°C ou plus entre la première et la seconde capture (inférieure à 10°C à la première capture, supérieure à 10°C à la seconde apuyaient) également l'hypothèse selon laquelle le changement de répartition est associé à la température ambiante. Enfin, une petite expérience dans laquelle des oiseaux très infestés capturés un jour où la température de l'air se situait entre 9 et 11°C ont été amenés à l'intérieur pour se trouver temporairement (20 min) à une température ambiante plus élevée avant d'être réexaminés et relâchés, a également confirmé que les déplacements des acariens étaient reliés à la température du milieu ambiant. Nous concluons que les changements saisonniers dans la répartition sont régis par des changements microclimatiques, en partie par des changements de température.

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Introduction

The feathers of birds provide a variety of microhabitats for ectoparasites (Choe and Kim 1988), and not surprisingly, different species of feather mites are often restricted to certain types of feathers and to particular regions of those feathers. In birds supporting more than one species of mite, there are characteristically different patterns of distribution of the species across the wings (Dubinin 1951, 1956; Atyeo and Perez 1988). Furthermore, the niches occupied by a single species of feather mite may vary in relation to ambient conditions. Dubinin (1951) observed a change in the distribution of feather mites when their hosts were exposed to two temperature ranges and to differences in humidity. Mites on the flight feathers of the European starling (*Sturnus vulgaris*) moved to the body feathers when the birds were subjected to low temperatures (11–14°C) and returned to the flight feathers when their hosts were in warmer surroundings (24–28°C). Similarly, when the relative humidity was high, mites migrated to feathers on or closer to the body (Evans et al. 1961). McClure (1989) noted a reverse trend with respect to humidity in the hot dry environment of Ventura County in California. However, all of these studies were based on an unquantified, subjective assessment of the distribution of mites, and statistical evaluation was not carried out.

In this paper we first report observations that the distribution of *Proctophyllodes stylifer* (Buckholz, 1869) across the flight feathers on the wings of blue tits (*Parus caeruleus*) varies with season. Mites of the genus *Proctophyllodes* are found primarily but not exclusively on the feathers of passerine birds, and it is usual for only one species of the genus to occur on a host species or on related host species (Gaud and Atyeo 1996). Although little is known about the life cycles of this group and its relationships with hosts, its biology and taxonomy were reviewed by Atyeo and Braasch (1966) and more recently by Gaud and Atyeo (1996). We tested the specific hypotheses that the distribution of this species of feather mite on blue tits is influenced by seasonal changes and is dependent in part on ambient air temperature. We used blue tits in our study because in the United Kingdom these birds predominantly carry just a single species of mite on their flight feathers, *P. stylifer*, and are easily netted in numbers suitable for quantitative observations throughout the year, but especially in the winter period, when temperatures drop close to freezing. We tested the predictions of our hypotheses in three regions of the U.K., and employed three distinct approaches.

Materials and methods

Study sites and capture and treatment of birds

The work presented in this paper was carried out independently in three regions of the U.K. by three groups of workers. Blue tits were mist-netted in a range of habitats, usually woodland, gardens, or scrubland, in the South Midlands (within a 50-km radius of Buckingham in north Buckinghamshire; n = 322), the West Midlands (within a 50-km radius of Uttoxeter in Staffordshire; n = 223), and northwest Lancashire (within a 25-km radius of the campus of the University of Lancaster; n = 289). In the winter, blue tits were mist-netted when they visited feeding stations baited with peanuts or sunflower seeds, or were netted at communal roosts. During the breeding season birds were trapped near nest boxes or mist-netted in their breeding territories. Some birds were also netted at banding stations where migrating passerines are routinely monitored.

All the birds were caught in standard mist nets and handled in accordance with established procedures of the British Trust for Ornithology (Spencer 1984) by trained, licensed bird banders.

Examination of birds for mites

After banding and on completion of morphometric measurements, the wing of each bird was extended and held up to ambient light or viewed against light from a battery-operated electric torch. At the Lancashire and South Midlands study sites we used only the right wing, whereas at the West Midlands sites we alternated the right and left wings; mite infestations do not differ between the two wings (Behnke et al. 1999). The primary feathers were exposed along their complete length, the primary coverts and underwing coverts being moved gently aside if necessary, and both sides of each feather were examined by eye. Feather mites were visible along the shaft of each infested feather and, in more intense infestations, along the barbs and barbules. It was thus possible to examine each of the flight feathers in a consistent and rapid manner (about 2–5 min per bird) without causing undue distress to the birds. At the South Midlands and Lancashire sites we employed the technique of Behnke et al. (1995), originally a modification of that reported by McClure (1989) and recently critically evaluated by Behnke et al. (1999). Briefly, mite-infestation scores in the range 0–3 (0 = no mites; 1 = 1–10 mites; 2 = 10–30 mites; 3 = ≥31 mites) were assigned to individual flight feathers, based on visual assessment of the number of mites present. At the West Midlands sites we used a further modification to this technique, extending the range by introducing scores of 0.5, when just a single mite was evident on a feather, and 4, when more than 50 mites were estimated to be present.

We followed Svensson's (1992) ascendant numbering scheme for feathers, i.e., from the outside of the wing in towards the body. All the flight feathers from p1 (the outermost primary feather) to p10, across the secondary feathers (s1–s6), and the 3 tertiary feathers (t1–t3) were assessed visually for evidence of mite infestation.

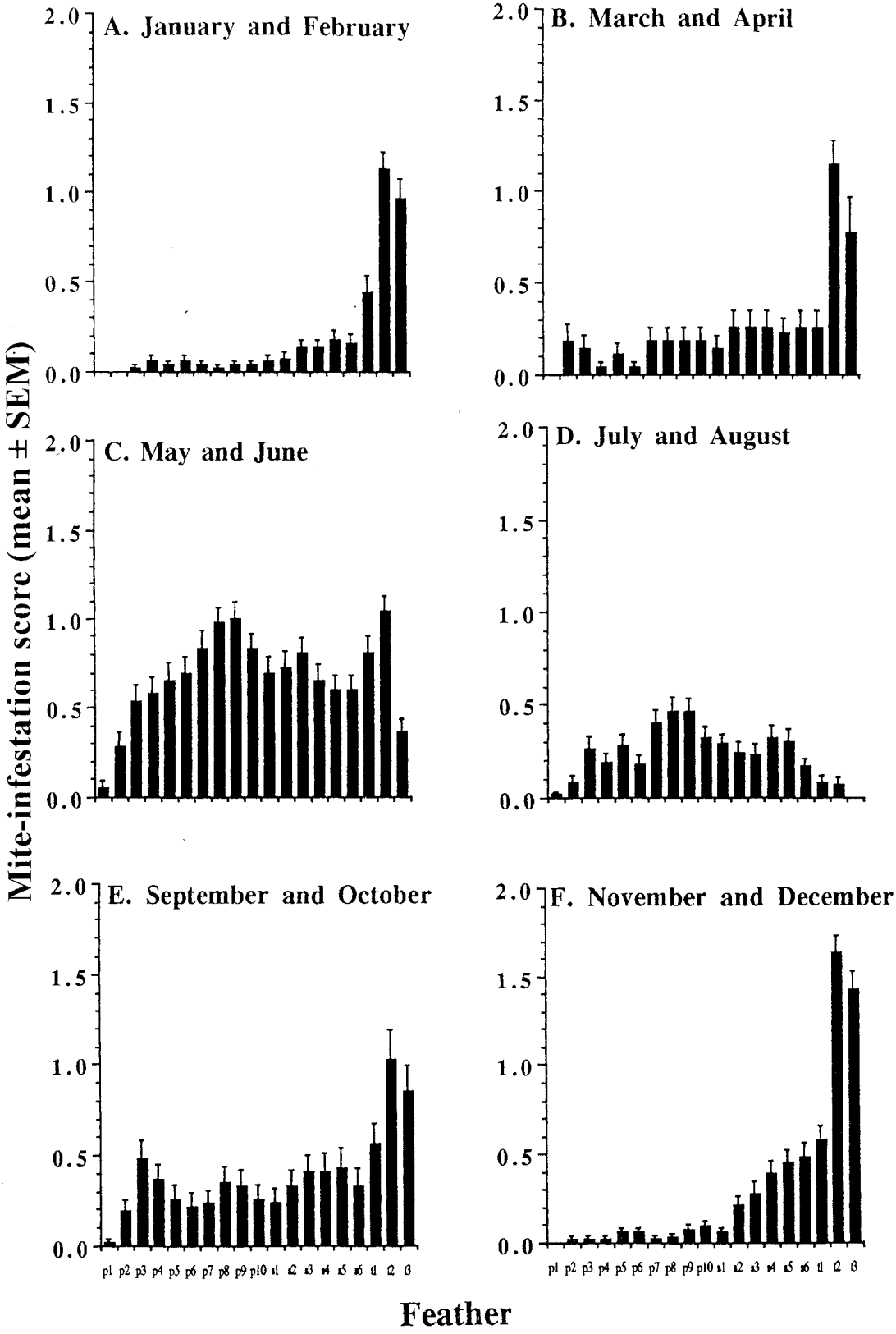
The only species of feather mite recorded on blue tits in this study was *P. stylifer*, identified from the keys of Atyeo and Braasch (1966).

Data presentation and statistical procedures

Where appropriate the data are presented as the mean ± the standard error of the mean (SEM). Except in the generalised linear model (GLIM) analysis (see below), nonparametric statistical procedures were employed because ordinal data were involved. To avoid Type I errors we did not compare distributions against each other. Following Day and Quinn (1989) we refrained from any post hoc multiple comparisons. We first removed all recaptures of birds from each data set to avoid pseudoreplication (the total number of recaptures removed was 132: 80 from Lancashire, 32 from South Midlands, and 20 from West Midlands sites), so that analyses were based on independent samples, i.e., the record from the first netting of each bird (we refer briefly to the data on recaptures in the Discussion). We then calculated for each bird the mean mite-infestation scores for the primary, secondary, and tertiary feathers separately, and then recorded for each bird the feather group that yielded the highest mean value.

To test for the effect of season, months were combined in pairs and the effect of temperature was analysed in specified temperature ranges. For each combination of months or temperature ranges we calculated the number of birds with peak scores among the primary, secondary, and tertiary feathers. The small number of birds (4.9%) that did not show a clear peak in a particular feather group (i.e., their mean mite-infestation scores for the secondary and ter-

Fig. 1. Seasonal changes to the pattern of distribution of mites on the wings of blue tits at the South Midlands study sites (n = 52 in A; n = 27 in B; n = 52 in C; n = 62 in D; n = 46 in E; n = 83 in F).



tiary feathers or other combinations were equal) had to be excluded from this analysis (12 from 322 birds at the South Midlands sites, 4 from 223 birds at the West Midlands sites, 18 from 289 birds at the Lancashire sites). The resulting frequencies were analysed by χ^2 tests (contingency tables) and the accompanying figures (Figs. 3 and 6) show the percent distribution of birds

Table 1. Tests for the effect of season and air temperature on the distribution of *Proctophyllodes stylifer* feather mites on the wings of blue tits.

Sites	N^a	χ^2 (season)[a]	Temperature[b] χ^2	Temperature[b] r_s
South Midlands	322	173.7***	—	
West Midlands	223	—	133.0***	–0.62***
Lancashire	289	42.3***	23.7**	–0.22***

Note: N is total sample size.

[a]For the χ^2 tests using season, we accumulated the frequencies of birds having the three peak-distribution feather groups and five or six bimonthly groups, hence these tests had 10 (South Midlands sites) or 8 degrees of freedom (West Midlands and Lancashire sites). We excluded 12 of the 322 South Midlands birds from the χ^2 test, 18 of the 289 Lancashire birds because they had no clear peak mite density in one feather region, and 7 birds netted in June because of a small sample size.

[b]The χ^2 tests using temperature had 8 degrees of freedom (5 temperature-range categories × 3 peak-distribution feather groups): we excluded 4 of the 223 West Midlands birds from the χ^2 test and 18 of the 289 Lancashire birds because they had no clear peak mite distribution in one feather region. The correlations involved the temperature at capture and the peak-distribution feather group for individual birds.

**$P < 0.01$.

***$P < 0.001$.

among the three feather groups for each combination of months or temperature range. The distribution arising from expected values from the χ^2 contingency test are also given for comparison, to show the direction of any significant changes relative to random expectation.

Correlations between ambient temperature in the field and the numerical sequence of feather groups (primaries = 1; secondaries = 2; tertiaries= 3) on sampled birds showing peak infestation were tested by Spearman's rank correlation test. In a few cases we were unable to record ambient temperatures, therefore sample sizes are slightly smaller than the total number of birds caught. In a simple manipulation experiment, birds were inspected when freshly caught and then re-inspected after 20 min indoors. For this data set, analysis of distributions before and after treatment was by Cochran's Q test for k-related samples (Siegel and Castellan 1988).

Finally, birds from all three sites for which we had relevant data were combined for analysis using a GLIM model with Poisson errors (South Midlands sites, $n = 300$; West Midlands sites, $n = 223$; Lancashire sites, $n = 288$; total, $n = 811$). We determined the effects of bird age (2 levels: first year versus older), temperature (5 levels: <4.9°C = 1; 5.0–9.9°C = 2; 10.0–14.9°C = 3; 15.0–19.9°C = 4; >20.0°C = 5), and site (3 levels: South Midlands, West Midlands, Lancashire) on the distribution peaks of mites between the primaries, secondaries, and tertiaries. The total mite-infestation score (the sum of the individual scores assigned to all 19 feathers of a bird on one wing, as described by Behnke et al. 1995, 1999) was entered as a covariate. Sex was not included because many birds were not sexed reliably. Thus, the dependent variable was feather group (1 = primaries; 2 = secondaries; 3 = tertiaries) of individual birds showing the highest mean mite-infestation scores. The statistical significance of each factor was determined by calculating the change in deviance of the model associated with deletion of the factor. The change in deviance is distributed asymptotically as χ^2 for the appropriate degrees of freedom of the factor. The full model was simplified following the procedures of Crawley (1993): starting with the highest order interactions, terms were removed from the model in turn and left out. However, the main effects were reinstated after subtraction before the next main effect was removed. In a second stage of this analysis we examined the minimum sufficient model, in which only the significant factor was entered.

Throughout, probabilities are two-tailed and $P < 0.05$ was considered to indicate a significant departure from the null hypothesis.

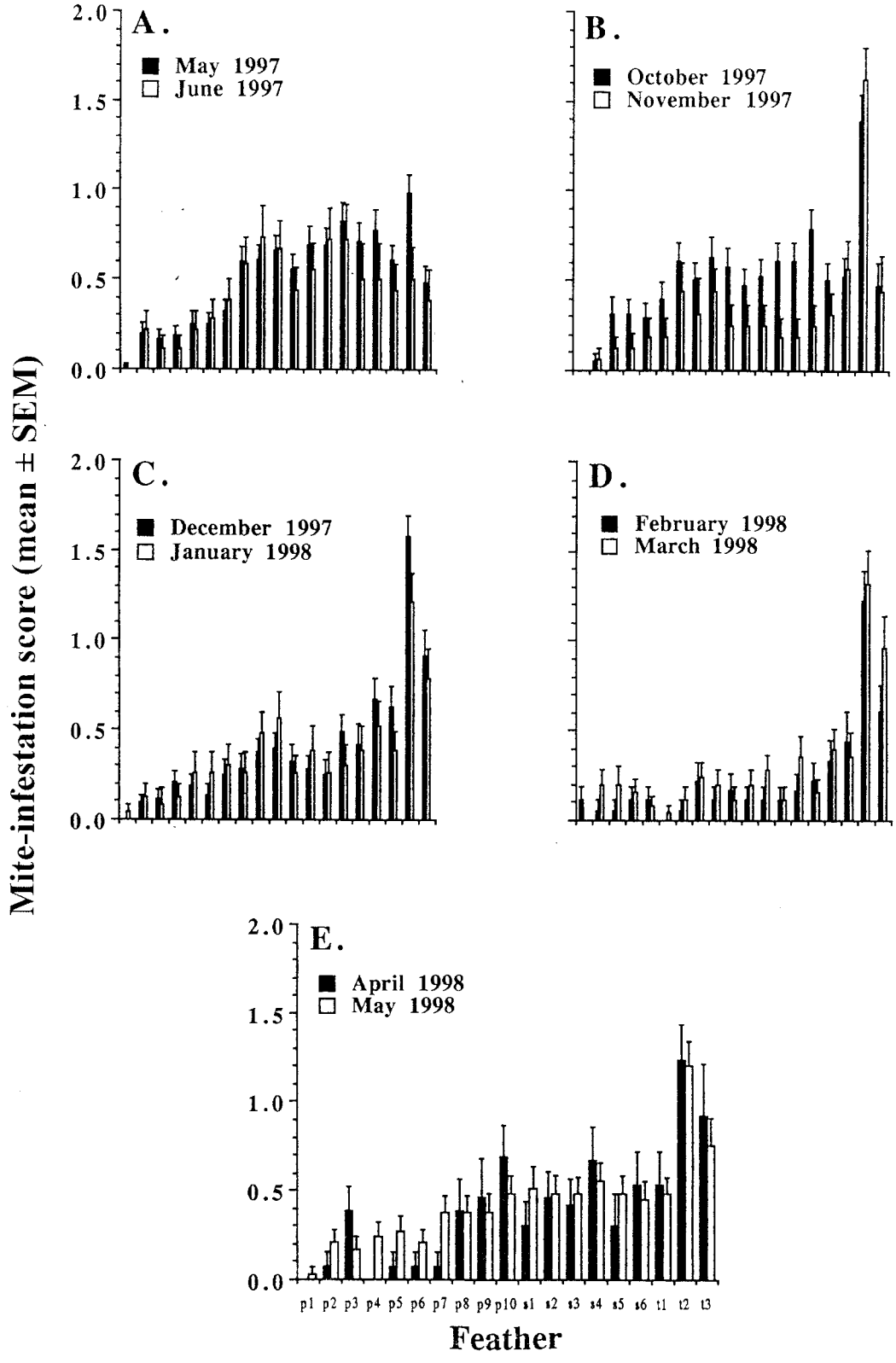
Results

Annual variation in the pattern of distribution

At the South Midlands sites, netting ($n = 322$) took place between dawn and noon during the period 1994–1997. It is clear (Fig. 1) that in January–February, mites were predominantly clustered on the tertiary feathers (96.2% of the birds showed a peak in mite distribution among the tertiaries, 2% among the secondaries, and none among the primaries), but by March–April mites began to spread out onto the primaries and secondaries. In May–June most birds still showed a peak intensity among the tertiaries, but by July–August, peak mean mite-infestation scores had quite clearly shifted to the primaries and secondaries (47.5 and 45.9% of birds, respectively). The following months saw a gradual return to the winter distribution. By September–October, peak infestation was again among the tertiaries (65.9% of birds) and by November–December, 98.8% of birds showed a peak in this feather group. From the number of birds showing peak scores among each of the three feather groups ($n = 310$, excluding the 12 birds with no obvious peak), separated into 2-month periods, there were significant changes in distribution with season (Table 1). The random expectation was that 15.5, 17.1, and 67.4% of birds would show peak infestations among the primaries, secondaries, and tertiaries, respectively, and that these would not change through the year.

At the Lancashire sites, birds were examined in May and June 1997, and then in each month from October until May 1998. The mean mite-infestation scores on the flight feathers are illustrated in Fig. 2. In May 1997, the highest mean mite-infestation score was recorded on t2 (Fig. 2A), but there was a long plateau of scores in the range 0.55–0.82 stretching across to p8. A shift in distribution was evident by June (Fig. 2A), when the highest scores were recorded on p9, s3, and s4 and no peak was evident among the tertiaries. By October (Fig. 2B), mite-infestation scores had increased on t2, with moderate scores still apparent among the primaries. This trend was more marked in November, with a higher mean mite-infestation score on t2 and a lower plateau among the primaries and secondaries. Mean mite-infestation scores continued to fall among the primaries and secondaries and increase among the tertiaries throughout December 1997 and January 1998 (Fig. 2C) and February and March (Fig. 2D), but by April and March (Fig. 2E) the pattern appeared to be returning to that recorded in May 1997, although the peak among the tertiaries was still evident. Combining months in pairs, and from the number of birds showing peak scores among each of the three feather groups (total $n = 264$), there was again a significant effect of season on the patterns of mite distribution across the wing (Table 1). The random expectation was that 10.2, 21.6, and 68.2% of birds would show peak infestations among primaries, secondaries, and tertiaries, respectively, remaining unchanged throughout the year, much as in the data from the South Midlands sites. This pattern closely reflected that in October–November (11.3, 20.8, and 67.9%, respectively) and April–May (4.8, 21.4, and 73.8%, respectively). However, in December–January (6.8, 8.5, and 84.8%, respective-

Fig. 2. Seasonal changes to the pattern of distribution of mites on the wings of blue tits at the Lancashire study sites (n = 59 for May 1997; n = 18 for June 1997; n = 38 for October 1997; n = 16 for November 1997; n = 43 for December 1997; n = 23 for January 1998; n = 18 for February 1998; n = 25 for March 1998; n = 13 for April 1998; n = 29 for May 1998).



ly) and February–March (7.5, 5.0, and 87.5%, respectively) more birds showed peak intensity on the tertiaries, whilst in May–June (17.1, 42.9, and 40%, respectively) more showed peak intensity on the secondaries.

Effect of ambient air temperature on the distribution of mites

Preliminary fieldwork showed that on particular occasions, especially in winter, birds showed wider distributions

Fig. 3. Changes in the percentages of birds showing peak mite-infestation scores (MIS) on the primary, secondary, and tertiary feathers in relation to ambient temperature at the time of inspection at the Lancashire study sites. For details see the text.

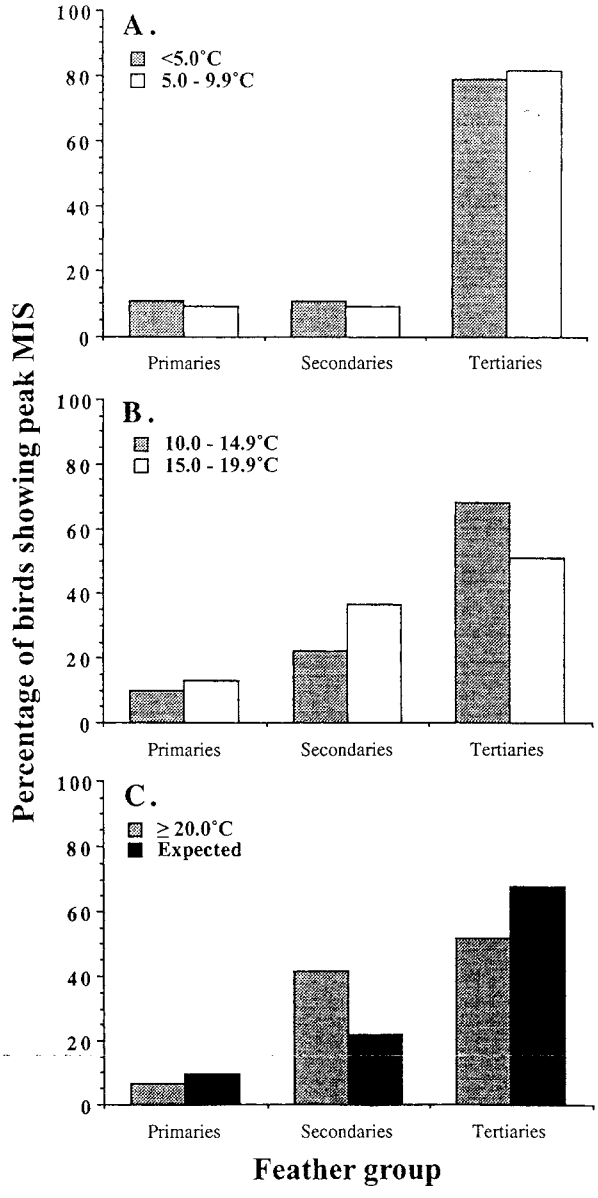
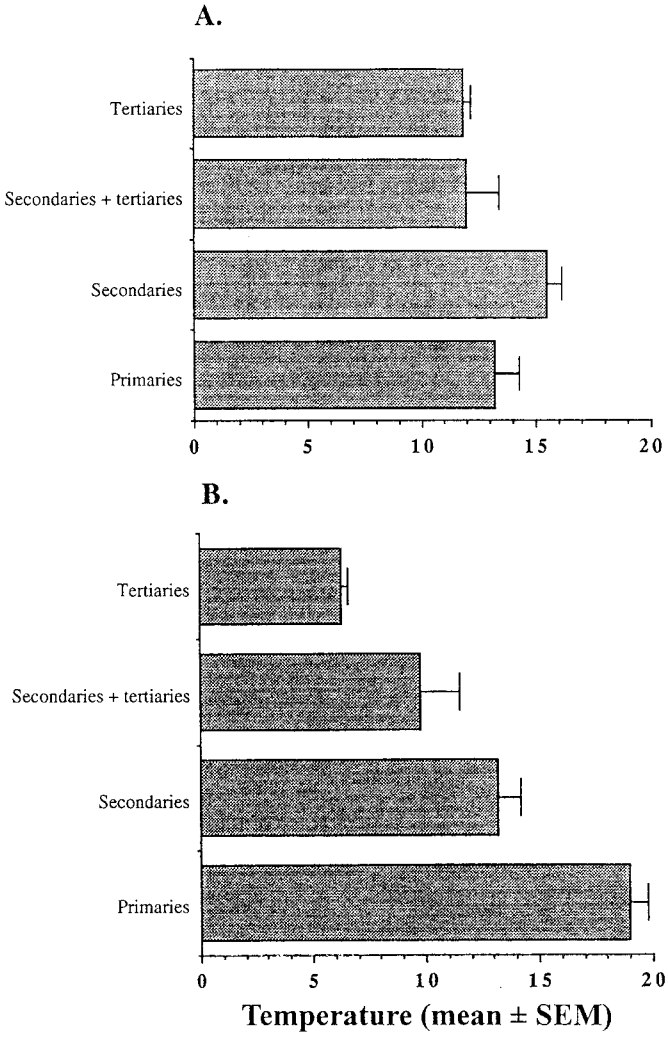


Fig. 4. Relationship between the feather group showing the peak mean mite-infestation score and ambient temperature. For details see the text. (A) Lancashire sites (n = 27 for primaries; n = 60 for secondaries; n = 17 for secondaries + tertiaries; n = 184 for tertiaries). (B) West Midlands sites (n = 25 for primaries; n = 54 for secondaries; n = 4 for secondaries + tertiaries; n = 140 for tertiaries).



of mites stretching into the primary and secondary feathers than would be expected for the time of year. These occasions often coincided with cold days when large numbers of birds, mainly winter flocks flying into the nets, were caught simultaneously. When kept in individual bird bags but held together in a cluster during the waiting period before inspection and banding, birds might have generated sufficient heat to warm and humidify the surrounding air. This suggests an initial hypothesis that temperature may have been an underlying factor determining seasonal distribution of mites across the wings of birds.

We reanalysed the Lancashire data set, for which meteorological data were also available (n = 271). Birds were allocated to groups depending on ambient daytime temperature, in the ranges shown in Fig. 3, since netting at the Lancashire sites was predominantly carried out in midafternoon. Figure 3 shows that as predicted, birds inspected when the temperature was low (<10°C) predominantly showed peak mite-infestation scores on the tertiaries. As the ambient temperature increased, there was a significant shift in the distribution, with greater numbers of birds showing peak mite-infestation scores on the secondaries (Table 1). We also tested the correlation between ambient temperature and peak-infestation feather group (1, 2, and 3 for primaries, secondaries, and tertiaries and 2.5 for the 18 previously excluded birds that had identical mite-infestation scores for secondaries and tertiaries). The relationship was highly significant (Table 1), although the correlation coefficient was low. As can be seen from Fig. 4A, whilst the mean ambient temperature increased with a shift in peak distribution from tertiaries to secondaries, birds showing a peak distribution among the primaries were associated with a lower mean ambient temperature.

Table 2. Statistical analysis of the factors affecting the blue tits' feather group showing peak infestation with *P. stylifer* by site, age, and temperature, through a three-way ANOVA with Poisson errors, and total mite infestation score (TOTMIS) as a covariate.

Source of variation	Change in deviance[a]	df	Residual deviance	Residual df	*P*
Temperature	35.88	4	172.03	810	<0.0005
Age	0.361	1	136.16	806	ns
Site	1.948	2	135.80	805	ns
TOTMIS	0.000	1	133.85	803	ns
Site × TOTMIS	0.283	2	133.85	802	ns
Age × TOTMIS	0.181	1	133.57	800	ns
Age × site	0.181	2	133.38	799	ns
Temperature × TOTMIS	5.459	4	133.20	797	ns
Temperature × site	11.80	8	127.74	793	ns
Temperature × age	0.602	4	115.95	785	ns
Temperature × age × TOTMIS	1.669	4	115.35	781	ns
Temperature × site × TOTMIS	1.402	8	113.68	777	ns
Age × site × TOTMIS	0.968	2	112.27	769	ns
Temperature × age × site	1.498	8	111.31	767	ns
Temperature × age × site × TOTMIS	0.541	7	109.81	759	ns

Note: The full model deviance was 109.27 with 752 degrees of freedom; ns, not significant.

[a]Change in deviance following removal of the combination specified in the "source of variation" column from the full factorial model. We began by removing the four-way interaction, followed by the three-way interactions, and then the two-way interactions. The remaining main effects, however, were removed to assess the change in deviance but then replaced before proceeding further. In a model with Poisson errors, the scale parameter is always 1 and the change in deviance is distributed as χ^2.

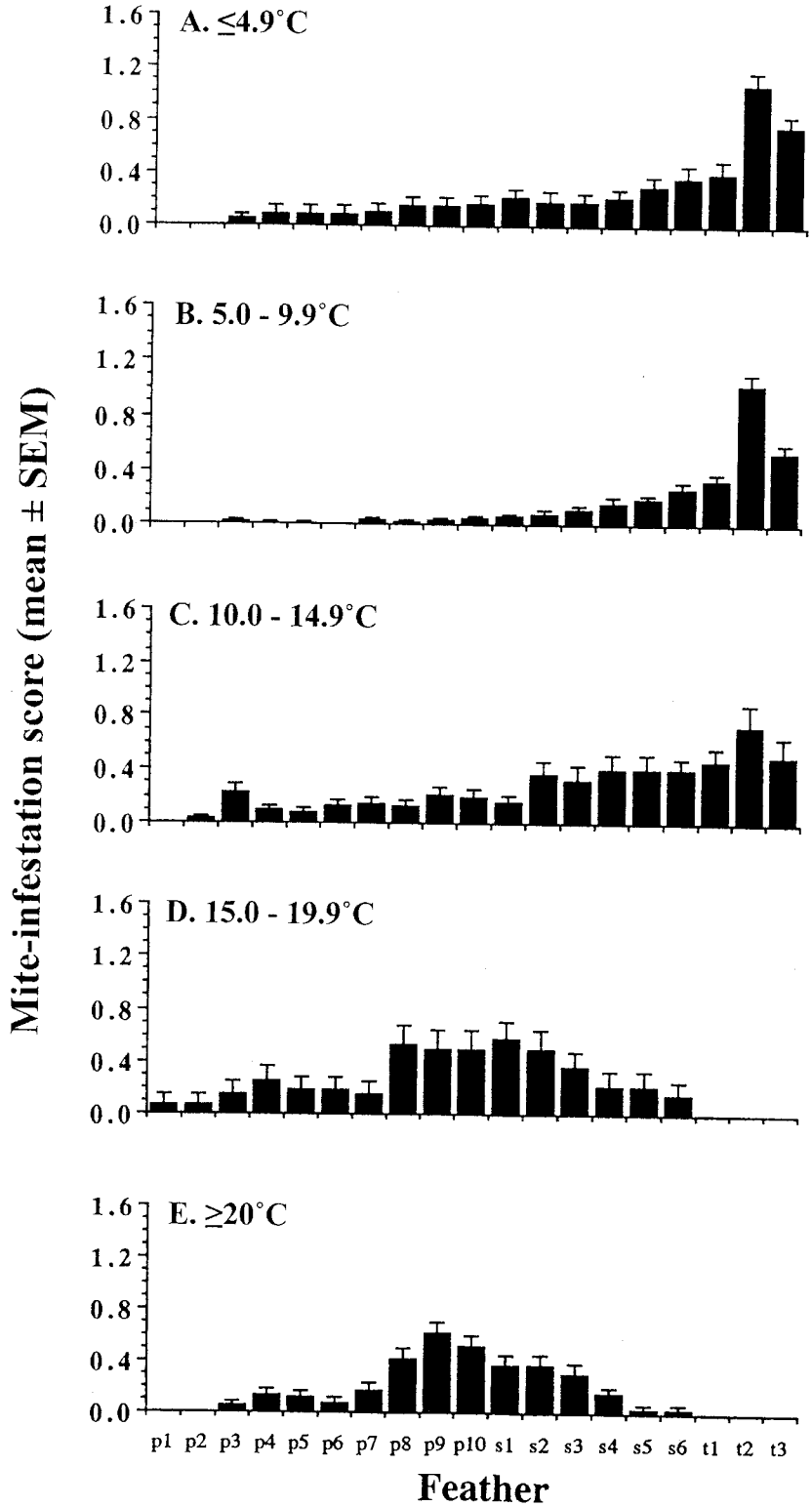
In the period June 1997 to March 1998 we recorded the distribution of mites on blue tits (n = 223) netted at our West Midlands study sites, but on each occasion we recorded the ambient air temperature at the time and in the precise location where birds were being inspected. Figure 5 shows that in the two lower temperature ranges, mites were clearly clustered predominantly on the tertiary feathers. In the temperature range 10.0–14.9°C, mite-infestation scores were higher on the primaries and secondaries and in both of the higher temperature ranges mites were clustered on p8–s3. Closer scrutiny of the raw data indicated that movement onto the secondaries was already apparent at 10–11°C. There was a highly significant shift in peak distribution (Table 1) associated with temperature categories. Figure 6 shows that at lower temperatures most birds had peak mite-infestation scores among the tertiaries, whilst at 10.0–14.9°C the pattern was much as predicted by the expected values from the χ^2 test. At 15–19.9°C most birds had peak mite-infestation scores among the secondaries, and at higher temperatures the majority of birds showed peak mite-infestation scores among the primaries. We again tested the correlation between ambient temperature and the feather group associated with peak mite intensity, and the relationship was highly significant (Table 1; see Fig. 4B). Again, birds showing peak mite distribution among the primaries were caught at higher mean ambient temperatures.

The GLIM analysis (Table 2) demonstrates that the only significant effect was a clear, strong relationship between temperature category and peak mite position; peak position was independent of total mite-infestation score, site of capture, and age of birds. The minimum sufficient model (in which only temperature was entered) revealed a steady shift of the arithmetic average of the peak-distribution feather group: 2.90 ± 0.03 for temperature category 1 (n = 171); 2.81 ± 0.03 for temperature category 2 (n = 253); 2.43 ± 0.05 for temperature category 3 (n = 225); 2.16 ± 0.08 for temperature category 4 (n = 80); and 1.88 ± 0.08 for temperature category 5 (n = 82). Peak mite-infestation scores occurred significantly more often on the inner flight feathers at lower temperatures and more often on the outer feathers in warmer conditions.

Effect of temporarily keeping birds indoors at a temperature higher than the ambient external temperature

Finally, we carried out a simple experimental manipulation. Birds netted on a cold day (9–11°C) were initially kept well spaced out in bags to prevent undue warming, and were assessed as soon as possible. Those showing a high total mite-infestation scores (n = 14) were then taken indoors into a warm room (20°C) and kept there for 20 min. Each bird was then reexamined before being released. At low temperatures (Fig. 7) the mites were clustered on the proximal secondary and tertiary feathers. Some mites were noted more distally along the wing, but the temperature range unfortunately partially coincided with 10–11°C, the temperatures at which an outward movement of mites was first seen (see above). Nevertheless, it is obvious that after 20 min indoors, mite-infestation scores on the primary and secondary feathers increased quite markedly. We compared statistically the feather group showing peak mite-infestation scores for each bird before and after treatment and found a significant change in distribution (Q = 10, df = 2, P < 0.01). Therefore, significantly fewer birds showed a peak mite-infestation score among the tertiary feathers after being kept indoors for 20 min on a cold day, when the external ambient air temperature ranged from 9 to 11°C.

Fig. 5. Changes in the pattern of distribution of mites on the wings of blue tits at the West Midlands study sites in relation to ambient air temperature (n = 45 in A; n = 94 in B; n = 39 in C; n = 14 in D; n = 31 in E).

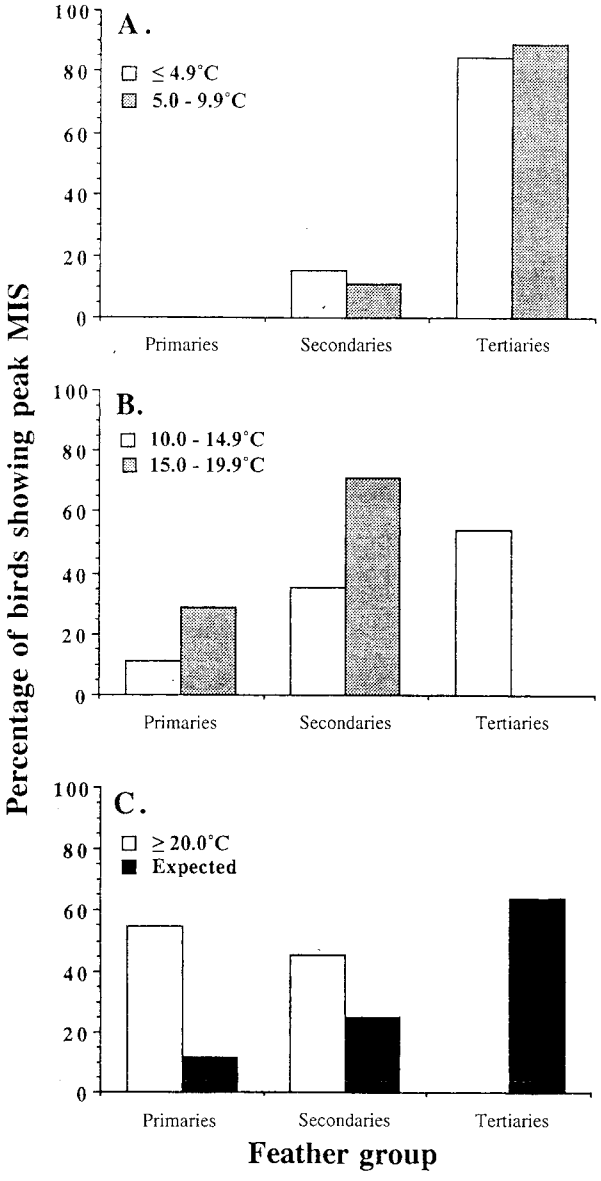


Discussion

The data presented in this paper confirm that the distribution of *P. stylifer* across the flight feathers of the blue tit varies with season. In the winter months mites tended to cluster on the tertiary feathers, but in the summer and autumn they showed a wider distribution, and on occasion could be observed on the distal secondary feathers and even as far away from the body as the outermost primary feathers. The question then arises as to why mites bother to change their distribution across the wings of their host during successive seasons?

It could be argued that the apparent seasonal redistribution was a by-product of a population increase following breed-

Fig. 6. Changes in the percentages of birds showing peak mite-infestation scores (MIS) among primary, secondary, and tertiary feathers in relation to ambient temperature at the time of inspection at the West Midlands study sites For details see the text.



ing in the late spring – early summer, leading to overspill of the increased mite burden and invasion of feathers distal to those normally occupied when population densities are lower. Although nothing is known about the timing of reproduction in *P. stylifer*, nor about seasonal changes in parasite burden on blue tits, intuitively increases in mite infestation might be expected around the time of nesting in spring, and during the period when nestlings are being raised (in the U.K. blue tits rear only one brood per annum (Perrins 1979)), to allow transfer of mites to new, susceptible generations of hosts. However, in our study, when the mite-infestation scores increased on the primary and secondary feathers, whether seasonally and (or) in response to changes in microclimate, this redistribution was always associated with a reduction in the mite-infestation scores on the tertiaries (Figs. 1, 2, 3, 5, and 6). If the tertiaries are the site preferred by these mites, we might have expected mite-infestation scores to remain high even when increased on the outer flight feathers. Moreover, the main effect, mite burden, as reflected in the total mite-infestation score, had no significant effect on distribution and there were no significant interactions between total mite-infestation score and the other factors we entered into the GLIM model. Therefore, we can reject the above explanation with some confidence. Instead, on the basis of our analyses, we propose that the underlying mechanism involved a response to changes in ambient temperature and (or) its correlates (principally humidity). Our data support this conclusion from three distinct perspectives.

Firstly, among individual birds examined throughout the autumn, winter, and spring, when ambient air temperature varied, those netted when the air temperature was below 10°C had mites clustering on the innermost feathers, whilst those netted when the air temperatures was higher had mites distributed out towards the primary feathers. This conclusion was based on two data sets that were collected independently from the Lancashire and West Midlands study sites, where slightly different approaches were used. At the Lancashire sites the relationship with ambient temperature was established only at the end of the study, by entering daily temperatures from meteorological records; the likely discrepancies from actual local temperature at the time of netting may have been responsible for the low (although significant) χ^2 values and correlation coefficients obtained when the relationships between peak mite distribution and temperature were tested. At our West Midlands study sites we measured temperature precisely when and where birds were being processed, and obtained a correspondingly higher χ^2 value and correlation coefficient. Both data sets (Figs. 3–5) support the idea that at temperatures below 10°C, mites cluster on the tertiary feathers, and that movement away from the feathers closest to the body of the host commences when the ambient air temperature rises above 10°C. The slight discrepancies between these data sets (compare Figs. 3 and 6) can be explained by the difference in the approach adopted (i.e., the range of scores used) and (or) the geographical location of the study sites, in addition to the possibilities presented earlier.

Secondly, a comparison of the distribution of mites across the wings of multiply recaptured individual birds revealed in all cases that the mites were clustered on the tertiary feathers at low temperatures and were more widely distributed on the same birds when the ambient air temperature was higher (data not shown). We did not analyse these observations quantitatively because of a small sample size and confounding variables, but even among such recaptures the movement of mites away from the tertiary feathers at higher temperatures was repeatedly observed.

Thirdly, the small-scale experiment in which birds netted on a cold day were temporarily kept in bird bags in a warm house revealed that between the first examination (in the cold) and the second (in the warm), mites had spread out from the tertiary feathers onto the primaries. This experiment established that mites could change their distribution in a relatively brief period of time, but the fundamental question is whether this was a response over time to being kept in a bird bag or a response to the change in ambient microclimate. The obvious control would have been to leave some