Feather mites on group-living Red-billed Choughs: a non-parasitic interaction?

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Blanco, G., Tella, J. L. and Potti, J. 1997. Feather mites on group-living Red-billed Choughs: a non-parasitic interaction? – J. Avian Biol. 28: 197–206.

Most reports of interactions between feather mites and their avian hosts have assumed that mites have detrimental effects on their hosts, i.e. that they behave as parasites. We investigate the effects of feather mites *Gabucinia delibata* on the body condition of Red-billed Choughs *Pyrrhocorax pyrrhocorax*, a highly social, medium-sized corvid species. Feather mites were absent in fledglings at the nest and were probably acquired by Choughs from 1 to 5 months after fledging, when they joined communal roosts. The abundance of feather mites on both wing and tail increased with age and development of social habits in non-breeding Choughs, but decreased when they reached breeding status. Mated Choughs had similar abundances of feather mites. The abundance of mites correlated positively with body condition (computed as the residuals of mass on a "size factor") in both males and females, and body condition was in general better for Choughs holding mites than for those lacking mites. The conclusion that feather mites do not have detrimental effects on Choughs was reinforced by the fact that feather mite abundance did not differ between Choughs with normal and crossed bills, respectively, suggesting that preening does not remove mites from the feathers. This particular association thus could be labelled as non-parasitic, suggesting at least a commensal, and possibly a mutualistic relationship. In the latter case, the hypothesised benefits accrued to Chough hosts from their association with mites may derive from an improved feather cleaning, and from the supposed protection against pathogenic organisms achieved primarily by preemption of resources by more benign species, such as feather mites.

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With the recent upsurge of interest in host-parasite interactions the effects of mites, ticks, lice, fleas and bugs living on birds have been studied as antagonistic relationships (Borgia and Collis 1989, Møller 1990, Møller et al. 1990, Loye and Zuk 1991, Lehman 1993, Loye and Carroll 1995, Potti and Merino 1995) with a detrimental effect on the fitness of the avian host as implicit in definitions of parasitism (Price 1980, Anderson and May 1982, Thompson 1994). Extensive evidence indicates that some ectoparasites reduce host fitness (references above), but some studies found no obvious detrimental effects of supposed parasites (e.g. feather lice, Potti and Merino 1995; hippoboscid flies, Tella et al. 1995, Tompkins et al. 1997). Commensalism, in which hosts are unaffected by symbionts (sensu

Thompson 1994), and mutualism in which both host and symbiont benefit, are common in nature (Thompson 1994), although nothing is known of their occurrence or frequency among birds and their symbionts.

Because of their ubiquity and enormous diversity (OConnor 1982), astigmatid mites hold much promise for the study of the diversity of potential interactions with their hosts. The Astigmata (order Acariformes) represent the largest radiation of mites living in close association with both vertebrates and invertebrates. Some astigmatid mites, namely burrowers grouped together under the name "Psoroptidia" are known as agents of disease in mammals (e.g. mange, sheep scab) and birds (scaly leg of poultry caused by members of Knemidokoptidae; Kettle 1984, see also Gaud 1968).

However, among astigmatid mites associated with birds there are other taxa in the lineages Pterolichoidea and Analgoidea, collectively known as feather mites, that feed on detritus and feather oil on the host's epidermal surface (Fain 1965, OConnor 1982). Feather mites are common symbionts of birds and usually assumed to act as parasites. However, little is known about the relationships of birds and their feather mites (OConnor 1982) despite the cosmopolitan distribution of birds and the presence of feather mites in all major avian groups except penguins (Peterson 1975), and their abundance in comparison with other avian-living arthropods (Fowler and Williams 1985, Choe and Kim 1987, McClure 1989). In fact, the few studies dealing with feather mites and birds (Fowler and Williams 1985, Choe and Kim 1987, 1989, McClure 1989) have also assumed the existence of a host-parasite interaction, although the functional significance of the interactions between feather mites and their avian hosts has not been adequately documented.

Irrespective of the type of interaction little information exists on the effect of host age (but see Potti and Merino 1995), season, environmental conditions, or social context when mites and other arthropods living on the body of birds are acquired. In this paper, we examine the mode of acquisition and the temporal patterns of variation in prevalence and abundance of a species of feather mite living on Red-billed Choughs *Pyrrhocorax pyrrhocorax* (Choughs hereafter), a highly social medium-sized corvid. We focus on the effects of host age and sociality on the abundance of mites to assess the hypothesis that group-living by hosts increases prevalence and abundance of mites (Poulin 1991). Furthermore, we analyse correlations between mite abundance and body condition of Choughs to test two alternative hypotheses regarding the functional nature of this interaction. If mites have detrimental effects on host fitness, that is, they behave as parasites, we predict that body condition of Choughs should be negatively affected by the abundance of mites. Ironically, an alternative explanation may be derived from this one-tailed hypothesis championed by most researchers who are just looking for detrimental effects of parasites. Under this view, which places intensity of infection as the predictor variable, we should expect that high abundances of feather mites should not impair or even improve the body condition of Choughs. This could be achieved if mites improve the efficiency of feather cleaning and compete for resources with other organisms living on the host body.

Methods

Study area and field work

The study was conducted from 1992 to 1994 in Los Monegros, Ebro Valley, NE Spain (41°20′N, 0°11′W). The study area is a plain of nearly 250 km², between 300–360 m a.s.l., mostly devoted to cereal crops (wheat, barley). The climate is continental Mediterranean semiarid, with c. 350 mm of total rainfall concentrated in spring and autumn and temperature extremes of −5°C in winter and 40°C in summer.

In this area, Choughs breed and roost almost exclusively inside abandoned farm houses and other old buildings (Blanco et al. 1997), where they can be easily captured throughout the year. Choughs were trapped with large butterfly nets from about three hours after sunset until sunrise and were released where caught after data collection. Breeding Choughs were captured at their nesting sites where both members of the pair normally roost together. Non-breeding Choughs were captured at communal roosting sites holding variable numbers of birds. We categorised roosting sites as either large or small based on the number of captures and especially on observations of the flocks before they entered roost sites. Large roosting sites are traditionally occupied across years and attract large numbers of birds (>40 Choughs, usually 70–200 in the study area) throughout the year, especially in autumn and winter (Blanco et al. 1993). In contrast, small roosting sites are used irregularly throughout the year by small- to medium-sized flocks (≤40 birds, usually 10–30).

Age and sex determination

We distinguished birds in their first year of life from second-year birds and non-breeding adults, i.e. birds ≥3 years old captured at communal roosts and previously unrecorded as paired breeding individuals in nesting sites. We aged birds by assessing moulting patterns and plumage features of birds undergoing moult of flight feathers (Blanco et al. 1996).

The sex of breeding Choughs was determined by means of both observations of breeding behaviour of marked birds and by size using linear discriminant functions (Tella and Torre 1993). Non-breeding birds subsequently captured as breeders were assigned to the sex determined when breeding. The rest of non-breeding Choughs were sexed by size using a discriminant function based on morphological measurements of breeding conspecifics (Blanco et al. 1996).

Analysis of hosts' size and condition

Upon capture and banding, each bird was weighed (to the nearest 1 g) and several measures of size (taken with digital calipers, precision 0.01 mm) were taken (see Tella and Torre 1993 for measurement procedures and definitions). Four of these measures (bill, head, wing and central tail feather lengths) were selected for subse-

quent analyses as representative of body size dimensions. All body measurements were taken in all months of the year, but wing and tail lengths of moulting Choughs captured in August–September and June, respectively, were excluded because these are periods of feather growth (authors' unpubl. data). Females weighed in March and April were also excluded because of substantial increases in mass near to egg laying. Measurements of broken feathers and bills were also discarded. No logarithmic transformations were applied because of the good fit of the data to normal distributions.

Since multivariate measures of size are preferable to univariate measures (Freeman and Jackson 1990), we used Principal Component Analysis (PCA) to combine morphological measurements and extracted the first principal component (PC1), which usually explains most of the variance and can be used as a multivariate index of overall body size (Grant 1986, Bortolotti and Iko 1992, Kirk and Gosler 1994). Because of the high degree of sexual size dimorphism in this species (Tella and Torre 1993, and unpubl. data), separate analyses were performed for males (n = 337) and females (n = 294). PC1 accounted for 66% and 57% of the variance in the set of measurements for males and females, respectively. An index of body condition was calculated as the residuals from the linear regression of body mass on PC1 factor scores (r = 0.63, p < 0.001 and r = 0.41, p < 0.001, for males and females respectively). We removed any variation of body condition due to season, year and age by using the residuals of a 3-way ANOVA of condition on these factors and then looked for relationships between body condition and mite load scorings.

Mite species and quantification

Mites living on Chough feathers were identified as belonging to the species *Gabucinia delibata* (Robin 1877), order Astigmata, superfamily Pterolichoidea, family Gabuciniidae. This species is distributed across Europe and North Africa, and has previously been recorded on other corvid species in the genus *Corvus* and in Magpies *Pica pica* where it presumably feeds on feather oil and debris (Dubinin 1951, cited in OConnor 1982, T. W. Atyeo, pers. comm.).

We conducted a log-linear analysis (Sokal and Rohlf 1981) to investigate the variation in mite prevalence, i.e. the proportion of hosts infested, across seasons and birds' age and sex. This procedure resembles analysis of variance in that the total variance of frequency data is partitioned into different factors, which allows one to test for interactions between them. The test was run hierarchically, beginning with the highest order (4) interaction and proceeding backwards until all terms/interactions retained by the model reached significance

(p < 0.05), so that dropping any of them would result in a lack of fit of the model. We included all Choughs captured over the 3-year period because they were not captured in all seasons each year. Three seasons were considered, namely winter (December to February), spring-breeding season (March to June), and summer-autumn period (July to November) which coincides with the moulting of flight feathers.

Mite abundance was estimated by scoring the number of mites attached to the wing (primary and secondary feathers) and tail feathers when they were extended and exposed against a lamp. Feather mites occurred ventrally, usually near the rachis, in the slots between the pennaceous barbs. Mite abundance was assessed for each feather of a single wing (16 feathers) and for each feather of the tail (12 feathers). The number of mites was scored in intervals based on the usual degree of variation in their abundance as assessed by previous observations. That is, we used scores which could be rapidly assigned in accordance with the natural variation in mite abundance. Thus, the numbers of mites was scored as 0 (no mites), 1 (<5 mites per feather), 2 (6–75), 3 (76–100 mites), and 4 (>100 mites). Since we searched each feather for mites and mite abundances usually differed somewhat among feathers of the same bird, we also used intermediate scores (i.e. 0.5, 1.5, etc.) when a similar number of feathers were assigned to two different, consecutive, scores. To reduce possible biases, only one of us (GB) examined the birds and scored mite abundance. The variation in mite abundance scores was analysed using non-parametric Kruskal-Wallis ANOVAs.

To see whether Choughs attempt to remove the mites by preening their feathers (Clayton 1991), we compared mite abundance and mite prevalence between Choughs with normal and deformed (crossed) bills. A crossed bill is a frequent bill deformity in Choughs (authors' unpubl. data) preventing full occlusion of mandibles; therefore, it can be assumed that a crossed bill makes the bird unable to remove the mites from its feathers (see Clayton 1991).

Results

Mite prevalence

We found no mites attached to flight feathers of nestling Choughs (n = 89). A log-linear model taking into account the variation in mite prevalence on wing with season, age and sex of the birds showed no 4-way interaction (G = 4.43, d.f. = 6, p = 0.62). However, a significant 3-way interaction indicated that mite prevalence on the wing was related to age and season (G = 32.23, d.f. = 6, p < 0.001). The fit of the log-linear model containing these interactions was adequate (goodness-of-fit, G = 8.33, d.f. = 20, p = 0.99). In sum-

mary, these results indicate that mite prevalence on the wing of first-year birds increased greatly from the end of the breeding season, when they were still associated with their parents and nesting sites, to the winter when all first-year birds joined communal roosts. In summer, most first-year birds live together with subadults in large flocks and communal roosts but mite prevalence was only about 35% (Fig. 1a). For Choughs older than one year (Fig.1a) the prevalence of mites on wing feathers was very high and rather stable (72.5–100%) throughout the year.

The same analysis did not reveal significant 4-way (G = 4.25, d.f. = 6, p = 0.64) or 3-way interactions (p > 0.30 in all cases) for mites on tail feathers, while there were independent interactions with age (G = 12.72. d.f. = 3, p = 0.005), season (G = 23.76, d.f. = 2, p < 0.001) and sex (G = 7.03, d.f. = 1, p = 0.008). The fit of the log-linear model containing these interactions was adequate (goodness-of-fit, G = 26.20, d.f. = 28, p = 0.56). These results showed that during the winter, prevalence of mites on tail feathers decreased notably in both sexes with respect to the previous summer-moult period, when the highest prevalence was reached (Fig. 1b,c). Prevalence was higher in males than in females in most comparisons in which age and season were controlled (Fig. 1b,c). Overall, mite prevalence on the tail peaked in the birds' moulting period.

Mite abundance

The abundance of feather mites on both wing and tail increased with age and development of social habits (see above) in non-breeding Choughs, but decreased when they reached breeding status (Kruskal-Wallis ANOVAs; H = 43.94, p ≪ 0.001, d.f. = 3, n = 598, and H = 55.02, p ≪ 0.001, d.f. = 3, n = 598, for wing and tail respectively; Fig. 2).

No between-sex differences in wing mite abundances were detected for any of the age-status classes (Table 1). However, differences between seasons were highly significant for all age-status classes (Table 1). Seasonal profiles of mite abundance for each age-status class are depicted in Fig. 3. Among first-year birds, mite abundance on the tail was significantly higher in males than in females, and the same trend, albeit not quite reaching statistical significance, was found in breeding adults (Table 1). Mite abundance scores for the tail differed between seasons for non-breeding Choughs older than one year (Table 1), being highest during the summer-moulting period (Fig. 3). The highest abundance of mites on the wing was reached when the abundance of mites on the tail decreased (Fig. 3), suggesting migration of mites from tail to wing feathers during winter. Overall, mite abundance peaked during the moult-summer period in the tail feathers and during the winter in the wing feathers.
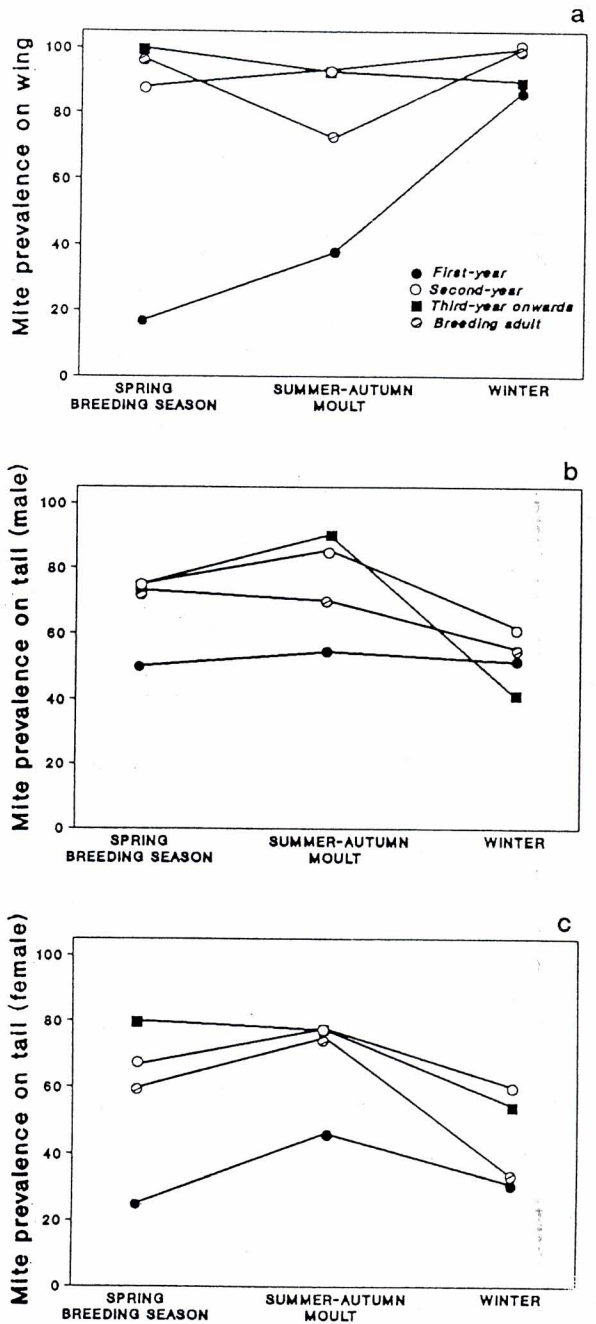

Fig. 1. Seasonal variation in mite prevalence on wing (a) and tail feathers (b: males; c: females) of Choughs in relation to age and breeding status. See text for statistics.

Mite acquisition

The above results were based on the analysis of overall prevalence and median values of mite abundance scores of different Choughs. When the analysis was restricted to individual Choughs captured in their first year and later recaptured in the second year, the results confirmed that first-year birds acquired mites once they
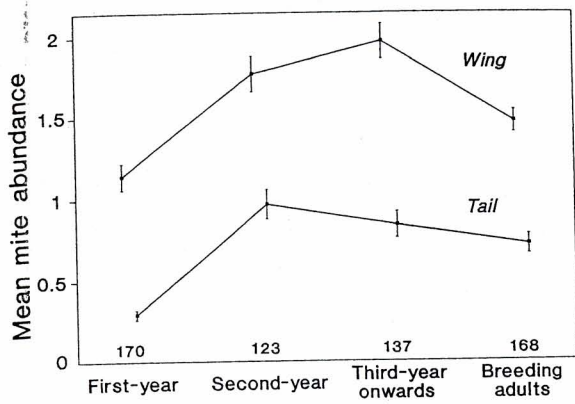
Fig. 2. Abundance (mean ± SE) scores of mites on the wing and tail feathers of Choughs in relation to age and breeding status. See Table 1 for statistics. Numbers at the bottom are sample sizes.

joined roosts, usually large communal roosts, from 1 to 5 months after fledging (authors' unpubl. data). Mite prevalence on wing feathers in 28 first-year Choughs which were later recaptured in their second year increased from 64.3% to 100% (Fisher's exact test, $p = 0.0007$). Prevalences on the tail increased from 60.7% to 71.4%, but the difference was not significant ($\chi_1^2 = 0.32$, $p = 0.57$). Mite abundance on the wing also increased within individual birds from their first (mean score $= 1.02$, SE $= 0.21$) to their second year (mean $= 2.21$, SE $= 0.21$) (Wilcoxon test for matched-pairs, $Z = 3.39$, $p = 0.0007$, $n = 28$). Mite abundance on the tail also

Table 1. Results of non parametric Kruskal-Wallis ANOVAs (H statistics) of the scores of mite abundance in the wing (A) and tail (B) feathers of Choughs in relation to bird sex, age and breeding status.

|	H	d.f.	n	P
(A) Wing				
Sex comparison (seasons pooled)				
First-year	0.16	1	166	0.68
Second-year	0.44	1	123	0.51
Third-year onwards	0.38	1	134	0.53
Breeding adults	3.63	1	168	0.057
Seasonal comparison (sexes pooled)				
First-year	24.17	2	170	<0.0001
Second-year	28.80	2	123	<0.0001
Third-year onwards	13.70	2	137	0.001
Breeding adults	19.13	2	168	<0.0001
(B) Tail				
Sex comparison (seasons pooled)				
First-year	7.20	1	166	0.0073
Second-year	0.02	1	123	0.90
Third-year onwards	0.07	1	134	0.80
Breeding adults	3.48	1	168	0.062
Seasonal comparison (sexes pooled)				
First-year (♂)	1.14	2	91	0.56
First-year (♀)	1.07	2	75	0.59
Second-year	17.68	2	123	0.0001
Third-year onwards	24.36	2	137	<0.0001
Breeding adults	5.35	2	168	0.068
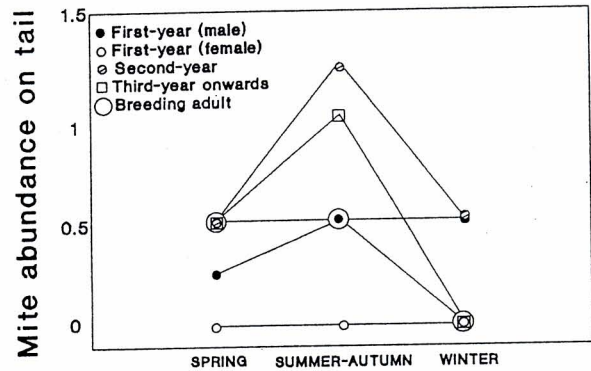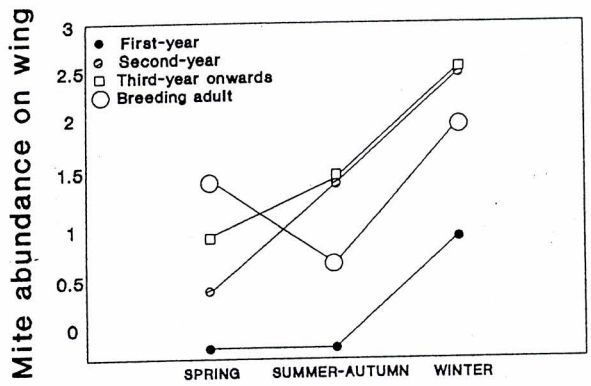
Fig. 3. Seasonal variation in abundance (median scores) of mites on the wing and tail feathers of Choughs in relation to age and breeding status. See Table 1 for statistics.

increased from the first to the second year of life albeit non-significantly ($0.52 + 0.09$ vs $0.86 + 0.18$, respectively; $Z = 1.81$, $p = 0.07$, $n = 28$ pairs). Although they were forming part of the flocks from the summer onwards, many of these first-year Choughs were captured for the first time in winter and so the estimated increase in prevalence and abundance of mites from the first to the second year should be conservative.

Mite distribution within individual Choughs and mated pairs

Some non-random distribution patterns of mites among Chough flight feathers were detected. Mite abundance on the wing feathers correlated positively with that on the tail when pooling seasons and ages (Spearman rank correlation, $r_s = 0.40$, $n = 643$, $p \ll 0.001$). The same analyses were performed separately across seasons to test for variations of this pattern in relation to the possibility of seasonal movements of mites between wing and tail feathers. Results were similar for the three seasons, with the trend being more marked during the summer-moult period ($r_s = 0.80$, $n = 180$, $p \ll 0.001$)

than during the breeding ($r_s = 0.43$, n = 158, p ≪ 0.001) and winter ($r_s = 0.39$, n = 305, p ≪ 0.001) seasons. These findings are consistent with the above results and suggest movement of mites from tail to wing feathers within particular Choughs in winter. Accordingly, the correlation between mite abundance on tail and wing feathers was highest when the distribution of mites was more even, as indicated by the seasonal variation in mite prevalence (Fig. 1) and abundance (Fig. 3).

The abundance of feather mites on breeding female Choughs correlated positively with that on their pair mates for both wing (Fig. 4) and tail ($r_s = 0.38$, n = 53, p = 0.0065) feathers.

Mite prevalence and abundance in relation to roost size

Mite prevalence did not differ between roosting sites of different size, for mites on either tail ($\chi_1^2 = 0.22$, p > 0.05) or wing ($\chi_1^2 = 0.06$, p > 0.05) feathers. However, mite abundance for Choughs older than two years was higher in large than in small communal roosts during the summer–autumn period (Fig. 5). During winter, mite abundance increased on wing and decreased on tail feathers (Figs. 3 and 5) so that no significant difference in mite abundance among roosting sites was evident except for higher abundances of mites on the wings of non-breeding Choughs older than two years captured at small roosts (Fig. 5).

Mite abundance and hosts' body condition

A positive relationship between mite abundance on the tail and the bird's body condition was found in males ($r_s = 0.19$, p = 0.003, n = 239) as well as in females ($r_s = 0.15$, p = 0.048, n = 172). Similarly, mite abundance on the wing correlated positively with body

Fig. 5. Abundance (mean + SE) scores of mites on the wing and tail feathers of Choughs in relation to size of their roosting group. Data are presented separately for birds in their second year (a) and birds of 3 years or older (b); ●: small roosts; ○: large roosts ∗: p < 0.05; ∗∗: p < 0.01; n.s.: not significant.

condition of female Choughs ($r_s = 0.18$, p = 0.018, n = 172). The same trend, albeit not reaching statistical significance, was found for males ($r_s = 0.10$, p = 0.10, n = 239). The overall abundance of mites (pooling tail and wing mites) correlated positively with body condition of males ($r_s = 0.16$, p = 0.01, n = 239) and females ($r_s = 0.19$, p = 0.01, n = 172).

Choughs which had mites attached to their tail feathers were in better condition than those without mites (t-tests: males: t = −2.14, p = 0.03, d.f. = 237; females: t = −2.48, p = 0.014, d.f. = 170). Body condition was better for Choughs with mites on their wings than for those lacking mites, the difference being significant for females (t = 4.76, p ≪ 0.001, d.f. = 170) and approaching significance for males (t = 1.58, p = 0.11, d.f. = 237), respectively. Similar trends were obtained when tail and wing mites were pooled (for females: t = 4.55, df = 170, p ≪ 0.001; for males, t = 1.67, p = 0.09, df = 237).

Since larger hosts may offer more living space to mites, we tested whether mite abundance was related to host size. We removed the effects of year, season and
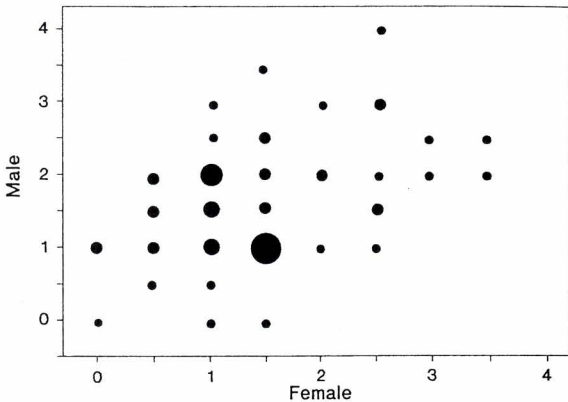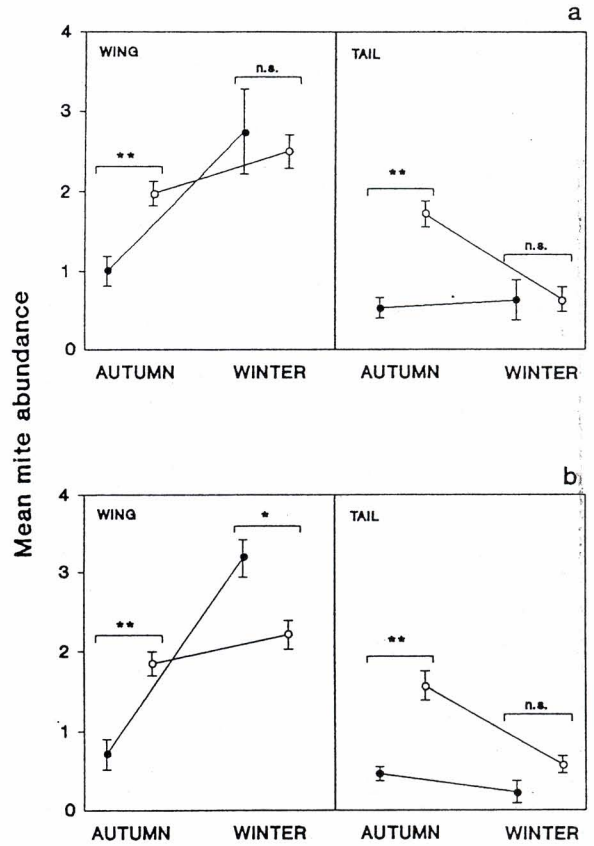

Fig. 4. Relationship between mite abundance scores of paired Choughs. Dots of increasing size indicate 1, 2, 3, 4 and 6 overlapping data points; $r_s = 0.42$, n = 53, p = 0.0027.

age on PC1 factor scores and compared them with mite abundance scores. All correlations were extremely low and far from statistical significance in males or females.

Mite prevalence and abundance in relation to preening ability

Pooling sexes and seasons, no differences in mite abundance were found on wing and tail feathers between breeding Choughs with normal (n = 151) or crossed bills (n = 17; Mann-Whitney tests, Z = 0.01, p = 0.99 for wing and Z = 0.54, p = 0.59 for tail). When mite abundances were analysed separately by sex and season, again no differences were found between Choughs with normal and crossed bills (in all cases p > 0.70 for wing and p > 0.30 for tail). In the case of non-breeding Choughs older than two years, we restricted the analysis to the winter period, when Choughs with crossed bills were captured. Most non-breeding Choughs older than two years with crossed bills were males (7 out of 8), so we only considered males in this comparison. Again, mite abundance on wing (Z = 0.74, p = 0.45, n = 44) and tail (Z = 1.64, p = 0.09, n = 44) feathers did not differ for Choughs with normal and crossed bills. The number of Choughs in the other two age-classes which had crossed bills was insufficient to analyse differences in mite abundance. The prevalence of feather mites on wing and tail was always lower or similar in Choughs with crossed bills in all comparisons (chi-squared tests applying Yates' correction, p > 0.05 in all cases). In conclusion, birds with bill deformities were not associated with higher mite infestations.

Discussion

The main findings of our study are two. In the first place, our work suggests that the mode of acquisition of feather mites and the variation in prevalence of these supposedly parasitic symbionts are linked to the development of the social habits in their host. Three of our results suggest a cause-effect relationship here: the increase of mite prevalence with age and contact with large roosts, the correlation between pair mates in mite abundance, and the pattern of variation in mite abundance in large vs small roosts. Second, mites had no apparent detrimental effects on host condition. On the contrary, high numbers of feather mites were clearly associated with increased body condition of the hosts, leading us to argue that the interaction between Choughs and *Gabucinia delibata* mites could be considered at least commensalistic and possibly mutualistic rather than parasitic.

Mites were acquired by individual Choughs in their first year of life, and both mite abundance and prevalence increased after the first-year birds joined large flocks, where they remain during the subsequent two, three or more years until they reach breeding status, usually at 3 or 4 years old (E. Bignal, pers. comm., authors unpubl.). Communal roosts, which hold large numbers of individuals during winter (Blanco et al. 1993) therefore seem likely to act as both reservoirs and sources of infestation. Thus, mites are probably transmitted from birds older than two years to first-year birds by contact when they roost close together, sometimes in close contact, in the same roosting sites night after night. The transmission of mites presumably was more likely among Choughs sharing large roosting sites, which attracted most first-year birds after fledging, hence had the largest numbers of individuals during autumn and winter (Blanco et al. 1993), than either among Choughs integrated in small flocks or isolated pairs roosting in their nesting sites. Although it could be argued that our results might as well be explained by better preening ability or more time spent in grooming by adult birds, these alternative hypotheses do not explain why breeding Choughs with crossed bills were not infected with more mites. This finding is in stark contrast to studies of other epizootic taxa, such as ectoparasitic chewing lice (Brown 1972, Clayton 1991), although it could be explained by mites being too tiny to be removed with the bill or mites inserting themselves in such a way as to be inaccesible to the bill. No information on either of these possibilities is available in this particular system.

By aggregating, individuals of group-living species attract more ectoparasites and come into more frequent inter-individual contacts with conspecifics holding parasites and other organisms (Poulin 1991, Hubálek 1994). Although, to our knowledge, there are no previous studies on the acquisition of symbionts by communally roosting birds, our results are in agreement with other studies which have documented increases in the rate of infestation by ectoparasites with increases in host colony size and development of group living (Shields and Crook 1987, Poulin 1991, Poiani 1992, Arnold and Lichtenstein 1993). Moreover, even within mated pairs where both individuals hold lower mite abundances than non-breeding birds, apparent "assortative" mating based on "parasite" abundances was observed, which may be most parsimoniously explained by transfer of mites between birds maintaining frequent contacts. Thus, our results sum up to one of the more pervasive patterns of host-parasite interactions, i.e. increasing host density favouring an increase in the likelihood of parasite transmission and/or acquisition of infectious diseases (Brown and Brown 1986, Møller et al. 1990, Poulin 1991), which has been thought to act as a force counterbalancing the benefits of social living (Hoogland and Sherman 1976). The relationship between feather mite abundance and sociability of Choughs emphasizes that, notwithstanding different effects on their hosts (see below), mechanisms of dispersal may converge

among different types of interaction, with most differences being in the effect they have on host fitness (Thompson 1994).

The seasonal pattern of mite abundance and prevalence suggests the existence of movements of mites between wing and tail, except in first-year birds where population growth of mites on individual birds is more likely explained by mite reproduction once mites were acquired in the flocks. Movements of mites from the tail causing higher abundances in wing feathers during winter could be explained by microhabitat selection of mites (Choe and Kim 1987, 1989) regulated by microclimatic conditions (McClure 1989). Wing feathers could be the preferred microhabitat during winter since they provide better protection against cold weather conditions, because of the closer contact with the host body during foraging and roosting. In fact, most mites recorded in the tail during winter were attached to the proximal part of the rectrices, where they were covered by the undertail-coverts. A correlation between mite movements on the host and weather conditions has been noted previously (Dubinin 1951, 1953, 1956 cited in McClure 1989). For instance, Dubinin found that flight feather mites of Starlings *Sturnus vulgaris* experimentally subjected to cold temperatures retracted to body feathers, and returned to their wing niches when warmer temperatures were restored. The higher prevalence and abundance of mites on the tail during the summer may also be due to movements caused by environmental conditions or by physiological changes involved in feather moult of the host (McClure 1989). Alternatively, mites could show a preference for new freshly moulted or developing feathers, as recorded among species in the family Laminosioptidae (OConnor 1982), which may explain the differences in abundance and prevalence of mites on tail and wing because new tail and wing feathers are present in summer and the start of the winter due to different moult chronology of these feathers (authors' unpubl. data).

Feather mites did not cause apparent harm to Choughs, a result that violates the definition of parasitism as based on current evolutionary theory (Price 1980, Anderson and May 1982). In fact, Choughs with high mite abundances in their flight feathers were in better condition than uninfested or only lightly infested birds. One possible reason, namely that larger hosts offer more space to mites, can be rejected because of the absence of a relationship between bird size and mite abundance and the nature of the condition index used, which is independent of bird size.

Feather mites in the family Gabuciniidae are reported to feed on feather oil, and feather debris (Dubinin 1956, cited by W. T. Atyeo, pers. comm.; Philips 1990); however, the nature of their mouthparts most likely makes them unable to feed on solid material, except for that dissolved in oil. Thus, *Gabucinia delibata* mites probably live on their hosts totally on the oil

secreted by the uropygial gland. One possible explanation for the positive relationship between mite abundance and bird condition would be that birds in prime condition may be able to produce larger volumes of feather oil (see Jacob and Ziswiler 1982) and hence support larger populations of oil-feeding mites than birds in lower condition. Apparently, the high numbers of mites on these birds (which, in fact, the birds do not seem to remove) do not impair their plumage quality, at least in the short term, as no damage (holes, feather debris) is externally visible in the wing or tail feathers of heavily "parasitized" birds. According to this hypothesis feather mites of Choughs would therefore qualify as merely commensal, not parasitic, symbionts, causing no harm to their hosts. Because of the correlative nature of our study, however, the relationship between mite abundance and bird condition could come about for a variety of reasons. For instance, an alternative hypothesis could be that birds in good condition have less need to control parasites. However, this fails to explain why Choughs with mites, irrespective of their abundance, were in better condition than Choughs lacking mites.

Under the one-tailed hypothesis which places intensity of infection as the predictor variable when examining host-parasite interactions, we should conclude that high abundances of *Gabucinia delibata* mites may improve the body condition of Choughs, i.e. the association between mites and Choughs might be mutualistic, in the sense that mites may potentially control population growth of some pathogenic microorganisms such as feather-growing fungi (Hubálek 1994) or bacteria living on the oily film formed over feathers by secretions of the uropygial gland (Jacob and Ziswiler 1982). In fact, feather mites also ingest fungal spores and other material trapped in this oil (OConnor 1982, Phillips 1990). If the mites are removing the old oil and the microorganisms contained there, they may improve the efficiency of preening and, at the same time, compete for resources with bacteria and fungi which can degrade feathers (E. H. Burtt Jr., pers. comm.). In addition, some astigmatid mites are known as hyperparasites of lice and hippoboscid flies (Fain 1965) which were, respectively, rare and nonexistent on the body of Choughs (authors' unpubl. data). Under the hypothesis of a mutualistic interaction, benefits accrued to Chough hosts from their association with mites would derive from the supposedly defensive characteristics of these symbionts. Along this line of reasoning, Price et al. (1986) have reviewed examples of the protection against pathogenic parasites achieved primarily by "preemption of resources by more benign species", and Jacob and Ziswiler (1982: 307) have also speculated on the role that certain non-pathogenic fungi may have in controlling overcrowding by pathogenic dermatophytes in the feathers. However, it is often difficult to distinguish cause from effect in host-parasite interactions (Forbes

1993, Møller 1994, 1997, Richner and Heeb 1995) and, because our study was correlational, there remains uncertainty as to the directionality of the interaction between Choughs and their feather mites. Future work should distinguish between alternative hypotheses by means of experiments, as predictions can be made that defaunating Choughs of feather mites should have no effect on bird condition or should worsen it, depending on whether the relationship is commensal or mutualistic. At any rate, this study may serve as a cautionary note to the current efforts of identifying detrimental effects of parasites on host fitness, as not all arthropods living epizootically on birds can be assumed to act as parasites.

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