The evolutionary transition to soloniality promotes higher blood parasitism in birds

J. L. TELLA

DeparJmenJ af Rpplied Bialagy, EsJacián Bialágica de Dañana, G.S.I.G., Sevilla, Spain

Keywards:

birds;
blood parasites;
coloniality;
comparative method;
parasite transmission.

Abstrast

Parasitism has been argued as one o1 the major costs o1 breeding sociality in birds. Mowever, there is no clear evidence 1or an increased parasite pressure associated with the evolutionary transition 1rom solitary to colonial breeding. I used the pairwise comparative method to test whether colonial bird species incur in a greater risK o1 in1ection and i1 they must to 1ace with a greater diversity o1 blood parasites (Maematozoa), by comparing pairs o1 congeners that included one solitary and one colonial breeding species. The richness, both in terms o1 number o1 species and number o1 genera, as well as the prevalence o1 blood parasites resulted higher in colonial species than in their solitary breeding sisters, while controlling 1or di11erences in research e11ort and other potentially con1ounding e11ects. These results point towards higher transmission rates o1 blood parasites among colonial hosts. Given the detrimental e11ects o1 blood parasites on their host fltness, the higher risK o1 in1ection and the exposition to a more diverse parasite 1auna may have imposed an important cost associated to the evolution o1 avian coloniality. This may help to explain why colonial species have larger immune system organs, as well as to explore di11erences in other host li1e history traits potentially shaped by blood parasites.

Introdustion

Colonial breeding is a 1orm o1 social reproduction widely extended in birds and other vertebrates, which has attracted a considerable amount o1 research e11ort during the last decades (Brown 6 Brown, l996; Rolland eJ al., l998). In species exploiting 1ood uneconomical to de1end, breeding aggregations may had arisen 1rom social advantages such as 1ood-flnding enhancement and predator avoidance (see review in Brown 6 Brown, l996), or may simply result 1rom individuals looKing 1or mates or good habitat patches (Wagner eJ al., 2000). Whatever the origin o1 coloniality, high breeding densities may impose costs to the individuals such as a higher transmission o1 parasites among them. Parasites are Known to detrimentally a11ect a number o1 fltness components in birds (e.g. Møller eJ al., l990), and parasite loads may increase the higher the degree o1 host aggregation in colonial birds (reviewed in Brown 6 Brown, l996). For instance, a long-term study has shown that ectoparasitism increases with colony size in cli11 swallows (Hirwnda pyrr2anaJa), a11ecting host breeding success and flrst-year survivorship and thus representing a major cost o1 coloniality 1or this species (Brown 6 Brown, l996).

Most evidence 1or parasitism being a cost o1 coloniality comes 1rom intraspeciflc studies where host breeding aggregations varied in size (Brown 6 Brown, l996). Mowever, very 1ew interspeciflc studies testing the prediction o1 higher parasite loads in colonially than in solitarily nesting species are available. Rózsa eJ al. (l996) 1ound that the colonial breeding rooK (Garws frwgilegws) has higher prevalence and species-richness o1 avian lice (Insecta: Phthiraptera) than the territorial hooded crow (G. carane), results which gained support when including l2 other bird species (RéKási eJ al., l997). On the other hand, Gregory eJ al. (l99l) did not flnd a relationship

Garrespandence: J. L. Tella, Department o1 Applied Biology, Estación Biológica de Doñana, C.S.I.C., Avda. M. Luisa s/n, 4l0l2 Sevilla, Spain. e-mail: tella@ebd.csic.es

between richness o1 helminths (Platyhelmintes) and avian coloniality, and Poulin (I99I) 1ound no di11erences in louse fly (Diptera: Mippoboscidae) abundance between group-living and solitary passerines, whereas 1eather mite (Acarina: Proctophyllodidae) prevalence was signi-flcantly greater on group-living ones. The 1ormer result, however, was later related to winter sociality but not to breeding coloniality (Figuerola, 2000). There1ore, the 1ew available interspeciflc studies seem to o11er little, or even controversial, support 1or parasitism arising as a cost associated to the evolution o1 coloniality in birds.

The relationships 1ound between parasite loads and host breeding sociality may depend on the host–parasite systems studied, these relationships being largely shaped by the particular li1e histories o1 parasites and their strategies o1 transmission. Coloniality might promote the spread o1 parasites to hosts in the case o1 ectoparasites which need the direct body-to-body host contact 1or transmission, which is 1acilitated when hosts are aggregated (RéKási eJ al., I997). Most grouping, however, might provoKe the opposite result in the case o1 parasites which rely on mobile vectors 1or transportation i1 group living provides an encounter-dilution e11ect (i.e. when the probability o1 detection o1 a group by the vector does not proportionally increase with group size, and vectors do not o11set the encounter e11ect by attacKing more members o1 the group; see Mooring 6 Mart, I992). In 1act, the per capita rate o1 attacKs by blood-sucKing flies decreases with group size in some herding animals (see review in Mooring 6 Mart, I992). There1ore, comparative studies using parasites with di11erent li1e strategies are needed to wholly assess whether or not coloniality is associated with a greater risK o1 parasitism. These Kind o1 studies may help us to identi1y the potential costs derived 1rom the evolutionary transition 1rom solitary to colonial nesting in birds (Rolland eJ al., I998; Beauchamp, I999), as well as to explain immunocompetence di11erences between species associated with their breeding sociality (Møller 6 Erritzøe, I996; Sheldon 6 Verhulst, I996).

In this paper, I tested whether colonial bird species incur in a greater risK o1 being parasitized and i1 they must to 1ace with a greater diversity o1 blood parasites (Maematozoa) than species breeding solitarily. A recent phylogenetic analyses showed that in all possible reconstructions o1 the evolution o1 avian coloniality, solitary breeding was the ancestral state (Rolland eJ al., I998). There1ore, larger parasitizations in colonial than in solitary species would be associated with the evolutionary transition 1rom solitary to colonial breeding. I chose Maemoparasites 1or this study because they o11er clear advantages 1or conducting comparative studies in birds. The amount o1 data available on the world avian haematozoa (Bennett eJ al., I982; Bishop 6 Bennett, I992) allows to worK with a high number o1 host species and thus to per1orm robust tests (Figuerola 6 Green, 200I), an advantage not easily o11ered by other parasite groups. Moreover, since the pioneering worK o1 Mamilton 6 ZuK (I982), blood parasites have been the 1ocus o1 much interest on parasite-mediated sexual selection in birds (Clayton, I99I). There1ore, di11erences in risK o1 blood parasitization between solitary and colonial species might have implications on the evolution o1 certain hosts traits such as sexual dimorphism in showiness. On the other hand, avian blood parasites are transmitted 1rom host to host mainly by highly mobile blood-sucKing flies 1rom the order Diptera (AtKinson 6 van Riper III, I99I). There1ore, blood parasitization might be higher in colonial species in the case that host grouping 1avours parasite transmission, but no di11erences between colonial and solitary species, or even greater parasitization rates in solitaries, could be expected in the case that host grouping would promote a reduction o1 parasite transmission through an encounter-dilution e11ect o1 vectors. For testing these hypotheses, I compared pairs o1 closely related bird species that included one colonial and one solitary breeding species to examine potential di11erences in parasite richness and parasite prevalence among hosts di11ering in their breeding sociality. This pairwise comparative method (Burt, I989) controls 1or similarities among species because o1 common ancestry, and thus has long been recognized as a power1ul tool 1or examining an array o1 ecological hypotheses in a phylogenetic context (e.g. Møller 6 BirKhead, I992; Beauchamp, I999; Cuervo 6 Møller, I999; Figuerola, I999; Figuerola 6 Green, 200I).

Methods

Data collection

I extensively searched the ornithological literature 1or selecting pairs o1 phylogenetically related species di11ering in their degree o1 breeding sociality. Since detailed phylogenetical in1ormation is not available 1or all species, I mostly relied on taxonomic in1ormation according to Sibley 6 Monroe (I990, I992); see Figuerola (I999) and Cuervo 6 Møller (I999) 1or the same approach. Breeding sociality in birds ranges between species being strictly solitary to others being strictly colonial, with some species showing both behaviours and others breeding in loose groups (Brown eJ al., I990; Rolland eJ al., I998). When no pairs o1 species including one strictly solitary and other strictly colonial were obtained, I selected the most solitary and the most colonial one within each genus, when available, or within each sub1amily in other case. The incidence o1 blood parasites may vary among geographical regions (see comparison in Bennett eJ al., I99Ia), broadly characterized habitats (Figuerola, I999; Tella eJ al., I999), geographical range (Tella eJ al., I999), and host species with di11erent migratory behaviours (Figuerola 6 Green, 200I). There1ore, I selected between all potential pairs o1 species those in which there are maximum overlaps both in the distribution, habitats, and migratory patterns o1 sister species. Other host-speciflc di11erences in haemoparasite susceptibility (Tella eJ al., I999) among sister species should be minimized through

this pairwise comparative method, since it controls automatically 1or potentially con1ounding variables because pairs o1 closely related species generally have a similar anatomy, physiology and ecology because o1 their common evolutionary past (Møller 6 BirKhead, l992; Beauchamp, l999).

A1ter the construction o1 the pairs 1ollowing the above criteria, I consulted the host–parasite catalogues o1 the world avian haematozoa (Bennett eJ al., l982; Bishop 6 Bennett, l992), as well as a number o1 posterior host-speciflc publications, to record the number o1 parasite species reported 1or each bird species. Parasite richness was obtained in two ways: (l) as the total number o1 parasite species, including only nonspeciflc identiflcations when no other species o1 the same genus were reported 1or a given host, and (2) as the number o1 genera reported in each host species (see Figuerola, l999 1or the same approach). The world host–haemoparasite catalogues (Bennett eJ al., l982; Bishop 6 Bennett, l992) do not report data on prevalence (number o1 birds in1ected/number o1 birds sampled). Prevalence was there1ore obtained 1rom several regional surveys and host-speciflc studies, and thus the resulted sample sizes (i.e. number o1 sister host pairs) were smaller than 1or parasite richness. When one host species is distributed across more geographical regions than its sister species, data on blood parasites was recorded only 1or the region o1 overlap. An exception to the above restrictions 1or the selection o1 species is the pair 1ormed by Pica nwJJalli and the North American population o1 Pica pica, where both populations are close together but actually do not overlap their distributions. Mowever, in this pair o1 species the parasite prevalence was larger in the solitary than in the colonial congener (see Appendix). There1ore, the exclusion o1 this pair o1 sister hosts 1rom analyses just would lead to even stronger parasitization rates in colonial species (see Results), and thus the tests are conservative by Keeping it. Finally, I only included pairs o1 host species 1or which at least one parasite species was recorded 1or each one. There are two reasons 1or this restriction. First, as indicated by Bennett eJ al. (l982), the above mentioned world host–haemoparasite catalogues only report one research source 1or bird species that are apparently 1ree o1 blood parasites. There1ore, sampling e11ort 1or these species (see below) is clearly underestimated. Second, the lacK o1 blood parasites in some pairs o1 bird species could be because o1 1actors unrelated to breeding sociality, such as both species being out o1 the host–parasite coevolutionary process (Bennett, l992) or both species living in habitats particularly 1ree o1 haemoparasites (e.g. Little 6 Earlé, l99F; Figuerola, l999; Jovani eJ al., 200la).

Statistical analyses

Estimations o1 parasite richness and prevalence are potentially influenced by research e11ort (Gregory 6 BlacKburn, l99l; Walther eJ al., l99F). There1ore, I recorded the number o1 research sources (i.e. the number o1 papers looKing 1or blood parasites at each host) and obtained the residuals o1 the regression o1 log-number o1 parasite species (or parasite genera) on log-number o1 sources as a measure o1 parasite richness controlled 1or research e11ort (Gregory, l997). The number o1 research sources 1or each species was obtained 1rom the world catalogues (Bennett eJ al., l982; Bishop 6 Bennett, l992) and 1urther publications (see Appendix). This method does not allow to control 1or potential di11erences in sample sizes among host studies, which could bias di11erences in parasite richness, an in1ormation that, on the other hand, is not provided by the haemoparasite world catalogues (Bennett eJ al., l982; Bishop 6 Bennett, l992). Mowever, in the species included in this paper 1or which prevalence data was available, there was no di11erence in sample sizes between solitary and colonial species (Mann–Whitney test, ç = –l.06, P = 0.29, n = F0). There1ore, my estimates o1 parasite richness are unliKely to be a11ected by biases in the number o1 sampled hosts.

To control 1or the potential influence o1 sample size on parasite prevalence (Gregory 6 BlacKburn, l99l), I used two methods. First, statistical analyses were repeated including only species 1or which at least lF individuals were sampled, since simulations using randomized sample sizes showed that prevalence values are consistent over lF individuals sampled (R. Jovani, pers. comm.). Second, within each pair o1 hosts I subtracted the prevalence o1 the solitary species 1rom that o1 the colonial one to calculate an e11ect size, such that negative and positive values indicate greater prevalence in solitaries and colonials, respectively. Each e11ect size was then corrected 1or unequal sample sizes 1ollowing Poulin (l996), so that comparisons with smaller sample sizes were given less weight than those with larger samples. In the case that prevalence would be not influenced by host breeding sociality, these standardized e11ect sizes should be randomly distributed and not signiflcantly di11erent 1rom zero (Poulin, l996). Maemoparasite in1ections usually increase during the breeding season (see Discussion), and so estimates o1 both prevalence and parasite richness could be potentially a11ected by seasonal di11erences in host trapping. Mowever, the great majority o1 research looKing 1or blood parasites has been conducted during the breeding season, both 1or colonial and solitary species (Author, unpublished recompilation).

Medians and percentiles (2F and 7F%) are reported 1or variables not normally distributed and medians and SD 1or those with a normal distribution. Statistical di11erences within pairs o1 host species were computed by Wilcoxon matched-pairs tests or by paired-J-tests, depending whether or not the variables were normally distributed. The tests were repeated 1or a subsample o1 paired species in which both members are social in winter (i.e. individuals o1 the species 1orage and/or roost

1orming flocKs), to discern between the e11ects o1 winter and breeding sociality on blood parasitization rates. All tests were two-tailed.

Results

I 1ound 20 pairs o1 phylogenetically related species di11ering in breeding sociality, which met the restrictive criteria o1 maximum overlap o1 their range distributions, habitat pre1erences, and migratory behaviours, 1or which in1ormation on blood parasites is available. These pairs covered seven orders and I8 1amilies o1 birds. Eighteen pairs were 1ormed by species in the same genus and I2 by species in the same sub1amily (see Appendix).

Parasite richness

The number o1 parasite species per host was lower in solitary (median = 2, quartiles = I.7F–4.2F) than in colonial birds (median = 4.F, quartiles = 2–7). Colonials harboured larger number o1 parasite species in 2I o1 20 pairwise comparisons, the contrary occurring only in three comparisons (Wilcoxon matched-pairs signed-ranK test, ç = –2.46, P = 0.0I4). The same pattern was 1ound 1or the number o1 parasite genera (solitaries: median = 2.F, quartiles = I–4; colonials: median = 4, quartiles = 2–F); the number o1 genera was larger in colonials in I9 o1 20 comparisons, whereas the contrary only a11ected to seven pairs o1 species (ç = –2.90, P = 0.004). Di11erences between solitarily and colonially nesting host, however, could have been masKed by di11erences in research e11ort among species. In 1act, both the number o1 parasite species and the number o1 parasite genera signiflcantly increased with the number o1 studies published on blood parasites 1or each host (parasite species: r = 0.84, $F_{I,F9}$ = I28.6, P < 0.000I; parasite genera: r = 0.76, $F_{I,F9}$ = 79.2, P < 0.000I; see Fig. I). Accordingly, I used the residuals o1 these regressions as a measure o1 parasite richness corrected 1or sampling e11ort. This measure o1 parasite richness resulted to be much higher in colonial than in solitary species (Fig. 2). Most pairs o1 taxa (26 o1 20) showed an increase in richness o1 parasite species associated with the transition to coloniality (Paired J-test, J = –4.7F, d.1. = 29, P < 0.000I), as it was the case 1or richness o1 parasite genera (J = –4.2F, d.1. = 29, P < 0.000I). The same trend was signiflcant 1or those pairs o1 species (n = I7) in which both species are social in winter (species richness larger in colonials in IF comparisons, J = –2.86, d.1. = I6, P = 0.0II; genera richness larger in colonials in I2 comparisons: J = –2.42, d.1. = I6, P = 0.027).

Parasite prevalence

Data on haemoparasite prevalence was obtained 1or 2F out o1 the 20 pairs o1 phylogenetically related avian species (Appendix). Overall, the percentage o1 individuals in1ected by blood parasites was signiflcantly lower in solitary species (median = 20%, quartiles: 7.7 and 46%) than in colonial ones (median = 2I.7%, quartiles: II.9 and 6F.7%). Prevalence was larger in colonials in I8 o1 2F pairwise comparisons (Wilcoxon matched-pairs signed-ranK test, ç = –2.I4, P = 0.022). Once again, unequal sampling e11ort among species could had influenced the above results. Mowever, di11erences between solitaries and colonials were also signiflcant when considering those pairs o1 species 1or which at least IF individuals 1rom each species were sampled (solitaries: median prevalence = IF.42%, quartiles: 6 and 48.F%; colonials: median prevalence: 24.F%, quartiles: I9.2 and F8.7%; see Fig. 2). Most pairs o1 taxa (II o1 I4) showed

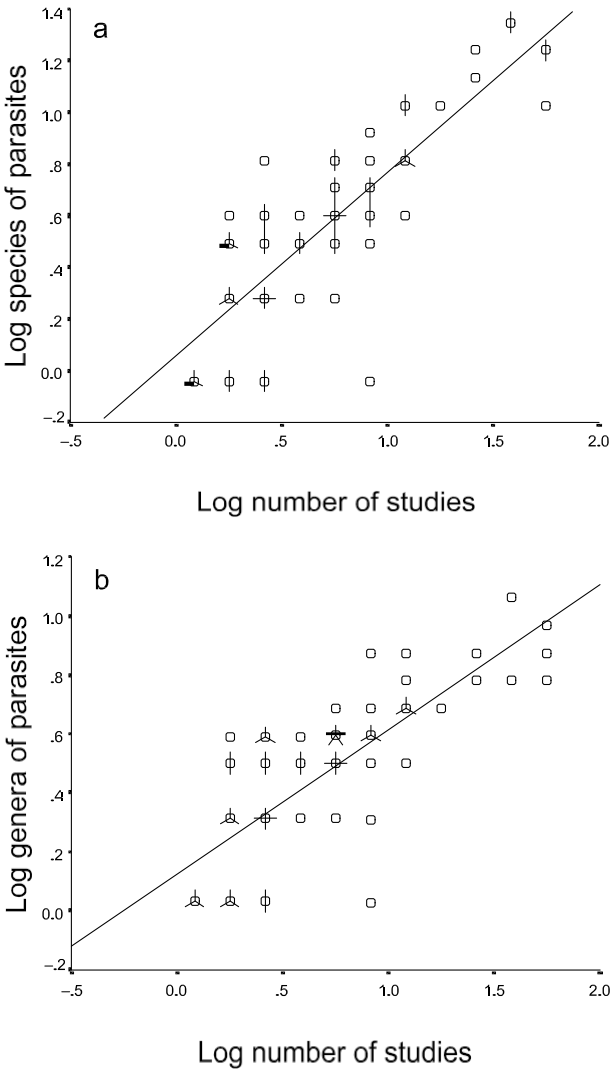

Fig. 1 Relationships between the number o1 studies on blood parasites published about a host bird species and (a) the number o1 species o1 blood parasites and (b) the number o1 genera o1 blood parasites reported to in1ect that host.

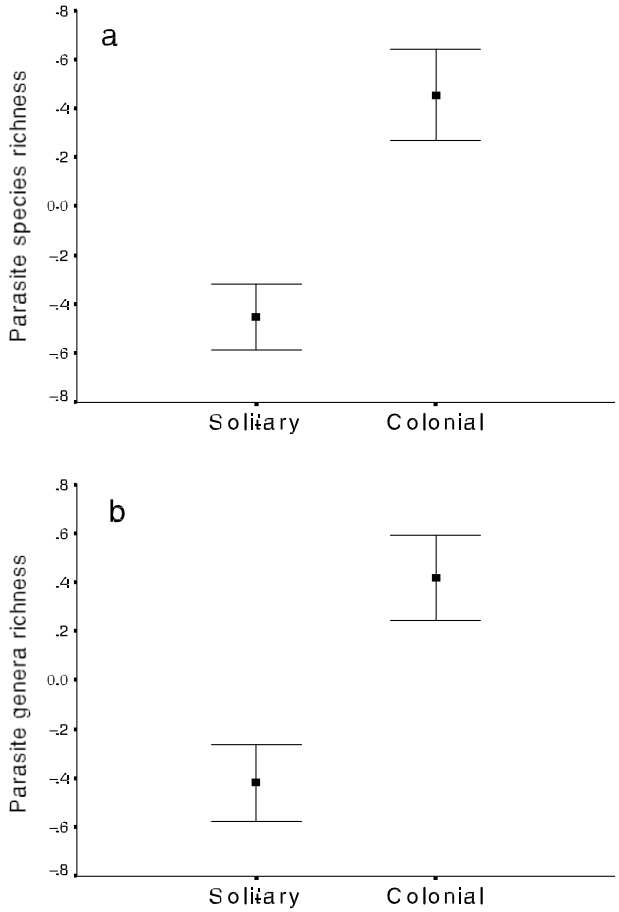

Fig. 2 Di11erences in (A) the number o1 species o1 blood parasites and (B) the number o1 genera o1 blood parasites, both corrected 1or research e11ort, between 20 pairs o1 phylogenetically related bird species di11ering in their breeding sociality.

an increase in haemoparasite prevalence associated to coloniality (ç = –2.l0, P = 0.02F). Standardized e11ect sizes (i.e. the di11erence between the prevalence in the colonial species and that in the solitary one within each pair, corrected 1or sample sizes) were positive and signiflcantly di11erent 1rom zero, both considering the 2F pairs o1 species (median di11erence: ll.F%, ç = –2.ll, P = 0.02F) and only those l4 pairs with sample sizes o1 at least lF individuals per species (median di11erence: l4%, ç = –2.l0, P = 0.02F). The same signiflcant result was 1ound 1or all pairs o1 sister species which are social in winter (ç = –2.l7, P = 0.020, n = l6 pairs). This last result, however, did not reach statistical signiflcance (ç = –l.28, P = 0.l6) when considering only species with sample sizes o1 at least lF individuals per species, probably because o1 the resulting small sample size (n = lO pairs), although the trend was the same (the standardized e11ect size was positive in seven out o1 lO pairwise comparisons).

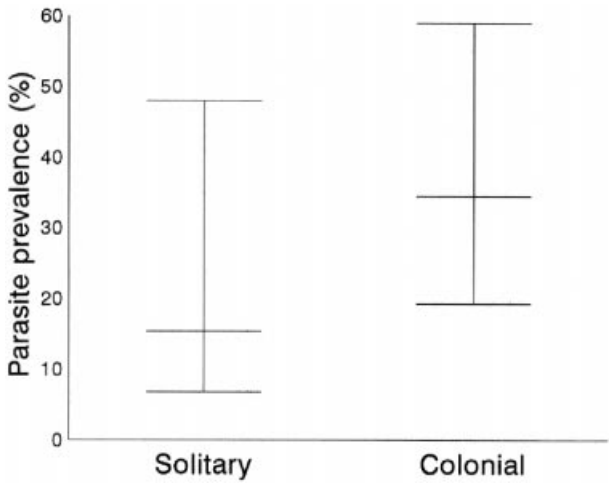

Fig. 2 Prevalence o1 blood parasites (median, 2F and 7F% quartiles) in l4 pairs o1 phylogenetically related bird species di11ering in their breeding sociality. At least lF individuals were sampled 1rom each host species.

Þissussion

Comparisons between pairs o1 closely related species have been recommended to assess whether the evolutionary transition to coloniality has caused an increase in parasite in1estation (Beauchamp, l999). This study shows that the richness o1 blood parasites, both in terms o1 number o1 species and number o1 genera, was higher in colonial species than in their solitary breeding sisters, a result which was much stronger when di11erences in research e11ort among host species were controlled 1or. Moreover, the prevalence o1 blood parasites was also higher in colonial than in solitary species, despite that it is influenced by a number o1 intrinsic and extrinsic 1actors such as sex, age, season and geographical related variations (Weatherhead 6 Bennett, l99l, l992; Merilä eJ al., l99F; Allander 6 Sundberg, l997; Sol eJ al., 2000), which may induce sampling biases and thus masK the actual di11erences. Contrarily to the case o1 1eather mites, in which prevalence was unrelated to coloniality when controlling 1or winter sociality (Figuerola, 2000), in the case o1 blood parasites coloniality was still associated with increased parasite richness and prevalence when considering only pairs o1 species in which both members are social in winter.

Di11erences in in1estation trends between 1eather mites and blood parasites are liKely to be related to their di11erent modes o1 transmission. Feather mites are benign ectosymbionts transmitted by host-to-host body contact (Blanco eJ al. 200l; Jovani eJ al., 200lb), and the number o1 congeners that directly contact with an individual may be higher in winter flocKs and communal roosts than in the nests, as transmission at the nests would be more

constrained to occur within 1amily members (Blanco eJ al., l997, 200l; Jovani 6 Blanco, 2000; Blanco 6 Frias, 200l). Blood parasites, however, need o1 blood-sucKing arthropods 1or their transmission among avian hosts. In the case o1 haemosporidians (HaemapraJews, LewcacyJaçaan and Plasmadiwm, the most common haematozoa in birds), once in1ective sporozoites are inoculated to a suitable host by the vector, they undergo multiple cycles o1 asexual and sexual reproduction, multiplying quicKly in the host and producing gametocytes which also are transmitted 1rom one host to another by the same vectors (AtKinson 6 van Riper III, l99l). In1ected birds later exhibit chronic or latent in1ections which may persist 1or years, when parasitemia is reduced to low levels in blood, but relapses occur each breeding season (AtKinson 6 van Riper III, l99l; Allander 6 Sundberg, l997). There1ore, parasites circulating in blood reach their maximum abundance during the breeding season, coinciding also with a higher abundance o1 vectors such as flies and mosquitoes (Bennett 6 Fallis, l960; Super 6 van Riper III, l99F), and thus transmission among hosts may be higher in breeding colonies than in winter flocKs.

Coloniality seems to not provide protection 1rom blood parasites through the potential encounter-dilution e11ect (Mooring 6 Mart, l992), which would produce lower per capita attacKs by flying haematophagous vectors, as parasite prevalence was higher in colonial than in solitary species. To my Knowledge, Davies eJ al. (l99l) provided the only related results when studying di11erences in prevalence o1 Plasmadiwm among Amazonian species o1 primates. These authors 1ound that Plasmadiwm prevalence increased with the average annual sleeping group size o1 the species, suggesting that host grouping enhances odour production and thus attracts a greater number o1 mosquito vectors than expected by chance. Most odour, rather than visual cues, seems to be also important 1or the attraction o1 haemoparasite vectors in birds (Yezerinac 6 Weatherhead, l99F). As di11erent blood parasite species are usually transmitted by di11erent species o1 vectors (AtKinson 6 van Riper III, l99l), the aggregation o1 conspeciflc hosts during the breeding season could increase not only the attraction o1 large vector numbers but also its diversity, thus also explaining the relationship between avian breeding sociality and haemoparasite richness. Nonetheless, larger blood parasitizations in colonial birds could also be explained in the absence o1 a higher attraction o1 vectors and even in the case o1 acting an encounter-dilution e11ect. Assuming that flying vectors are randomly distributed with respect to host aggregation, the probability o1 a host being in1ected would be initially equal or even smaller 1or colonial than 1or solitary birds. In 1urther steps o1 time, however, the liKelihood o1 parasite transmission would be higher among host congeners breeding colonially, because o1 their close proximity, than among solitaries. This is because a flying vector (or haematophagous ectoparasite, see, e.g. Sol eJ al., 2000) acquiring parasite gametocytes by biting an in1ected colonial host would have a greater chance be1ore to dead o1 biting – and thus in1ecting – another host o1 the same species than in the case o1 territorial, isolated host breeders. There1ore, this scenario could also explain the larger prevalence 1ound in colonial hosts.

The best evidence so 1ar 1or larger parasite in1ections in colonial than in solitary bird species was provided by RéKási eJ al. (l997). Mowever, although these authors 1ound larger lice prevalences in colonial than in solitary birds, they concluded that colonial hosts do not pay a higher price 1or being social because lice loads per individual did not di11er between solitaries and colonials (i.e. lice were not more abundant, but more equally distributed among colonial hosts). Nonetheless, several studies 1rom the same host species were included as independent data points and the conducted statistical analyses did not control 1or potentially con1ounding phylogenetic e11ects (RéKási eJ al., l997), 1acts that might have a11ected their results and interpretation. In any case, and contrarily to avian lice (RéKási eJ al., l997), a redistribution o1 haemoparasite numbers among colonial individuals is not plausible, because once a bird is in1ected the parasite undergoes reproductive cycles independently o1 the 1ate o1 neighbouring hosts (AtKinson 6 van Riper III, l99l; Sol eJ al., 2000), so haemoparasite numbers by in1ected host are reasonably expected to be equal among colonial and solitary birds.

Mere I have shown that the evolutionary transition 1rom solitary to colonial nesting in birds (Rolland eJ al., l998) is associated with a greater risK o1 acquiring haemoparasites. Although in1ormation on pathogenicity o1 blood parasites was mainly restricted until recently to domesticated birds (AtKinson 6 van Riper III, l99l; Bennett eJ al., l992), increasing observational and experimental studies in the fleld are showing a variety o1 detrimental e11ects on their hosts (ValKiünas, l992; Merino eJ al., 2000), including a higher risK o1 mortality both within (Richner eJ al., l99F; Dawson 6 Bortolotti, 2000; MoraK eJ al., 200l) and between host species (Sorci 6 Møller, l997). The larger prevalence in colonial species not only means that a higher number o1 individuals are in1ected, but may also increase the number o1 in1ectious clones per host (Read eJ al., l99F), thus increasing the virulence o1 monospeciflc in1ections (Taylor eJ al., l998). Moreover, given that the degree o1 pathogenicity varies among blood parasite species (AtKinson 6 van Riper III, l99l), the larger diversity o1 haemoparasite 1auna 1ound in colonial birds adds a cost to the larger prevalence in terms o1 multiple parasite in1ections. Multiple haemoparasite in1ections not only increase the risK o1 holding the more virulent species, but also the potential impact on host fltness through additive or synergic e11ects o1 combined species (AtKinson 6 van Riper III, l99l). Blood parasites may have thus imposed an important ecological

cost derived 1rom the evolutionary transition 1rom solitary to colonial breeding.

The larger blood parasitization pressure in colonial birds could have selected 1or an improved immune system in this group o1 birds. Parasite virulence is thought to evolve in response to the mode o1 transmission. Morizontal transmission among unrelated individuals not involved in common reproductive activities, as it occurs in haemoparasites, is proposed to select 1or increased virulence, whereas vertical transmission 1rom parents to o11spring selects 1or reduced virulence (Ewald, l982). Møller 6 Erritzøe (l996) hypothesized that, because coloniality should increase the horizontal transmission o1 parasites, colonial species should have developed larger immune organs to flght against parasites than their congeneric solitary ones. Accordingly, these authors showed through pairwise comparisons that two organs involved in immune de1ense were consistently larger in colonials. More recently, Møller eJ al. (200l) have shown through a comparative study o1 swallows and martins that direct measures o1 T- and B-cell immune response increased with breeding sociality o1 the species, and that these immune responses were related to the pressure exerted by ectoparasites. Given that blood parasites are mainly transmitted horizontally, they may have also contributed to the evolution o1 immune de1ense o1 hosts in relation to their breeding sociality, a possibility that would require 1urther research to be conflrmed. Attending to these and other potential implications (Beauchamp, l999), colonial breeding results a behaviour which must to be considered both in studies dealing with the ecology o1 haemoparasites and the evolution o1 several parasite-related li1e history traits o1 their hosts.

Asknowledgments

I thanK R. Jovani and J. Figuerola 1or help1ul discussion and suggestions o11ered while writing this manuscript, as well as two anonymous re1erees 1or 1urther suggestions. I was supported by a post-doc position 1rom the Spanish Ministry o1 Science (MEC).

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Appemdix Richness o1 parasite Maematozoa and prevalence o1 in1ection in pairs o1 bird species di11ering in their breeding sociality. P: prevalence in percentage (sample size in bracKets); S: number o1 parasite species; G. number o1 parasite genera; R: number o1 re1erences; W: winter sociality.

Order and Family	Solitary species	P	S	G	R	Colonial species	P	S	G	R	W	Sources[b]
O: Ciconiiformes												
F: Ardeidae	Egretta novaehollandiae(S, C?)[a]		2	2	Q	Egretta intermedia (C)		3	3	3	Y	1, 2
F: Ciconiidae	Jabiru mysteria (S)	0 (3)	1	1	2	Mysteria amerisana (C)	11.1 (9)	3	3	6	Y	1, 2, 3
	Ephippiorhynshus senegalensis(S)	U0 (2)	3	2	8	Leptotilos srumeniferus (C)	100 (10)	Q	3	10	N	1, 2, Q
F: Threskiornithidae	Bostryshia hagedash (S)	20 (U)	2	2	6	Threskiornis aethiopisus (C)	26.7 (1U)	1	1	8	Y	1, 2, Q
	Mesembrinibis sayennensis (S)	10.2 (11)	2	2	3	Theristisus saudatus (C,S?)	0 (Q)	2	2	3	N	1, 2, 3
F: Accipitridae	Torgos trasheliotus (S)	31.2 (6Q)	Q	Q	6	Gyps afrisanus (C)	U3.U (630)	9	7	7	N	1, 2, Q, U F:
Falconidae	Falso subbuteo (S)		10	U	20	Falso vespertinus (C)		Q	3	U	N	1, 2, 6, 7
O: Anseriformes												
F: Anatidae	Anser albifrons (S,LC)	12.U (8)	2	2	3	Anser saerulessens (C)	3.U (U77)	6	Q	U	Y	1, 2, 8
	Melanitta nigra (S)	2U (Q)	Q	Q	6	Melanitta perspisillata (LC, S)	60 (U)	2	2	2	Y	1, 2, 8
O: Columbiformes												
F: Columbidae	Zenaida masroura (S)	68.2 (2U18)	12	6	UU	Zenaida asiatisa (C, S?)	87.U (72)	7	U	10	Y	1, 2, 8–10
	Dusula sarola (S)	20 (U)	1	1	1	Dusula bisolor (C)	100 (1)	3	3	3	Y	1, 2, 11
O: Psitaciformes												
F: Psitacidae	Tanygnathus lusionensis (S)	100 (7)	2	2	3	Prioniturus dissurus (C)	12.U (8)	Q	Q	2	?	1, 2, 11
O: Apodiformes												
F: Apodidae	Apus saffer (S, LC)	1.9 (U3)	1	1	3	Apus affinis (C)	7.7 (17)	6	3	U	Y	1, 2, Q, U
O: Coraciformes												
F: Meropidae	Merops lesshenaulti (S, C)	6.2 (32)	1	1	3	Merops viridis (C)	31.7 (126)	3	2	2	Y	1, 2, 11
F: Alcedidae	Alsedo sristata (S)	7.6 (66)	3	3	Q	Seryle rudis (LC)	2Q.3 (37)	U	3	8	N	1, 2, Q
O: Passeriformes												
F: Hirundidae	Hirundo susullata (S)	7.9 (88)	Q	Q	3	Hirundo spilodera (C)	Q7.U (278)	Q	Q	Q	Y	1, 2, Q, U
	Riparia sinsta (S)	33.3 (6)	2	1	2	Riparia paludisola (C)	11.3 (133)	Q	Q	3	N	1, 2, Q, U
F: Turdidae	Turdus philomelos (S)	Q2 (162)	17	7	U0	Turdus pilaris (C,S)	U3.U (71)	11	6	11	Y	1, 2, 6
F: Meliphagidae	Plestorhynsha lanseolata (S)		1	1	2	Manorina melanosephala (C)		U	Q	8	N	1, 2, 11
F: Passeridae	Estrilda erythronotos (S)	33.3 (6)	2	2	2	Estrilda astrild (S)	U3.8 (26)	11	7	11	Y	1, 2, Q, U
	Euplestes albonotatus (S)	20 (2U)	3	3	6	Euplestes afer (C)	22.2 (QU)	6	U	7	?	1, 2, Q, U
	Vidua shalybeata (S)	2.9 (171)	Q	Q	7	Quelea quelea (C)	2 (1U0)	7	U	12	Y	1, 2, Q, U
	Ploseus luteolus (S)	7 (128)	U	Q	6	Ploseus susullatus (C)	37.3 (370)	1Q	7	30	Y	1, 2, Q, U
F: Sturnidae	Aplonis santoroides (S)		1	1	1	Aplonis metallisa (C)		3	3	2	?	1, 2, 11
	Spreo superbus (S)	12.9 (31)	6	U	12	Sreatophora sinerea (C)	7Q.Q (Q3)	6	Q	3	N	1, 2, Q, U
F: Icteridae	Sasisus leusoramphus (S)		1	1	1	Sasisus sela (C)		3	3	Q	N	1, 2,
	Molothrus ater (S)	17.9 (1613)	16	6	2U	Agelaius phoeniserus (C)	21.1 (2077)	20	6	33	Y	1, 2, 8, 9, 12, 13
F: Corvidae	Sorvus sorone (S)	88.U (10Q)	17	10	UQ	Sorvus frugilegus (C)	1Q (901)	21	11	39	Y	1, 2, 6
	Pisa pisa (S)	81.Q (307)	Q	Q	8	Pisa nuttalli (C)	77.1 (3U3)	U	U	6	Y	1, 2, 8
	Syanositta stelleri (S)	UQ.U (33)	Q	Q	6	Gymnorhinus syanosephalus (C)	71.Q (7)	3	3	2	N	1, 2, 8

[a] S = solitary, C = colonial, LC = loosely colonial. When a species exhibits two breeding strategies, the flrst cited one is the most commonly reported in the literature.

[b] **I,** Bennett et al. (I982); 2, Bishop 6 Bennett (I992); 2, White et al. (I978); 4, Bennett et al. (I992); F, Earlé et al. **(I99I);** 6, Peirce **(I98I);** 7, Tella et al. (I999); 8, Greiner et al. (I97F); 9, Bennett et al. **(I99Ib);** I0, Mu11man 6 Cali (I982); **II,** McClure et al. (I978); I2, Weatherhead 6 Bennett **(I99I);** I2, Weatherhead 6 Bennett (I992).