Experimental & Applied Acarology, 19 (1995) 443–458

Identity, prevalence and intensity of infestation with wing feather mites on birds (Passeriformes) from the Setubal Peninsula of Portugal

Jerzy M. Behnke[a], Peter K. McGregor[a], Mike Shepherd[a*], Roy Wiles[b], Chris Barnard[a], Francis S. Gilbert [a] and Jane L. Hurst[a]
[a]*Department of Life Science, University of Nottingham, University Park, Nottingham NG7 2RD, UK*
[b]*Department of Biology, University of Buckingham, Buckingham MK18 1EG, UK*

ABSTRACT

The results of a 4 year project investigating species of mites infesting wing primary feathers on 21 species of Passeriformes are reported. The majority of species were identified as belonging to the genus *Proctophyllodes* Robin, 1877 with one new host record. In addition *Pteronyssoides obscurus* Berlese 1884 was found on European swallows, also a new host record. A novel method to enable quantification of mite intensities without causing harm to the birds was devised and evaluated. This relied on visual inspection of wing primary feathers and assignment of subjective infestation scores to individual feathers, the sum of the individual scores comprising the primary feather total mite infestation score (PTMIS). Comparisons between species revealed that birds could be grouped into four categories depending on their infestation intensity with mites. Swallows, sand martins and greenfinches showed the highest prevalence and most intense infestations (mean PTMIS $\geq$ 6.8). Blackbirds, blackcaps, serins, goldfinches, Cetti's warblers, great tits and house sparrows showed moderate levels of infestation with prevalence in the range 60–90.9% but a mean PTMIS lower than in the former group (1.6–5.8). The third group comprised Sardinian warblers, nightingales and short-toed tree creepers and was characterized by a prevalence of mites $\leq$40% and a mean PTMIS of 0.6–1.4. The final group, representing wrens, chiffchaffs, fan-tailed warblers and waxbills were without detectable mites, the only exception being wrens on which mites were identified in only three birds of the 32 sampled. These results are interpreted in the light of published information and possible explanations for the observations are discussed.

Key words: Birds, feather mites, prevalence, intensity of infection, *Proctophyllodes, P. pinnatus, P. troncatus, P. sylviae, P. serini, P. clavatus, P. stylifer, Pteronyssoides obscurus.*

INTRODUCTION

The study of the biology and ecology of ectoparasitic arthropods of wild birds, particularly wing feather mites, has been relatively neglected in

*Present address: Scottish Natural Heritage, Anderson Place, Edinburgh, UK.

0168-8162

recent years apparently for several reasons. With the exception of domestic fowl there is little evidence that feather mites cause pathology or indeed any detectable loss to bird fitness and, hence, they do not represent parasites of economic importance (Evans *et al.* 1961). The taxonomy of relevant species is still incompletely understood and their differentiation at the species level is difficult, relying for the most part on the size and number of setae and the structure of the male genitalia (Trouessart, 1885; Atyeo and Braasch, 1966). Much of our knowledge about the different species is still based on reports published in the 1800s (Canestrini, 1886), some of which are difficult to trace, although many new species have been described since (Bonnet and Timon-David, 1932; Fritsch, 1961; Atyeo and Perez, 1988, 1990) and a considerable effort has been made in recent years to unravel the relationships between the higher taxa and to establish their phylogeny (Atyeo and Braasch, 1966; Faccini and Atyeo, 1981; Gaud, 1981; Atyeo and Perez 1990; Atyeo, 1992). Lists have been published of mite species from individual or groups of host species (Hull, 1934; Radford, 1953; Hollander 1956). Some authors have reported on host specificity (Cerný, 1973; Atyeo and Perez, 1990) and on site selection among different regions of the body (Dubinin, 1951; Fitzpatrick and Threlfall, 1977; Choe and Kim, 1988), in relation to feather types (Peterson, 1975; Perez and Atyeo, 1984) or regions of the feather (Atyeo and Perez, 1988; Choe and Kim, 1989). Nevertheless, the population dynamics of these parasites, seasonal changes in infestation rates (McClure, 1989), their ecology in relation to other ectoparasites (Choe and Kim, 1987a, b) and differences in prevalence of infestation between host species (Wheeler and Threlfall, 1986; McClure, 1989) in relation to host ecology (Atyeo and Gaud, 1979) or social behaviour (Poulin, 1991; Poiani, 1992) have been less well documented.

However, the biology and ecology of feather mites deserves more attention because (1) the appearance of harmlessness in parasitic associations has often turned out to be misleading on detailed investigation (Cooper and Bundy, 1988; Booth *et al.* 1993), (2) the wide variation in mite infestation and diversity within and between species demands explanation and (3) there are strong theoretical reasons for supposing that both ectoparasites and endoparasitic infestations have been important in the evolution of host external appearance and behaviour (Hamilton and Zuk, 1982; Read, 1990; Clayton, 1991b; Møller, 1991; Wedekind, 1992).

This paper reports on a 4 year study, conducted in Portugal, in which wing and breast feather mites were identified and the former quantified using a subjective scoring system, developed during initial pilot investigations. We present data to show that the technique can be used reliably to quantify the intensity of infestation and that it is based on a direct positive relationship with actual mite numbers. Data are presented comparing 21 bird species and the pronounced differences in infestation rates which were detected are discussed.

MATERIALS AND METHODS

Study site

The project was carried out over 14 days in mid April in 1990–1993. The work was conducted as part of the Department's Terrestrial Zoology Field Course and was carried out by second year undergraduate students under the strict supervision of academic staff. Most birds were caught at the Quinta de Sao Pedro in Sobreda near Lisboa, but two other sites were also used with the landowner's permission. These were the Quinta Niza, approximately 3 km further southeast and Pancas, a site near the Tejo estuary where the species range sampled earlier at Sobreda was extended with the addition of waxbills (*Estrilda astrild*), sand martins (*Riparia riparia*), Cetti's warblers (*Cettia cetti*), nightingales (*Luscinia megarhynchos*) and a single stonechat (*Saxicola torquata*). Throughout the study close contact was maintained with the Centro de Estudos de Migrações e Protecção de Aves (CEMPA) and the techniques used were approved by that organization for the study.

Capture and treatment of birds

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

Examination of birds for mites

Initial pilot studies established that it was not possible to conduct a thorough search of all feathers for mites without causing distress to most birds. Examination was therefore limited to all ten wing primary feathers on the left wing. In consequence, the data which we present cannot be regarded as reflecting total mite burdens for the birds. However, since sampling methods were consistent throughout the study, each bird being sampled in exactly the same manner, the data are likely to reflect the relative prevalances and intensities of infestations with reasonably accuracy.

On completion of morphometric measurements, the left wing of each bird was extended and held up to ambient light. The complete length of the primary feathers was exposed, primary covets and under wing covets 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 running along the barbs and barbules. It was thus possible to examine each of the ten primaries and to ascertain which carried mites in a consistent and rapid manner without undue distress to the birds. Such data were collected during all 4 years.

With experience it also became possible to compare the intensities of infestation on individual feathers using a novel procedure, based on a modification of that reported by McClure (1989). This involved a subjective scoring system in the range 0–3, where 0 represented feathers which were not detectably infested, 1 represented feathers with some mites congregating around the feather shaft (usually at the mid-shaft/base) and little or no evident spread to barbs, 2 represented feathers with mites along at least 50% of the length of the feather shaft and some limited spread to the barbs and 3 represented feathers in which mites were observed packing the feather shaft and extending along the barbs. Thus each of the ten feathers was given a subjective score and a total was calculated by adding all the individual scores. In this way a maximum possible score for a bird was 30. This was termed the primary feather total mite infestation score (PTMIS). In order to calibrate this subjective score with actual mite counts we regularly sampled feathers (never more than one primary from an individual bird) and counted the total number of mites with the aid of a dissecting microscope. These mites were preserved in 70% ethanol and 5% glycerol and mounted in Berlese's fluid for subsequent identification and description. Data of this type were only collected in 1991–1993, although samples of mites from earlier years were also preserved for taxonomic purposes.

Identification of mites

Feathermites of the genus *Proctophyllodes* Robin, 1868 were identified using the keys of Atyeo and Braasch (1966) and other genera using Zumpt (1961) and Dubinin (1951, 1953, 1956).

Statistical procedures

Where appropriate, the data are presented as the prevalence of infestation (% of birds infected). The mean ± the standard error of the mean

(SEM) and the median values are given for the number of infested feathers and the PTMIS. Non-parametric statistical procedures were employed because ordinal data, showing overdispersed distribution, were involved. Correlations between variables were examined with the Spearman rank order correlation test and r_s values are given as appropriate. For probabilities, p values ≤ 0.05 were considered to be significant, unless multiple analyses were undertaken, in which case a $p \leq 0.025$ was considered to be significant in order to prevent type I errors. The coefficient of skewness (g_l) was calculated by standard procedures.

RESULTS

Species and numbers of birds examined

A total of 473 birds of 21 species were caught and examined for wing feather mites. Table 1 shows the number of each species examined. It is evident from these data that blackcaps ($n = 138$) and house sparrows ($n = 95$) were the two dominant species sampled. Some species were caught in very small numbers and for this reason the quantitative parasite data given subsequently for blue and long-tailed tits, fan-tailed and garden warblers, sand martins, stonechats and waxbills should be treated with a degree of caution since in each case fewer than five individuals were sampled.

Species of mites recovered

It was not possible to check the identity of each specimen but samples from the host species showing most frequent infestations were examined and the majority of feather mites collected from the primary wing feathers were of the genus *Proctophyllodes* Robin 1868 (Table 2). Eggs, protonymphs and tritonymphs were also found but the vast majority were adults (deuteronymphs are absent in all feather mites). One species from the genus *Pteronyssoides* Hull, 1931 was also identified: this was *Pteronyssoides obscurus* Berlese 1884 (Faccini and Atyeo, 1981) from the swallows (a new host record).

Prevalence of infestation with wing primary feather mites

Of the total sample of 473 birds examined, 300 (63.4%) were infested with feather mites on wing primary feathers (Table 3). Only swallows, sand martins and greenfinches showed 100% prevalence of wing feather mites. A moderately high prevalence (> 50%) was also observed among goldfinches, serins, Cetti's warblers, blackcaps, blackbirds and house sparrows

TABLE 1

Number of birds of each species examined (1990–1993) and infested with feather mites on primary wing feathers

Family and species	Common name	Number examined	Number infested
Certhiidae			
Certhia brachydactyla	Short-toed treecreeper	15	3
Estrildidae			
Estrilda astrild	Waxbill	4	0
Fringillidae			
Carduelis carduelis	Goldfinch	53	40
Carduelis chloris	Greenfinch	21	21
Serinus serinus	Serin	11	10
Hirundinidae			
Hirundo rustica	Swallow	5	5
Riparia riparia	Sand martin	3	3
Silviidae			
Cettia cetti	Cetti's warbler	10	7
Cisticola juncidis	Fan-tailed warbler	4	0
Phylloscopus collybita	Chiffchaff	9	0
Sylvia atricapilla	Blackcap	138	116
Sylvia borin	Garden warbler	1	0
Sylvia melanocephala	Sardinian warbler	36	8
Turdidae			
Luscinia megarhynchos	Nightingale	5	2
Saxicola torquata	Stonechat	1	0
Turdus merula	Blackbird	21	18
Parida			
Aegithalos caudatus	Long-tailed tit	2	1
Parus caeruleus	Blue tit	2	1
Parus major	Great tit	5	3
Passeridae			
Passer domesticus	House sparrow	95	59
Troglodytidae			
T. troglodytes	Wren	32	3

but in each species some birds were without detectable feather mites. The three species of Paridae showed > 50% prevalence but the numbers sampled were very low. At the opposite extreme fan-tailed warblers, chiffchaffs and waxbills, stonechats and garden warblers were not infested. However, wrens, of which 32 were sampled, also ranked among the species showing very low prevalence, with mites only being detected on three birds.

TABLE 2

The more common species of mites found on birds in the study

Host species	Common name	Mites
C. carduelis	Goldfinch	*Proctophyllodes pinnatus* (Nitzsch, 1818)
C. chloris	Greenfinch	*Proctophyllodes pinnatus* (Nitzsch, 1818)
S. serinus	Serin	*Proctophyllodes serini* Atyeo & Braasch, 1966
H. rustica	Swallow	*Pteronyssoides obscurus* Berlese 1884[a]
S. atricapilla	Blackcap	*Proctophyllodes sylviae* Gaud, 1957
S. melanocephala	Sardinian warbler	*Proctophyllodes clavatus* Fritsch, 1961[a]
		Proctophyllodes sylviae Gaud, 1957
T. merula	Blackbird	*Proctophyllodes* sp[b]
P. major	Great tit	*Proctophyllodes stylifer* (Buchholz, 1869)
P. domesticus	House sparrow	*Proctophyllodes troncatus* Robin, 1877
T. troglodytes	Wren	*Proctophyllodes stylifer* (Buchholz, 1869)

[a]New host record.
[b]Not identified beyond genus, possibly new species.

Number of feathers with detectable mites

Table 3 shows the mean and the median number of primaries affected for each species. The mean values closely reflected the prevalence rates. Thus, swallows, sand martins and greenfinches had the highest mean number of infested feathers. The species showing intermediate prevalence rates (blackcaps, house sparrows, goldfinches, blackbirds, Cetti's warblers, great tits and serins) had mean values in the range 1–4.4. The relationship between the prevalence and mean number of affected feathers across species was highly significant ($r_s = 0.96$, $n = 22$, $p < 0.001$).

Primary feather total mite infestation score

The relationship between scores assigned to feathers and the actual number of mites on feathers which were selected for detailed microscopical inspection is illustrated in Fig. 1. As expected there was a strong positive relationship ($r_s = 0.785$, $n = 154$, $p < 0.0001$).

The mean values for primary feather total mite infestation scores (PTMIS) for each species are given in Table 3. It should be noted that sample sizes were smaller than in the data presented earlier because PTMIS were only collected in 1991–1993. It is evident from the data that greenfinches carried the most intense mite infestations as reflected in a mean PTMIS of 12.3 and a median score of 14.5. As in the earlier analyses, swallows and sand martins had high PTMIS values (> 6). The validity of using PTMIS was established by the highly significant positive relationship across species between the mean PTMIS and the prevalence

TABLE 3

Allocation of bird species to four categories according to prevalence and intensity of infestation

Species	*n*	Prevalence	Number of infested feathers[a]		PTMIS[b]		
			Mean ± SEM	Median	*n*	Mean + SEM	Median
Group 1: high prevalence and intensity of infestation							
C. chloris	21	100	6.7 ± 0.5	8	14	12.3 ± 1.7	14.5
R. riparia	3	100	4.7 ± 1.2	4	3	7.7 ± 1.8	7
H. rustica	5	100	6.4 ± 0.4	7	4	6.8 ± 0.6	7
Group 2: moderate prevalence and intensity of infestation							
S. serinus	11	90.9	2.8 ± 0.6	2	9	3.3 ± 0.7	4
T. merula	21	85.7	4.4 ± 0.7	5	18	5.8 ± 1.2	5
S. atricapilla	138	84.1	3.4 ± 0.2	3	92	4.6 ± 0.5	3
C. carduelis	53	75.5	2.5 ± 0.3	2	40	3.0 ± 0.5	2
C. cetti	10	70.0	2.2 ± 0.6	3	10	3.5 ± 1.0	4
P. domesticus	95	62.1	3.2 ± 0.3	2	79	5.6 ± 0.8	3
P. major	5	60.0	1.0 ± 0.4	1	5	1.6 ± 0.7	2
Group 3: low prevalence and intensity of infestation							
S. melanocephala	36	22.2	0.7 ± 0.2	0	25	1.3 ± 0.5	0
L. megarhynchos	5	40	1.0 ± 0.6	0	5	1.4 ± 1.0	0
C. brachydactyla	15	20	0.5 ± 0.4	0	13	0.6 ± 0.5	0
Group 4: negligible prevalence and intensity of infestation							
T. troglodytes	32	9.4	0.2 ± 0.1	0	26	0.3 ± 0.2	0
P. collybita	9	0.0	0.0	0	5	0.0	0
C. juncidis	4	0.0	0.0	0	2	0.0	0
E. astrild	4	0.0	0.0	0	4	0.0	0

Species for which $n < 3$ in 1990–1993 have been excluded from this table.
[a] Data based on 1990–1993.
[b] Primary feathers total mite infestation score. Data based on 1991–1993.

of mites ($r_s = 0.955$, $n = 22$, $p < 0.001$) and the mean number of feathers with evident mites ($r_s = 0.986$, $n = 22$, $p < 0.001$).

Frequency distribution of mites

Frequency distributions for the number of wing primaries with evident mites and PTMIS for blackcaps, house sparrows, goldfinches and greenfinches are shown in Figs 2 and 3, respectively. Although the most heavily infested birds were found among the house sparrows with two birds carrying scores in excess of 20, the negatively skewed distribution of the number of feathers with evident mites ($g_l = -0.71$) and PTMIS ($g_l = -0.398$) among greenfinches is clearly evident.

Allocation of bird species to overall infestation categories

On the basis of all the observations made during this project we were able

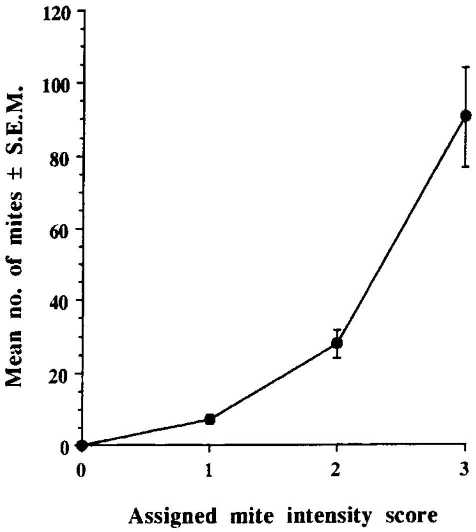

Fig. 1. Relationship between the subjective score (range 0–3) allocated to a feather and the actual number of mites attached based on microscopical inspection ($r_s = 0.785$, $n = 154$, $p < 0.0001$).

to allocate birds to four quite distinct categories as shown in Table 3. There was little overlap in values between these groups.

DISCUSSION

The approach which was used to quantify wing feather mites, was based on a novel procedure in which the method originally described by McClure (1989) was adapted to enable quantification of feather mite infestations and their subsequent statistical analysis. It was developed because of the difficulties involved in determining total mite infestations on live birds without rendering harm to the birds themselves. All of the birds in our study were ringed and released after our measurements had been taken and the handling time was minimal. Many were subsequently recaptured in the same year and in following years and none showed adverse effects of handling.

We concentrated on the primary feathers because these can be easily and conveniently examined during the brief period to which we were restricted when handling birds. However, feather mites also live among the secondary and tertiary wing feathers, covets and in other sites including the tail and body plumage. Quantification of infestations among the secondary and tail feathers is possible with the present system, but

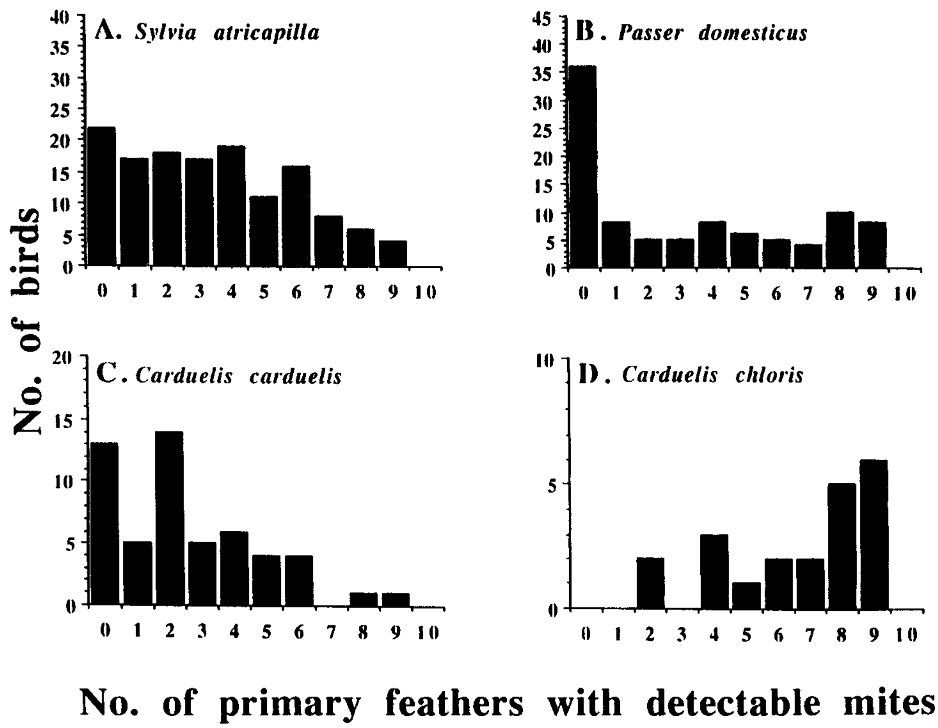

Fig. 2. Frequency distribution for the number of infected feathers in blackcaps (n = 138), house sparrows (n = 95), goldfinches (n = 53) and greenfinches (n = 21).

requires extension of the bird handling time, but not among body plumage and covets because these cannot be examined *in situ*. Whenever possible we scrutinized feathers removed from these latter sites but, overall, feather mites were rarely encountered in these alternative locations. Therefore, although our data do not quantify total mite infestations, we believe that they reflect and therefore are indicative of overall infestation intensities with mites. Our technique was accurate and repeatable, sampling feather mite populations in a semi-quantitative manner to provide information on mite infestations in individual hosts and in species of birds.

We attempted to identify the representative specimens from each bird species infested by mites. The majority of feather mites were of the genus *Proctophyllodes* and belonged to the '*pinnatus*' group (Atyeo and Braasch, 1966), characterized by a genital sheath supported by a heavily sclerotized ring. *Proctophyllodes pinnatus* (Nitzsch, 1818) is found on a wide range of avian hosts from Europe, Asia, North Africa and Central and North America and our detection of this species on greenfinches is consistent

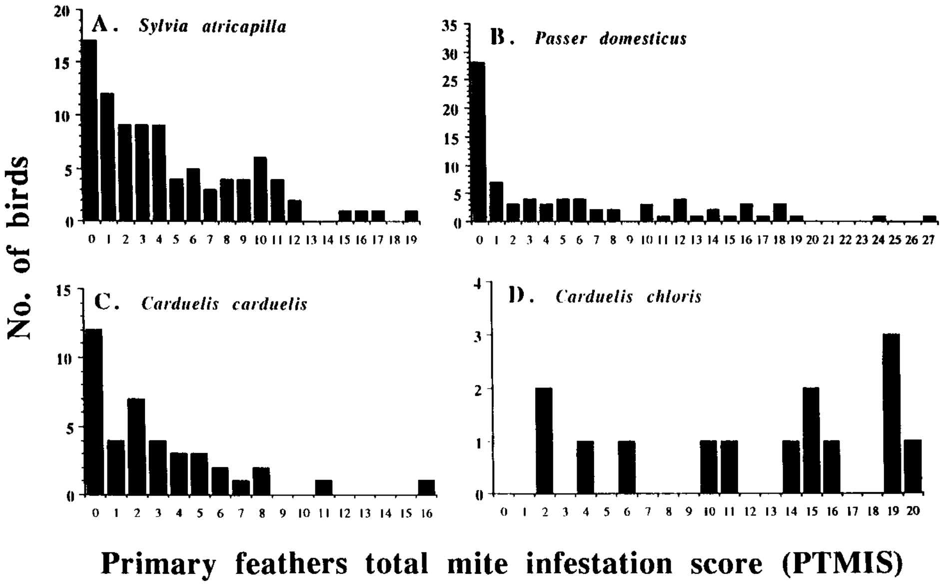

Fig. 3. Frequency distribution for PTMIS in blackcaps ($n = 92$), house sparrows ($n = 79$), goldfinches ($n = 40$) and greenfinches ($n = 14$).

with other reports (Atyeo and Braasch, 1966). *Proctophyllodes troncatus* Robin 1877 is generally restricted to birds from the genus *Passer* and hence our identification of this species on house sparrows is not unexpected. *Proctophyllodes sylviae* Gaud, 1957 is restricted to the two species on which we found it, Sardinian warblers and blackcaps (Gaud, 1957). *Proctophyllodes clavatus* Fritsch, 1961 is more wide ranging on European birds and our discovery of this species on the Sardinian warbler constitutes a new host record. *Proctophyllodes stylifer* (Buchholz, 1869) is generally restricted to birds from the family Paridae but slides in the Trouessart collection indicate that the species was found on '*Troglodytes europeaus*' (synonym of *Troglodytes troglodytes*) (Atyeo and Braasch, 1966) and our data confirm that this species does indeed occur on wrens. *Pteronyssoides obscurus* Berlese 1884 has been reported on various martins and African swallows but never previously on the European swallow, although this is not surprising in view of the migratory behaviour of European swallows (Zumpt, 1961).

The semi-quantitative methods enabled five related measures of infestation to be used in comparisons across species. All of these supported each other in so far as birds which showed a high prevalence of infestation, were also those which had the most infested feathers and which gave the highest PTMIS. The only exception to this generalization were the house sparrows which had a prevalence of infestation of 62.1% and yet had the fifth highest PTMIS in the study, with a mean value of 5.6. The explanation for this is clearly apparent from Figs 2b and 3b which emphasize the complex distribution of the PTMIS in house sparrows: there was a peak of birds among the low-intensity infestation levels and then birds with a range of mite loads with some carrying the most intense infestations detected in our study. This is an interesting finding in its own right, for which we offer several possible explanations. Firstly it is conceivable that despite our inability to distinguish more than one species affecting house sparrows, there may have been several with one species showing a high-intensity infestation in only a proportion of birds whilst the others presented lower levels of infestation. Secondly it is possible that genetic differences between individual house sparrows resulted in two infestation phenotypes, one susceptible to mites and the other resistant. There is ample precedent from studies of genetics of resistance to other parasites to make this suggestion feasible (Wakelin and Blackwell, 1988), although we do not know of any data suggesting that adaptive immunity can control wing feather mites. It is equally likely that behavioural differences, which might also be attributed to a heritable genetic component, led to the complex distribution pattern. Impaired preening, arising through experimental intervention affecting the bill (Booth *et al.* 1993), genetically determined abnormalities or accidental damage (Clayton 1991a) may result in the accumulation of high ectoparasitic burdens on birds. Finally, it could be that the two groups represented different communities of house sparrows, occupying different habitats (e.g. farm land versus urban environment) which intermingled in our study sites. We cannot offer a definitive explanation but it is hoped that future work will elucidate the explanation.

Finally, our conclusion that the birds which we sampled could be grouped into four categories based on the intensity of mite infestations also warrants some explanation. It is quite apparent from our data that swallows, sand martins and greenfinches showed 100% prevalence. Poulin (1991) reported that group-living species were more likely to show a high prevalence of feather mites than solitary species but there was no statistical support for this conclusion from our study. Moreover, two of the birds in the top category were insectivores (sand martins and swallows) and the other a granivore, so the explanation for variable mite infestations cannot reside solely in feeding strategies either. However, it is also quite apparent that the birds carrying low-intensity infestations or not infested at all, were, with one exception, all insectivores. The only exception was the waxbill, an introduced species in Portugal, the four specimens sampled in this study having no detectable mite infestations. Other granivores such as goldfinches, serins and house sparrows ranked in the intermediate group, showing moderate levels of prevalence and intensity of infestation. If there is an explanation to be found in the mode of feeding it might relate to the bill shape in relation to insectivorous and granivorous feeding strategies; insectivores may be more efficient at cleaning their feathers from mite infestation. While swallows and sand martins are insectivores, they are aerial plankton feeders with a very different bill morphology from the other insectivores in this study; their wide gape and short bill length could make preening difficult. However, Møller (1991) found that swallows were almost mite free except on the head where they cannot preen (86% of mites were located on the head). This suggests that they remove mites efficiently elsewhere on the body, but we cannot comment further on this disparity between our observations and those of Møller (1991) since our inspection of swallows was confined to wing feathers. It may also be pertinent that Clayton and Cotgreave (1994) concluded that no relationship between bill morphology and ectoparasite burden existed in the case of feather lice, birds compensating for inefficient bills by increased grooming with their feet.

An additional/alternative explanation for the mite intensity groupings may be that the population dynamics of mite species on specific hosts differ with maximum infestations being achieved at other times of the year, possibly in relation to climatic changes, the breeding or moulting cycles, availability of food or even migration. Indeed data to support season-dependent cycles in the prevalence of feather mites, movement on birds from wings to body feathers in relation to humidity and even circadian cycles with peak activity in the dark phase have been reported previously (McClure, 1989). Our study was conducted for only a 2 week period in each of four successive Aprils and it may be that some of the bird species showing low infestation rates have more intense infestations at other times of the year, although from April the climate in Portugal becomes hotter and drier and on the basis of McClure's (1989) data we would expect wing feather mite loads to decline towards mid-summer. This possibility will only be resolved when our study is extended to continue throughout the year and data become available for complete annual cycles of mites on each host species, a project which we intend to initiate soon. Furthermore, since all the birds were ringed it will be possible to compare infestation levels on birds which are recaptured in successive years and this will also aid in building a picture of the population dynamics of these parasites.

Whatever the explanation for the groupings, the results reported in this paper were derived from a novel approach to the study of bird wing feather mites and have already revealed interesting comparisons between species, which have not been reported previously. Our findings pose several intriguing problems which will require further investigation and analysis.

ACKNOWLEDGEMENTS

We wish to thank Mr A Pircher, the warden of the Quinta de Sao Pedro research station for his hospitality, advice and support throughout our study. We are also very grateful to Mr Antonio Arujo of CEMPA and his colleagues who arranged permission for us to study birds in Portugal, suggested one of our study sites and arranged appropriate support to enable us to incorporate this into our project. Last, but by no means least we are grateful to R. Samuelson, J. Salmon, M. Partington, A. White, P. Bowen, P. Bloomfield, P. Heaton, C. Hanson, A. Littlefield, J. Little, N. Allain, A. Kerfoot, J. Medlicott, A. Beale, M. Williams, D. Rose and S. Hodgson, the undergraduate students who so eagerly participated in this study and without whose assistance the work would not have been possible.

REFERENCES

Atyeo, W.T. 1992. The pterolichoid feather mites (Acarina, Astigmata) of the Megapodiidae (Aves, Galliformes). Zool. Scripta 21: 265–305.

Atyeo, W.T. and Braasch, N.L. 1966. The feather mite genus *Proctophyllodes* (Sarcoptiformes: Proctophyllodae). Bull. Univ. Neb. St. Mus. 5: 1–354.

Atyeo, W.T. and Gaud, J. 1979. Feather mites and their hosts. Recent Adv. Acarol. 2: 355–361.

Atyeo, W.T. and Perez T.M. 1988. Species in the genus *Rhytidelasma* Gaud (Acarina: Pterolichidae) from the green conure, *Aratinga holochlora* (Sclater) (Aves: Psittacidae). System. Parasitol. 11: 85–96.

Atyeo, W.T. and Perez, T.M. 1990. Feather mites of the *Aralichus canestrinii* (Trouessart) complex (Acarina, Pterolichidae) from New World Parrots (Psittacidae). II. From the genera *Aratinga* Spix, *Deroptyus* Wagler, *Letpositaca* Berlepsch and Stolzmann, *Ognorhynchus* Bonaparte, *Pionites* heine, and *Pyrrhura* Bonaparte, and conclusions to the study. Fieldiana Zool. (New Ser.) 62: 1–30.

Bonnet, A. and Timon-David, J. 1932. Sur quelques oiseux de provence et leurs acariens plumicoles. Bull. Soc. Linn. Provence 5: 23–29.

Booth, D.A., Clayton, D.H. and Block, B.A. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. Proc. R. Soc. Lond. B 253: 125–129.

Buchholz, R. 1869. Bemerkungen uber die Arten der Gattung Dermaleichus Koch: 19–21. Dreseden.

Canestrini, G. 1886. Famiglia degli Analgesini. Prospectto dell'Acarofauna Italiana, Padova 2: 248–303.

Černý, V. 1973. Parasite–host relationships in feather mites. In Proceedings of the Third International Congress of Acarology, M. Daniel and B. Rosicky (eds), pp. 761–764. Academic Publishing House of Czechoslovakian Academy of Sciences, Prague.

Choe, J.C. and Kim, K.C. 1987a. Community structure of arthropod ectoparasites on Alaskan seabirds. Can. J. Zool. 65: 2998–3005.

Choe, J.C. and Kim, K.C. 1987b. Ectoparasites of the pelagic cormorant, *Phalacrocorax pelagicus*, from the Pribilof Islands, Alaska, J. Med. Entomol. 24: 592–594.

Choe, J.C. and Kim, K.C. 1988. Microhabitat preference and coexistence of ectoparasitic arthropods on Alaskan seabirds. Can. J. Zool. 66: 987–997.

Choe, J.C. and Kim, K.C. 1989. Microhabitat selection and coexistence in feather mites (Acari-Analgoidea) on Alaskan seabirds. Oecologia 79: 10–14.

Clayton, D.H. 1991a. Coevolution of avian grooming and ectoparasite avoidance. In Bird–Parasite interactions: ecology, evolution and behaviour, J. E. Loye and M. Zuk (eds), pp. 328–348. Oxford University Press, Oxford.

Clayton, D.H. 1991b. The influence of parasites on host sexual selection. Parasitol. Today 7: 329–334.

Clayton, D.H. and Cotgreave, P. 1994. Relationship of bill morphology to grooming behaviour in birds. Anim. Behav. 47: 195–201.

Cooper, E.S. and Bundy, D.A.P. 1988. *Trichuris* is not trivial. Parasitol. Today 4: 301–306.

Dubinin, V.B. 1951. Feather mites (Analgesoidea). Part I. Introduction to the study. Fauna USSR Arachnida 6(5): 1–363. (In Russian.)

Dubinin, V.B. 1953. Feather mites (Analgesoidea). Part II. Families Epidermoptidae and Freyanidae. Fauna USSR Arachnida 6(6): 1–411. (In Russian.)

Dubinin, V.B. 1956. Feather mites (Analgesoidea). Part III. Family Pterolichidae. Fauna USSR Archnida 6(7): 1–813. (In Russian.)

Evans, G.O., Sheals, J.G. and MacFarlane, D. 1961. The Terrestrial Acari of the British Isles. An Introduction to their Morphology, Biology and Classification, Volume 1. Introduction and Biology. British Museum (Natural History), London, UK.

Faccini, J.L.H. and Atyeo, W.T. 1981. Generic revisions of the Pteronyssinae and the Hyonyssinae (Analgoidea: Avenzoariidae). Proc. Acad. Natl. Sci. Phil. 133: 20–72.

Fitzpatrick, C. and Threlfall, W. 1977. The ectoparasites of three species of seabirds from Newfoundland, Canada, Can. J. Zool. 55: 1205–1209.

Fritsch, W. 1961. Die Milbengattung *Proctophyllodes* Robin 1868. Z. Parasitenk. 21: 1–29.

Gaud, J. 1957. Acariens plumicoles (Analgesoidea) parasites des oiseaux du Maroc. I. Proctophyllodidae. Bull. Soc. Sci. Nat. Phys. Maroc 37: 105–136.

Gaud, J. 1981. Acariens Sarcoptiformes plumicoles des oiseaux Ciconiiformes d'Afrique. II. Parasites des Ciconiidae, Scopidae et Phoenicopteridae. Rev. Zool. Afr. 96: 335–357.

Hamilton, W.D. and Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? Science 218: 384–387.

Hollander, W.F. 1956. Acarids of domestic pigeons. Trans. Am. Microsc. Soc. 75: 461–480.

Hull, J.E. 1931. A new genus and species of Analgesidae (feather mites). Vasculum 17: 145–147.

Hull, J.E. 1934. Concerning British Analgidae (feather mites). Trans. Northern Nat. Un. 1: 200–206.

McClure, H.E. 1989. Occurrence of feather mites (Proctophyllodidae) among birds of Ventura County Lowlands, California, J. Field Ornithol. 60: 431–450.

Møller, A.P. 1991. Parasites, sexual ornaments and mate choice in barn swallows. In Bird–Parasite interactions: ecology, evolution and behaviour, J. E. Loye and M. Zuk (eds), pp. 328–348. Oxford University Press, Oxford.

Nitzsch, C.H. 1818. Acarina. In Allgemeiner encyclopadie der wissenschaften und kunste, Vol. 1, Ersch and Gruber (eds), pp. 246–252.

Perez, T.M. and Atyeo, W.T. 1984. Site selection of the feather and quill mites of Mexican parrots. In Acarology VI, Vol. 1, D. A. Griffiths and C. E. Bowman (eds), pp. 563–570. Ellis Horwood Ltd, Chichester.

Peterson, P.C. 1975. An analysis of host–parasite associations among feather mites (Acari-Analgoidea). Misc. Publ. Entomol. Soc. Am. 9: 237–242.

Poiani, A. 1992. Ectoparasitism as a possible cost of social life: a comparative analysis using Australian passerines (Passeriformes). Oecologia 92: 429–441.

Poulin, R. 1991. Group-living and infestation by ectoparasites in passerines. Condor 93: 418–423.

Radford, C.D. 1953. The mites (Acarina: Analgesidae) living on or in the feathers of birds. Parasitology 42: 199–230.

Read, A.F. 1990. Parasites and the evolution of host sexual behaviour. In Parasitism and host behaviour, C. J. Barnard and J. M. Behnke (eds), pp. 117–157. Taylor and Francis, London.

Robin, C. 1868. Memoire sur les Sarcoptides avicoles et sur les metamorphoses des Acariens. CR Acad. Sci., Paris 66: 776–786.

Robin, C. (and Megnin, P.) 1877. Memoire sur les Sarcoptides plumicoles J. Anat. Physiol., Paris 13: 629–656.

Spencer, R. 1984. The Ringer's Manual, 3rd edn. British Trust for Ornithology, Beech Grove, Herts, UK.

Trouessart, E.L. 1885. Note sur la classification des Analgesiens et diagnoses d'especes et de genres nouveaux. Bull. Soc. Angers 14: 46–89.

Wakelin, D. and Blackwell J. (eds) 1988. The Genetics of Resistance to Bacterial and Parasitic Infections. Taylor and Francis, London.

Wedekind, C. 1992. Detailed information about parasites revealed by sexual ornamentation. Proc. R. Soc. Lond. B. 247: 169–174.

Wheeler, T.A. and Threlfall, W. 1986. Observations on the ectoparasites of some Newfoundland passerines (Aves: Passerformes). Can. J. Zool. 64: 630–636.

Zumpt, F. 1961. The arthropod parasites of vertebrates in Africa south of the Sahara I.S. Afr. Inst. Med. Res. 9: 1–457.