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GEOGRAPHICAL STRUCTURING OF FEATHER MITE ASSEMBLAGES FROM THE AUSTRALIAN BRUSH-TURKEY (AVES: MEGAPODIIDAE)

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ABSTRACT: Populations of a host species may exhibit different assemblages of parasites and other symbionts. The loss of certain species of symbionts (lineage sorting, or ''missing-the-boat'') is a mechanism by which geographical variation in symbiont assemblages can arise. We studied feather mites and lice from Australian brush-turkeys (Aves: Megapodiidae: *Alectura lathami*) and expected to observe geographical structuring in arthropod assemblages for several reasons. First, because the brush-turkey is a sedentary ground-dwelling bird, we predicted that geographically close host populations should share more similar arthropod assemblages than distant ones. Second, because brush-turkeys do not brood their young, vertical transfer of arthropods is unlikely, and brush-turkeys probably acquire their mites and lice at social maturity through contact with other birds. Young birds could disperse and found new populations without carrying complete sets of symbionts. We predicted that young birds would have fewer species of arthropods than older birds; in addition, we expected that males (which are polygynous) would have more species than females. Birds were sampled from 12 sites (=populations) along the east coast of Queensland, Australia, that were separated by a distance of 12.5–2,005 km. In total, 5 species of mites from the Pterolichidae and 1 species from the Ascouracaridae were found. Two species of lice were collected but in numbers too low to be statistically useful. Differentiation of mite assemblages was evident; in particular, *Leipobius* sp. showed 100% prevalence in 3 host populations and 0% in the remaining 9. A dendrogram of brush-turkey populations based on mite assemblages showed 2 geographically correlated clusters of sites, plus 1 cluster that contained 2 sites near Brisbane and 1 approximately at a distance of 1,000 km. There was no strong effect of host age or sex on number of mite species carried. Horizontal transfer of feather mites by hippoboscid flies, in addition to physical contact between hosts, may play a role in homogenizing symbiont assemblages within populations.

Parasitologists have long sought for evidence of cospeciation between hosts and parasites (Klassen, 1992; Brooks and McLennan, 1993; Hoberg, 1997). The 'holy grail' in this quest is a perfect topological match between host and parasite cladograms. The grail has proven elusive, however, with most cladograms showing gaps and mismatches (e.g., Smith, 2001; Johnson et al., 2002; Ricklefs and Fallon, 2002). Recently, researchers have begun to view such mismatches not as flaws but as interesting phenomena in themselves (Paterson et al., 1999; Paterson and Banks, 2001). Incongruent cladograms can arise through several processes (Paterson and Banks, 2001), among which host switching (=host jumping) and lineage sorting (=''missing-the-boat'') are perhaps the most common. In host switching, a parasite from an unrelated host is acquired by the host of interest, for example, through shared nesting sites (e.g., Johnson et al., 2002) or predator–prey interactions (e.g., Gaud and Atyeo, 1996). In lineage sorting, parasite species are lost from certain host populations, either through founder effect, i.e., the founding hosts by chance lacked certain parasite species, or because a newly occupied habitat is inappropriate for the parasite, e.g., if an intermediate host is absent. Lineage sorting through founder effect also is applicable to mitochondrial DNA haplotypes (Rand, 2001) and indeed to any assemblage of symbionts, be they parasites, mutualists, or commensals.

Evidence of lineage sorting has been observed for many taxa of avian symbionts, including malarial parasites (Ricklefs and Fallon, 2002), feather mites (Dabert et al., 2001; Ehrnsberger et al., 2001), and feather lice (Paterson et al., 1999). In the most directed of these studies, Paterson et al. (1999) compared louse assemblages of birds introduced into New Zealand with louse assemblages on the hosts in their native ranges. Fifteen of 18 human-introduced bird species had reduced louse diversity, whereas only 3 of 10 self-introduced species did. The authors speculated that the difference was due to smaller founding populations for human-introduced birds compared with the (likely) constant immigration of self-introduced species. Of particular interest from a phylogenetic viewpoint was their finding that 16 of 20 closely related pairs of host species or subspecies showed lower louse diversity in the New Zealand member of the pair. This clearly demonstrates that missing-the-boat has repercussions at higher phylogenetic levels. However, it may be argued that New Zealand, with its ancient and extreme geological isolation, is a unique case. It may be that lineage sorting is less likely to occur among symbionts of birds located on contiguous mainland. We tested the possibility using arthropod ectosymbionts (feather mites and lice) associated with the Australian brush-turkey, *Alectura lathami* Gray (Aves: Megapodiidae). We also examined whether age and sex of the host affect the richness of ecosymbionts, as has been observed for some other taxa (e.g., Soliman et al., 2001).

MATERIALS AND METHODS

The host

Megapode birds are a group in which the potential for lineage sorting of symbiotic mites and lice seems very high. First, although megapodes can fly, they prefer to move on foot (Frith, 1959) and are not known for long-range migrations (Dekker, 1989). This should increase the probability of isolation of host populations and hence development of distinctive sets of symbionts. Second, there is effectively no contact between chicks and adults (Jones et al., 1995; Jones, 1998). Megapodes incubate their eggs by depositing them within substrata warmed by various sources of environmental heat, including geothermally heated soil, sun-warmed sand, and decomposing organic matter (Jones et al., 1995). After laying within the incubation site, there is no further direct contact between the egg or hatchling and an adult (Booth and Jones, 2001); even when 1 or both parents tend the incubation site, chicks and adults actively avoid one another. Indeed, megapode hatchlings are among the most precocial of all birds and commence their lives as independent and solitary individuals (Jones et al., 1995). There is some evidence for the importance of social contact in maintaining a high diversity of avian ectoparasites. Rósza et al. (1996) observed that individuals of the colonial rook (*Corvus frugilegus* L.) harbored a greater diversity of lice than individuals of the more solitary hooded crow (*Covus corone cornix* L.), even though each species as a whole hosted the

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same total number of lice. Thus, the potential seems high for young megapodes to carry an incomplete set of feather mites and lice. If young birds found a new population, then this new population may display only a subset of all possible symbionts.

We investigated these issues in the best-studied megapode, the Australian brush-turkey, *A. lathami*, an abundant species in eastern Australia (Marchant and Higgins, 1993). The first sustained social interactions among young brush-turkeys occur when the young birds are several weeks to months old; by the time they are about 100 days of age, they are seen regularly in similarly aged groups (Jones, 1990; Göth and Vogel, 2003). Direct contact between individuals is minimal, limited mainly to brief agonistic interactions (Göth and Vogel, 2002a). The only prolonged physical contact between brush-turkeys is during copulation, when mounting lasts only 10–20 sec (Jones, 1990). Even among roosting birds, individuals space themselves well away from their neighbors (Jones, 1990). We hypothesized that arthropod symbionts should accumulate on a bird as it ages because of chance encounters with other birds that happened to carry a different species of arthropod and hence predicted that older birds should have a greater richness of mites and lice than young birds. Reproductive behavior is centered on the incubation mounds constructed and defended by adult males (Jones, 1990). Females select among males and lay varying numbers of eggs in 1–4 mounds during the 4- to 8-mo breeding season. Because certain males control the most-favored nest mounds, and hence achieve the most matings, we predicted that there should be a greater variation in ectosymbiont richness in male than in female birds.

The current distribution of the Australian brush-turkey is far more fragmented than is evident from most published distribution maps (e.g., Marchant and Higgins, 1993). Although relatively robust in their reaction to habitat alteration, their use of large mounds of decomposing moist organic matter for incubation limits the species to the interior or edges of closed forest in higher rainfall areas. In addition, most sclerophyllous vegetation provides poor fuel for microbial decomposition, and brush-turkeys are relatively rare in eucalypt-dominated forest (Jones et al., 1995). Currently, brush-turkeys are found primarily in rainforest or other closed-forest areas along the eastern seaboard of Australia. Given the past and present reduction in the extent of rainforest habitats, the current distribution of brush-turkeys is distinctly patchy, with most populations now relatively isolated from one another (Marchant and Higgins, 1993). Fragmented habitat and low vagility are likely to restrict contact between geographically separated groups of brush-turkeys and possibly promote the development of distinctive population-level assemblages of arthropod ectosymbionts.

The symbionts

Brush-turkeys have previously been reported to host 4 species of feather mites from 2 families (Atyeo, 1992; Proctor, 1999): Pterolichidae—*Echinozonus leurophyllus* Atyeo & Pérez, *E. longisetosus* Atyeo & Pérez, *Ascetolichus ruidus* Pérez & Atyeo; and Ascouracaridae—*Gallilichus jonesi* Proctor. All species are unique to *A. lathami*. The first 3 species dwell on vanes of the flight feathers where they feed on feather oils and accumulated pollen and fungus (Proctor and Owens, 2000) and are likely to act as commensals or mutualists (Blanco et al., 1997). *Gallilichus jonesi* lives inside the quills of flight feathers, where it chews on feather pith (Proctor, 1999), and probably acts as a parasite. Palma and Barker (1996) report 6 species of feather lice from *A. lathami*: Philopteridae—*Goniodes macrocephalus* (Taschenberg), *G. fissus* (Rudow), *Lipeurus crassus* Rudow, *Oxylipeurus ischnocephalus* (Taschenberg); Menopodidae—*Colpocephalum alecturae* Price & Beer, *C. lathami* Price & Beer.

Study sites

Brush-turkeys were sampled from 12 locations from throughout the distribution of the species, an area spanning 2,005 km from north to south (Fig. 1; Table I). Sites can be divided among several geographic regions: southern Queensland (O'Reilly's [OR], Springbrook [SB], Brisbane Forest Park [BF], and Tamborine [TM]); central Queensland (Carnarvon George [CV] and Bunya Mountains [BM]); southern North Queensland (Mount Elliot [ME], Pallarenda [PR], and Paluma [PL]); Atherton Tablelands (Malanda [ML] and Lake Eacham [LE]); and Cape York (Iron Range [IR]). At all sites south of Cape York, brush-turkeys belong to the nominate subspecies *A. lathami lathami* Gray; IR birds

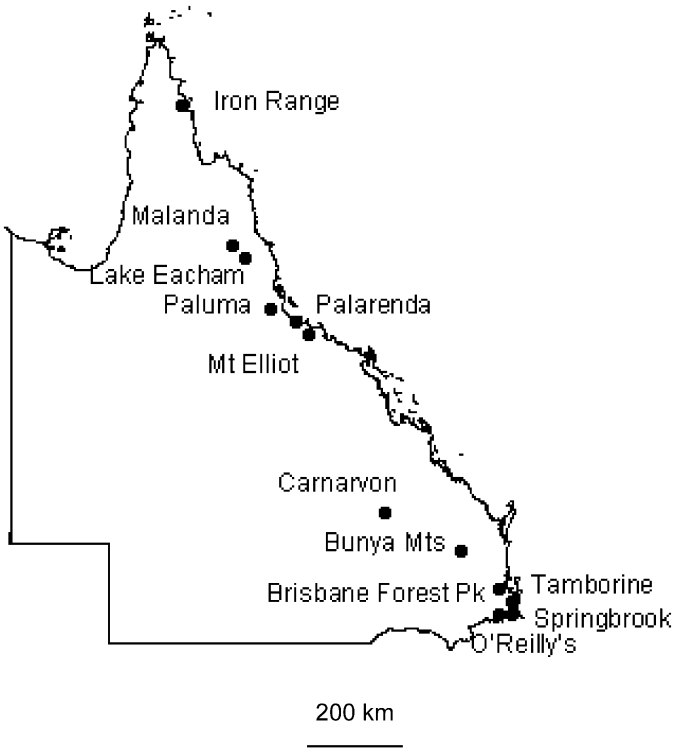


FIGURE 1. Map of Queensland, Australia, showing sites where brush-turkeys were sampled.

belong to the subspecies *A. lathami purpuricollis* (Le Souëf), the purple-collared brush-turkey. Members of the *purpuricollis* subspecies are differentiated from *lathami* in the male having a mauve rather than a yellow wattle and in both sexes having somewhat shorter tail feathers (Jones et al., 1995). At each site, birds were collected at picnic areas within or adjacent to reserves.

Field and laboratory methods

Feather collection: Feathers were collected from live brush-turkeys captured using a baited drop-trap or noose concealed on the forest floor. Immediately on capture, the bird was placed within a large cloth bag. Large, old feathers were selected from both wings (primary feathers only) and the tail (retrices). Two to 6 feathers were collected from each bird, with no more than 2 being plucked from the tail or from the same wing. Feathers from each bird were immediately placed in 2 airtight plastic bags, 1 for wing feathers and 1 for tail feathers (with the exception of those from the IR bird, which were not separated). The feathers were subsequently preserved in 70% ethanol.

Mites and lice: A dissection microscope was used to examine each preserved feather at ×10–40 magnification. All arthropods were removed from the external surface of the feather, then the quill was slit open using scissors, and quill-dwelling mites removed. Arthropods were stored in 80% ethanol until mounting. Mites and lice were mounted in Heinze polyvinyl alcohol (Evans, 1992), and slides were cured on a warming table at 50 C for several days. Mites were then identified following Atyeo and Pérez (1991), Atyeo (1992), and Proctor (1999). Exemplars of louse morphospecies were sent to experts for identification.

Statistics: Although lice were collected from many birds (see Results), identification to species was not possible for the majority of specimens, which were either juvenile or male. Because of this uncertainty, no statistical comparison was based on louse data. The feather mites *A. ruidus* and *G. jonesi* were sufficiently distinctive to be recognized at all life-history stages. For the other species of mites, both sexes of adults and older nymphs could be reliably identified. The number and identity of mites were recorded per individual host and per population. To examine site specificity (Pérez and Atyeo, 1984; Proctor, 2003), mite dis-

TABLE I. Prevalence and numbers of feather mites from brush-turkey populations. Sites are arranged roughly from north (top) to south (bottom).

Site: abbreviation (n = birds sampled)	*Ascetolichus ruidus*	*Echinozonus leurophyllus*	*Echinozonus longisetosus*	*Gallilichus jonesi*	*Goniodurus quadratus*	*Leipobius* sp.	Unidentifiable juveniles*
Iron Range: IR (1)	0.00† (0)	**1.00** (24)	**1.00** (22)	0.00 (0)	0.00 (0)	0.00 (0)	3
Malanda: ML (5)	**0.20** (3)	**1.00** (43)	**1.00** (201)	**0.80** (48)	**0.20** (2)	0.00 (0)	81
Lake Eacham: LE (2)	**1.00** (6)	**1.00** (31)	**1.00** (16)	**1.00** (6)	0.00 (0)	0.00 (0)	16
Pallarenda: PR (5)	0.00 (0)	**0.40** (7)	**1.00** (298)	**1.00** (170)	0.00 (0)	**1.00** (175)	1019
Mount Elliott: ME (5)	0.00 (0)	**1.00** (51)	**1.00** (195)	**0.60** (42)	0.00 (0)	0.00 (0)	19
Paluma: PL (5)	0.00 (0)	**0.80** (236)	**1.00** (92)	**0.80** (40)	0.00 (0)	0.00 (0)	108
Carnarvon Gorge: CV (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0
Bunya Mountains: BM (10)	**1.00** (549)	0.00 (0)	**0.60** (90)	**0.80** (185)	0.00 (0)	**1.00** (444)	120
Brisbane Forest Park: BF (5)	**0.80** (38)	**0.80** (42)	**1.00** (230)	**1.00** (176)	0.00 (0)	**1.00** (76)	102
O'Reilly's, Lamington Park: OR (10)	**0.80** (305)	**1.00** (330)	**1.00** (362)	**0.70** (40)	0.00 (0)	0.00 (0)	222
Tamborine: TM (8)	**0.75** (83)	**0.88** (273)	**1.00** (66)	**1.00** (153)	0.00 (0)	0.00 (0)	349
Springbrook: SB (5)	**0.60** (21)	**1.00** (472)	**1.00** (438)	**1.00** (422)	**0.20** (1)	0.00 (0)	638

* Unidentifiable juveniles include larvae and protonymphs of *Echinozonus* and *Leipobius* spp.
† Prevalence is expressed as a proportion of birds at each site with that mite; bold font indicates that prevalence was greater than 0.

tributions were further broken down according to feather type, wing, or tail. Mean and variation in mite species richness per host were compared between sexes using analysis of variance (ANOVA) (SPSS for Windows, Version 10.0.5). Regressions and scatter plots were used to compare the relationship between mite richness and host body weight and tarsus length, which were assumed to be positively related to host age (Jones, 1987). The multivariate software program PATN (Belbin, 1995) was used to create a dendrogram of site relationships based on proportion of birds in a population bearing each species of mite (Bray–Curtis distance matrix, flexible UPGMA fusion option). Only sites where 5, or more, birds were sampled were included (n = 9 sites). To test whether population structuring based on feather mite assemblages was correlated with geographic distance, Mantel's test (Belbin, 1995) was used to compare mite-based and geographically based distance matrices of the 9 sites.

Other collections and observations: Feathers from 4 brush-turkey chicks that had been killed by predators during a radiotracking study (Göth and Vogel, 2002b) were examined to ascertain that young chicks were free from feather mites and lice. The chicks had been released into the forest near Maleny, Queensland, 10–14 days before their deaths. Winged louse-flies (Diptera: Hippoboscidae) (n = 5) that had been casually collected from 5 live brush-turkeys were examined for the presence of phoretic feather mites and lice.

TABLE II. Prevalence of louse morphotypes on brush-turkeys as a proportion of birds at each site with that louse. Sites are arranged roughly from north (top) to south (bottom).

Site: abbreviation (n = birds sampled)	Squat morphotype*	Long morphotype†
Iron Range: IR (1)	0.00	0.00
Malanda: ML (5)	0.80	0.40
Lake Eacham: LE (2)	1.00	1.00
Pallarenda: PR (5)	1.00	0.20
Mount Elliott: ME (5)	0.60	0.40
Paluma: PL (5)	0.40	0.20
Carnarvon Gorge: CV (1)	0.00	1.00
Bunya Mountains: BM (10)	0.70	0.50
Brisbane Forest Park: BF (5)	1.00	0.60
O'Reilly's, Lamington Park: OR (10)	1.00	0.80
Tamborine: TM (8)	0.50	0.38
Springbrook: SB (5)	1.00	0.60

* Squat adult females identified as *Colpocephalum lathami*.
† Long adult females identified as *Lipeurus crassus*.

RESULTS

A total of 62 brush-turkeys were sampled, ranging from 1 bird each at CV and IR to 10, each at BM and OR (Table I). Sample size at the different sites reflected ease of capture; birds at popular tourist sites were less wary than those in more seldom-visited areas. In total, 9,181 mites were removed from the feathers, of which 6,504 could be unambiguously assigned to species (see comments on identification in Materials and Methods). In no case was a bird's mite load composed only of unidentifiable juveniles. With the exception of the single brush-turkey captured at CV, all birds carried at least 1 species of feather mite (Table I). The 4 species of mite previously known from brush turkeys were well represented, with *E. leurophyllus*, *E. longisetosus*, and *G. jonesi* having a higher prevalence than *A. ruidus*. In addition, 2 other species of vane-dwelling pterolichid mites were observed that had not previously been collected from brush-turkeys. *Goniodurus quadratus* (Trouessart) was very infrequently encountered (Table I). Because we found only 3 individuals in total, we suspect that this species is not actually an inhabitant of flight feathers and may be normally found elsewhere, e.g., on wing covert feathers. *Goniodurus quadratus* has previously been collected from *Talegalla cuvieri* Lesson and *T. jobiensis* Meyer (Megapodiidae) (Atyeo, 1992). The other pterolichid appears to be a new species of *Leipobius*. The only described member of this genus is *L. ocellatus* Atyeo from the mallee fowl *Leipoa ocellata* Gould (Megapodiidae) (Atyeo, 1992). The *Leipobius* species was found on all birds from 3 of the 12 populations and on none of the other populations (Table I). Because low sample size of hosts in some populations may have affected the observed mite richness, we examined the relationship between sampling effort and mite species richness using linear regression. The number of mite species observed per brush-turkey population was not significantly affected by number of birds sampled per site ($P = 0.27$; $R^2 = 0.13$) or by the total number of mite specimens per site ($P = 0.34$; $R^2 = 0.1$).

Only 2 species of lice were identified from a total of 78 specimens, the long-bodied *L. crassus* and squat *Colpocephalum lathami* (Table II). With the exceptions of sites where only

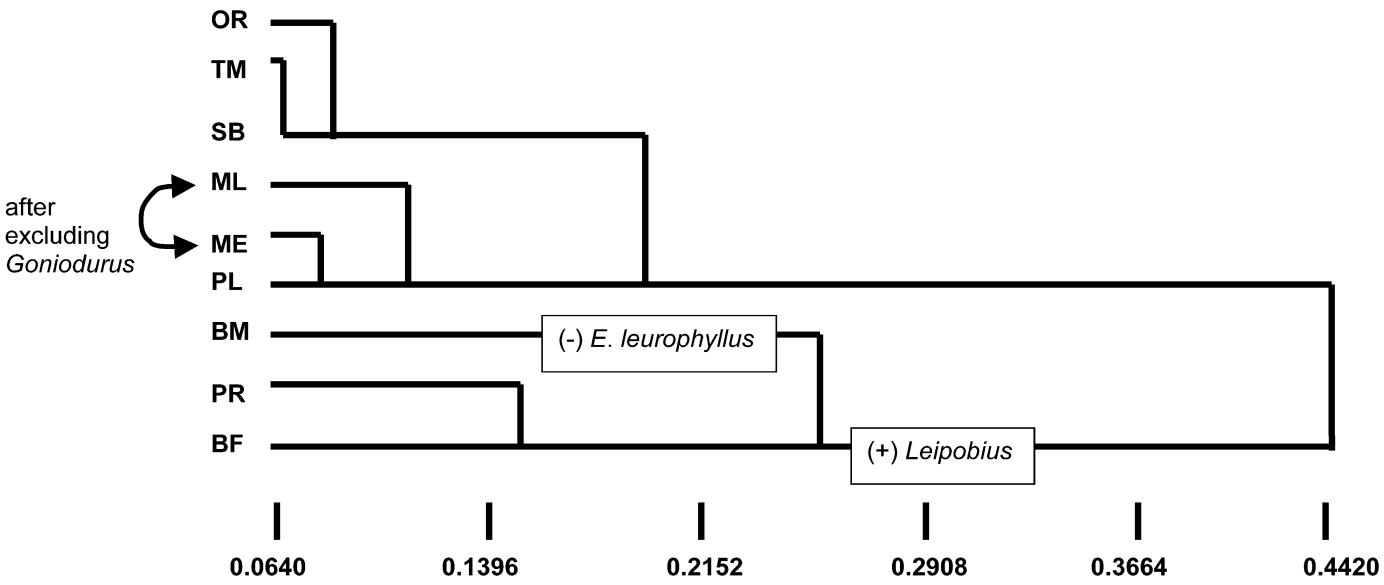


FIGURE 2. Flexible UPGMA dendrogram of site relationships based on mite assemblages (proportions of birds with each mite species); only sites with 5 or more birds were used. The double-headed arrow indicates sites that switch places when *Goniodurus quadratus* is excluded from the analysis. Sites BM, PR, and BF are characterized by the presence of *Leipobius* species in all sampled birds; BM was the only site where *Echinozonus leurophyllus* was completely absent.

1 bird was sampled, both morphotypes were present at all sites. Although lice were collected from most birds, usually fewer than 10 specimens were retrieved per host, compared with 10s to 100s of mites. Definite identification was possible only for mature female lice, which were rare compared with juveniles and males; thus, it is possible that the 'long' and 'squat' morphotypes represent more than 1 species each. Because of this uncertainty, we did not include lice in multivariate analyses.

None of the 4 field-killed brush-turkey chicks carried mites or lice; however, a hippoboscid fly was present on 1 of the corpses. Of the 5 hippoboscid flies that had been captured as they flew from adult brush-turkeys, 2 carried mites and 1 of these also carried lice of the long morphotype. Avian skin-mites of the family Epidermoptidae were present on 1 of the 2 flies. Epidermoptid mites are well known for their phoretic and parasitic relationships with hippoboscid flies (Madden and Harmon, 1998; Jovani et al., 2001). Protonymphs of pterolichoid feather mites were present on both hippoboscids. They were too small to be identified with certainty but were likely *Echinozonus* species. In contrast to epidermoptids, vane-dwelling feather mites have rarely been reported as phoretic on hippoboscid flies (Jovani et al., 2001).

Mite assemblages versus geographic distance

A dendrogram of site relationships based on mite assemblages (as proportions) is shown in Figure 2. The double-headed arrow indicates sites that switch places when *G. quadratus*, which may not normally occur on flight feathers, is excluded from the analysis. Its exclusion has little effect on the overall topology of the dendrogram. Some evidence of geographical structuring is present. Sites OR, TM, and SB are all in the mountainous southeast area of Queensland. ML, ME, and PL are in northern Queensland. The linking of BM and BF with the northern site PR was not expected on the basis of their geographical proximity; however, they are clearly connected by the presence of *Leipobius* sp. in all sampled birds. *Leipobius* sp. was found at no other site. BM is the only site where *E. leurophyllus* was completely absent. It is the most inland site with the exception of CV, where no mite was found on the 1 bird collected.

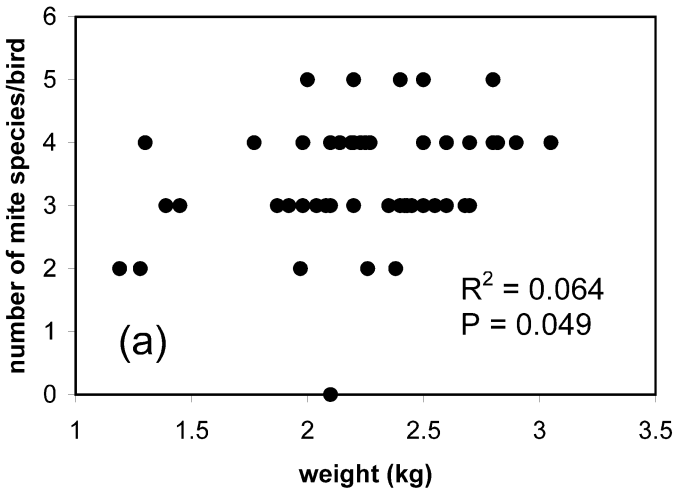
Perhaps because of the placement of PR together with 2 relatively distant sites, Mantel's test did not find a significant correlation between the distance matrix based on geographical distance between sites and that based on mite assemblages (mean randomized difference between matrices = 0.385, original difference = 0.407, percentage of randomization differences less than the observed value = 70.7; i.e., $P = 0.707$).

Mite richness versus host sex and size

Six birds were not sexed and so were excluded from this comparison. More male than female brush-turkeys were captured because of the greater boldness of the males (D. Jones, pers. obs.). The mean numbers of mite species per male and female were not significantly different: male (n = 39) 3.3 ± 0.16 SE; female (n = 17) 3.5 ± 0.17 SE; ANOVA $F = 0.268$, $P = 0.61$. There also was no significant difference in the variation in mite richness between the sexes (Levene Statistic 0.723, $P = 0.40$). The regression of mite species richness on host body weight was significant at $P = 0.049$ (Fig. 3a); however, R^2 was very low (0.064). There was no significant relationship between mite species richness and tarsus length ($P = 0.28$; $R^2 = 0.019$) (Fig. 3b).

Distribution of mites on wing and tail feathers

The majority of mites were found on (or in) wing feathers; the only species with an apparent preference for tail feathers was *Echinozonus longisetosus* (Fig. 4). Inadequate field notes were taken as to the total number of wing and tail feathers



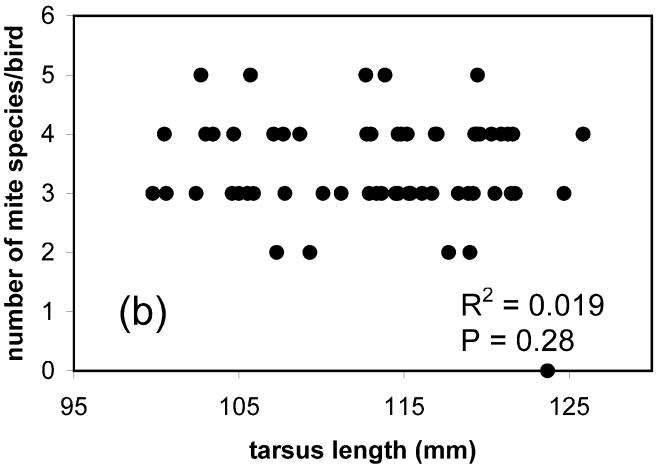


FIGURE 3. Relationship between number of mite species collected per bird and host age, as represented by (**a**) host weight and (**b**) host tarsus length.

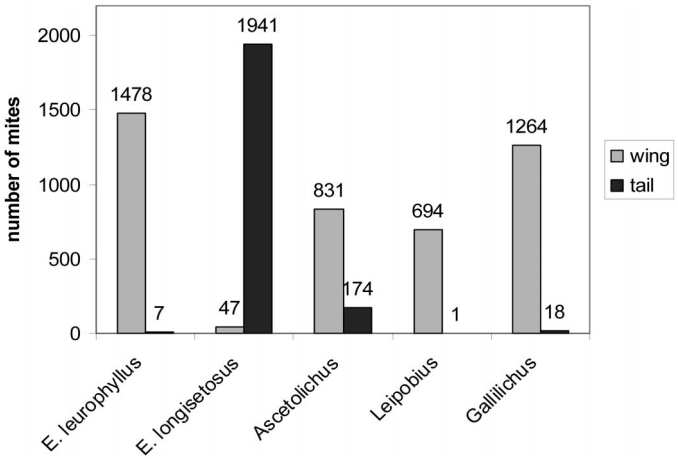


FIGURE 4. Distribution of feather mite species by feather location, excluding mites from the IR bird (whose feathers were not identified as 'wing' or 'tail'), and the 3 *Goniodurus quadratus* specimens (which were all found on wing feathers).

collected from each bird to allow legitimate statistical testing of whether more mites occurred on 1 feather type than would be expected. However, even if one considers the most extreme scenario of biased feather sampling (1 tail feather to 4 wing feathers per bird), only the distribution of *A. ruidus* approaches the 1:4 ratio one would expect if there was no preference for feather type.

DISCUSSION

There was obvious structuring in the feather mite assemblages from different brush-turkey populations (Fig. 2; Table I). This structure related to geographic distance in part, with 1 set of northern (ML, ME, PL) and 1 of southeastern (OR, TM, SE) sites. The sites in the remaining group (BM, PR, BF) did not share geographic proximity. They were distinguished by the shared presence of *Leipobius* sp., a mite that occurred nowhere else (Table I). Brush-turkeys from the BM site were further distinguished by the absence of *E. leurophyllus*, a species that was present (albeit sometimes in low numbers) at every other site. The brush-turkeys that originally colonized this inland site may have been without *E. leurophyllus* or this mite may have been lost soon after colonization. The only host individual in this study to completely lack feather mites was the single brush-turkey from CV, an even more isolated inland site. This also is suggestive of lineage sorting; however, the very small sample size hinders interpretation. Further sampling at this and other sites may reveal mites and lice that were not observed in this study.

The presence of a new species of *Leipobius* on a limited subset of geographically separated brush-turkey populations is intriguing. Clark's (1964) phylogeny of the megapodes placed the Australian brush-turkey as sister species to the mallee fowl (*Leipoa ocellata*), the only other megapode known to carry *Leipobius*. In contrast, Brom and Dekker (1992) and Birks and Edwards (2002) place *Alectura* and *Aepypodius* as sister taxa. *Aepypodius* and *Alectura* share mites in the genera *Goniodurus*, *Ascetolichus*, and *Echinozonus* (Atyeo, 1992; this study). This greater number of shared mite taxa supports Brom and Dekker's (1992) and Birks and Edwards (2002) hypothesis over Clark's (1964) and implies that the new *Leipobius* on the Australian brush-turkey may be the result of a relatively recent colonization event rather than shared ancestry between *Alectura* and *Leipoa*. Before the most recent contraction of rainforest, there was potential for contact between southern inland populations of brush-turkeys and mallee fowl (Rolls, 1981). Male brush-turkeys are notoriously amorous and have been known to copulate with domestic fowl (D. Jones, pers. obs.), providing potential for acquisition of mites from another species. If host switching rather than shared host ancestry explains the current hosts of *Leipobius* spp., one still must explain how *Leipobius* sp. came to occupy brush-turkeys in such geographically disjunct regions. The current distribution of the brush-turkey is likely to be its most restricted and fragmented for several millennia. Most of coastal eastern Australia was covered in virtually continuous rainforest until about 25,000 yr ago (White, 1994), suggesting the possible intermixing of brush-turkey populations over a large area. The retreat of the rainforest to their pre-European extent was complete by about 8,000 yr ago

(Smith, 1979). It appears likely that the small populations still extant in extremely isolated pockets of closed forests far inland are remnants of this period. Nonetheless, *A. lathami* is known to have prospered during the early 1900s when introduced prickly pear, *Opuntia* spp., had expanded rapidly throughout southern Queensland (Brookes, 1919). It is possible that some contact between previously separate populations of brush-turkey may have occurred during this time, although relatively few populations would have been involved. Perhaps this is how *Leipobius* sp. reached PR on the northern coast of Queensland.

A very important caveat to these speculations is the poor sampling effort to date for feather mites associated with mallee fowl. *Leipobius ocellata* is the only mite known from the mallee fowl, whereas most other megapode taxa host 3, or more, species (Atyeo, 1992). With more sampling of mallee fowl skins in museums, representatives of *Ascetolichus*, *Echinozonus*, and *Goniodurus* may be found. If they are, this would provide very strong support for a sistertaxon relationship between *Alectura* and *Leipoa* and would suggest that the absence of *Leipobius* sp. in many populations of Australian brush-turkeys was the result of repeated losses (lineage sorting) rather than 1 gain of this mite.

Feather mite colonization of brush-turkeys

The brush-turkey chicks that were examined postmortem lacked feather mites, which was expected given the noncontact incubation and lack of posthatching parental care in this species. Among the adults, the lightest, and hence possibly the youngest, carried fewer species of feather mites than the heaviest (=oldest) birds (Fig. 3a). This supports the idea that feather mites are gradually accumulated by body contact with conspecifics as the host ages. However, the relationship between weight and mite richness was weak and did not hold when tarsus length was used as a surrogate for age. It is possible that phoresy on winged hippoboscid flies, as was observed for at least 1 species of feather mite in this study, speeds colonization of hosts. A more extensive collection of hippoboscids from brush-turkeys is required to determine whether this is a common phenomenon. It also is possible that feather mites may be transmitted among brush-turkeys during agonistic interactions or when roosting.

Habitat partitioning among feather mites

Even accounting for the possibility that tail feathers may have made up only one third or one fifth of the total feathers taken from each bird, it is clear that most mite species showed a strong preference for either wing or tail (Fig. 4). *Ascetolichus ruidus* is the only potential exception. *Echinozonus leurophyllus*, *Leipobius* sp., and *G. jonesi* were more abundant on wing than tail feathers. In contrast, *E. longisetosus* preferred the tail to the wing. The Australian brush-turkey is not alone in having a pair of *Echinozonus* species. *Talegalla cuvieri*, *Aepypodius bruijnii*, and *A. arfakianus* also host 1 '*leurophyllus*'-like type I morphotype and 1 '*longisetosus*' type II morphotype (Atyeo, 1992). Atyeo and Pérez (1991) hypothesized that each morphotype may occupy a different feather group on the host, but their sampling methods (using museum study skins) did not allow them to test it. The clear separation of the 2 *Echinozonus* species in this study implies that the congeners may be subdividing niche space on the host through active competition; however, on the Bunya Mountain birds (which completely lacked the wing-dwelling *E. leurophyllus*), all *E. longisetosus* were located on tail feathers as usual. It also is possible that host grooming mediates location of these different morphotypes (Reiczigel and Rósza, 1998), an idea that could be tested with experimental impairment of the host's grooming ability (e.g., Clayton and Tompkins, 1995).

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