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On the origin of *Halipeurus heraldicus* on Round Island petrels: Cophylogenetic relationships between petrels and their chewing lice

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ABSTRACT

Lice phylogenetic relationships have often been used to elucidate host relationships and vice versa. In this study, we investigate the louse genus *Halipeurus* which parasitizes bird hosts in the families Procellariidae, Hydrobatidae and Pelecanoididae. The presence of two lice species on *Pterodroma arminjoniana* in different breeding grounds (*Halipeurus heraldicus* on Round Island, off Mauritius in the Indian Ocean and *Halipeurus kermadecensis* on Trindade Island in the Atlantic Ocean) has led to some confusion in the distribution of *Pt. arminjoniana* and its close relatives *Pt. heraldica* and *Pt. neglecta*. By using a cophylogenetic approach that incorporates uncertainties in phylogenetic reconstructions, we show significant overall coevolution between *Halipeurus* lice and their hosts. However, the study also indicates that the presence of *H. heraldicus* on *Pt. arminjoniana* and *Pt. neglecta* on Round Island and on *Pt. heraldica* on Gambier Island are the result of a host switch whereas *H. kermadecensis* is the ancestral parasite of *Pt. arminjoniana*. This suggests that *H. kermadecensis* was lost during or after colonisation of Round Island by *Pt. arminjoniana*. We conclude that cophylogenetic analyses are central to inferring the evolutionary history and biogeographical patterns of hosts and their parasites.

1. Introduction

Lice (Insecta: Phthiraptera) are a useful group for cophylognetic studies as they often show high levels of host specificity due to their life history (Price et al., 2003). They have limited mobility, depend mainly on host-to-host contact for transmission (Hafner and Nadler, 1988) and lice that leave the host die within a few hours or days (Tompkins and Clayton, 1999). Chewing lice in the genus *Halipeurus* exclusively parasitize petrels of the families Procellariidae, Hydrobatidae and Pelecanoididae and most species have exclusively been found on one host (Price et al., 2003). In the first cophylogenetic study of the genus *Halipeurus* and its hosts, extensive cospeciation was found between the five host–parasite associations analysed (Paterson and Banks, 2001). On the other hand, a later study with phylogenies of nine species of *Halipeurus* and a seabird supertree of their hosts (Kennedy and Page, 2002) showed limited congruence between the hosts and the parasites (Page et al., 2004). Storm petrels are the most basal species and are parasitized by the most basal louse lineage: *H. pelagicus* (Denny, 1842). However, *Halipeurus* from shearwaters (species of *Calonectris* and *Puffinus*) did not form a clade. The largest number of cospeciation events was 7, which was not significant.

Whilst cospeciation events occur when there is co-divergence between the host and the parasite, which results in strict congruence between the host and parasite phylogenies, incongruences could be the result of sorting events, host switches and/or duplications. Sorting events occur when the parasites have been removed from the host species. The parasite could either have been absent when the host diverged from an ancestral species ("missing the boat") or have gone extinct since the divergence ("drowning on arrival") (Paterson et al., 2003). Insufficient sampling of hosts could also be a reason for the absence of a particular parasite on a host (Page et al., 1996). Host switching events arise when a parasite colonizes a host other than the host it has co-diverged with. Finally, duplication events occur when the parasites diverge without their hosts speciating (Paterson et al., 2003).

In this study, we will focus on different *Halipeurus* species sampled from *Pterodroma* hosts. *Pterodroma arminjoniana* is parasitized by two different *Halipeurus* species in different breeding grounds: *H. heraldicus* Timmermann, 1961 on Round Island (22 km NE of Mauritius in the Indian Ocean), and *H. kermadecensis* Johnston and Harrison (1912) on Trindade Island, off Brazil. Additionally, *H. heraldicus* has been found on *Pt. neglecta* on Round Island and,

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although this petrel harbours *H. kermadecensis* in the Pacific Ocean, *H. kermadecensis* appears to be absent on Round Island. Whilst other bird species (*Gygis alba, Sula dactylatra, Anous stolidus*, *Onychoprion fuscatus*) breed nearby *Pt. arminjoniana* on Trindade Island, they do not breed in mixed colonies and do not harbour any *Halipeurus* lice (Price et al., 2003). Round Island provides nesting for two tropic-birds (*Phaethon lepturus* and *P. rubricauda*), which are not known to host any *Halipeurus* lice, and a shearwater (*Puffinus pacificus*), which hosts *Halipeurus mirabilis*.

This difference in *Halipeurus* species between the two sites is even more intriguing considering Round Island seems to have been colonized by petrels only recently. The first record of a gadfly petrel on Round Island was made by Jean-Michel Vinson in 1948 (Vinson, 1976). Murphy and Pennoyer (1952) were the first to associate the Round Island gadfly petrel with the Trindade petrel (*Pt. arminjoniana*), previously only known from Trindade Island in the south Atlantic Ocean. The calls and morphology of specimens from Round Island and Trindade Island are virtually indistinguishable (Brooke et al., 2000; Brown et al., submitted for publication-a,b; Gardner et al., 1985) and recent molecular work showed very little genetic divergence between *Pt. arminjoniana* from the two islands, i.e. they shared a number of haplotypes (Brown et al., submitted for publication-a).

The presence of different louse species of the genus *Halipeurus* on *Pt. arminjoniana* from the two different islands has been used to suggest the closer affinity of the Kermadec Petrel (*Pt. neglecta*) with *Pt. arminjoniana* on Trindade Island (Imber, 2004). Moreover, the presence of *H. kermadecensis* on *Pt. arminjoniana* from Trindade Island was used, together with other evidence, to suggest the presence of breeding *Pt. neglecta* on Trindade Island and their occurrence in the North Atlantic (Imber, 2004). This paper has been controversial (Bourne, 2005; Imber, 2005; Tove, 2005), and the presence of *Pt. neglecta* on Trindade Island has been rejected using diagnostic calls, white primary shafts and genetic data after many years of fieldwork by different scientists and after the inspection of over 100 bird skins in the National Museum in Rio de Janeiro dating back to the early 1900s (Luigi et al., 2009). On the other hand, the presence of *H. heraldicus* on *Pt. arminjoniana* and *Pt. heraldica* has also suggested close affinities between these petrels on Round Island (Brooke et al., 2000). However, these studies have not taken into account the phylogenetic relationships of the lice which are necessary to ascertain the origins of the different *Halipeurus* fauna on *Pt. arminjoniana* and its relatives (e.g. Hughes et al., 2007; Paterson and Banks, 2001).

In this paper, we analyse a larger dataset of *Halipeurus* species (i.e., 23 host–lice associations), which includes new sequences from *H. kermadecensis* from Trindade Island in the Atlantic Ocean, and *H. heraldicus* from Round Island, Indian Ocean, and Gambier Islands, Pacific Ocean. We also use sequence data from GenBank for the molecular phylogenetic reconstruction of petrels and their relatives. Additionally, we explore the effects of phylogenetic uncertainties and multi-host/multi-parasite associations on the inferences of cospeciation. Most methods are suited for the one-to-one parasite case such as tree comparison methods: TreeMap with Jungles (Charleston, 1998) and TreeFitter (Ronquist, 1995). These methods compare a range of trees representing alternative hypotheses of host and parasite relationships and reconstruct a plausible history of the host–parasite associations by trying to minimize the overall cost of events (e.g. cospeciation, duplication, loss). These methods are ideally designed for the one host-one parasite cases; but, as the numbers of hosts and parasites increases, the problem becomes highly computer-intensive, making optimal solutions hard to find. Additionally, tree comparison methods assume that the host and parasite phylogenies are known and do not take into account the uncertainties of phylogenetic reconstructions. Here, we avoid these problems by using ParaFit which employs a method that compares matrices of patristic distances (summed branch lengths along a phylogenetic tree) and allows for multi-host/multi-parasite associations and we summarize the results of the ParaFit analyses over a large number of alternative host and parasite topologies.

2. Methods and materials

2.1. Sampling and sequencing

Seventy-four *Pterodroma arminjoniana* sampled throughout Trindade Island were deloused, of which 73 were positive for *Halipeurus kermadecensis*. The number of *Halipeurus kermadecensis* lice from each bird ranged from 1 to 7. A total of 95 male lice and 94 female lice were examined. A further three samples (29 specimens) of *Halipeurus kermadecensis* from three Trindade *Pt. arminjoniana* were examined in a separate study. Fifteen birds were deloused on Round Island that tested positive for *Halipeurus heraldicus*. The total number of *Halipeurus heraldicus* collected was 9 males and 7 females with the number from each bird ranging from 1 to 2. Examination of *Pt. arminjoniana* on a separate occasion from at least one bird yielded a further 23 specimens of *Halipeurus heraldicus*.

Total genomic DNA was extracted from 7 specimens of *Halipeurus kermadecensis* sampled from *Pterodroma arminjoniana* from Trindade Island, 3 specimens of *H. heraldicus* (2 from *Pt. arminjoniana* and 1 from *Pt. neglecta*) from Round Island, and 1 specimen of *H. heraldicus* from *Pt. heraldica* from Gambier Islands (Fig. 1 and Table A1). A specimen collected from *Pt. madeira* not previously analysed in a phylogenetic context was also added. The head of each louse was separated from its body and both were incubated in lysis buffer over night using a DNeasy tissue kit (Qiagen). Two mitochondrial genes were amplified using insect specific primers 12Sai and 12Sbi for 12S rRNA (Simon et al., 1994) and L6625 and H7005 for COI (Hafner et al., 1994).

The PCR conditions were denaturation at 94 °C for 1 min followed by 40 cycles at 92 °C for 30 s, annealing at 45 °C for 40 s, and an extension at 72 °C for 10 min. Amplification products were gel purified using QIAquick Gel Extraction Kit (Qiagen) and sequenced for both DNA strands with an automated sequencer. These COI and 12S rRNA sequences were added to pre-existing sequences from GenBank (Table A2). Previously published mitochondrial cytochrome b sequences for the host birds were obtained from GenBank (Table A3).

2.2. Sequence alignment and analysis

COI and 12S rRNA sequences were aligned using Muscle (Edgar, 2004) and conserved blocks from the multiple alignment were selected using Gblocks (Castresana, 2000). The statistical significance of the incongruence length difference (ILD; Farris et al., 1994, 1995) between COI and 12S rRNA was assessed in PAUP v4.0b10 (Swofford, 1998) by executing 10,000 replicates with only the taxa common to both partitions included in the analysis.

To assess the relative stability of trees to methods of analysis, we used three different tree construction methods: parsimony, maximum likelihood and Bayesian. Phylogenies were estimated for each gene separately as well as the combined data set of lice. Maximum Parsimony (MP) phylogenies were estimated by heuristic searching all sites equally weighted, 1000 random addition replicates with tree-bisection-reconnection (TBR) branch swapping in PAUP. Bootstrapping (500 heuristic replicates) was used to determine the strength of support for individual nodes. The TVM model with invariable sites and a gamma distribution for substitution rate heterogeneity (TVM + G + I) was selected by ModelTest (Posada

and Crandall, 1998) and was used to run the maximum likelihood and Bayesian analyses. Phyml (Guindon and Gascuel, 2003) was used for maximum likelihood analysis. The robustness of the trees was assessed by bootstrapping (500 pseudoreplicates) with Phyml. MrBayes v3.0 (Ronquist and Huelsenbeck, 2003) was used for calculation of Markov chain Monte Carlo Bayesian posterior probabil-

Fig. 1. Map illustrating the breeding islands of the known hosts of *H. kermadecensis* (*Pt. neglecta* (□), *Pt. externa* (△), *Pt. arminjoniana* (☆)) and *H. heraldicus* (*Pt. heraldica* (○), *Pt. arminjoniana* (☆), *Pt. alba* (◇)) (Brooke, 2004). The symbols are filled black when *H. kermadecensis* was found and dark grey for hosts were *H. heraldicus* was collected in our study. Ri. Round Island, Ti. Trindade Island, Gi. Gambier Island.

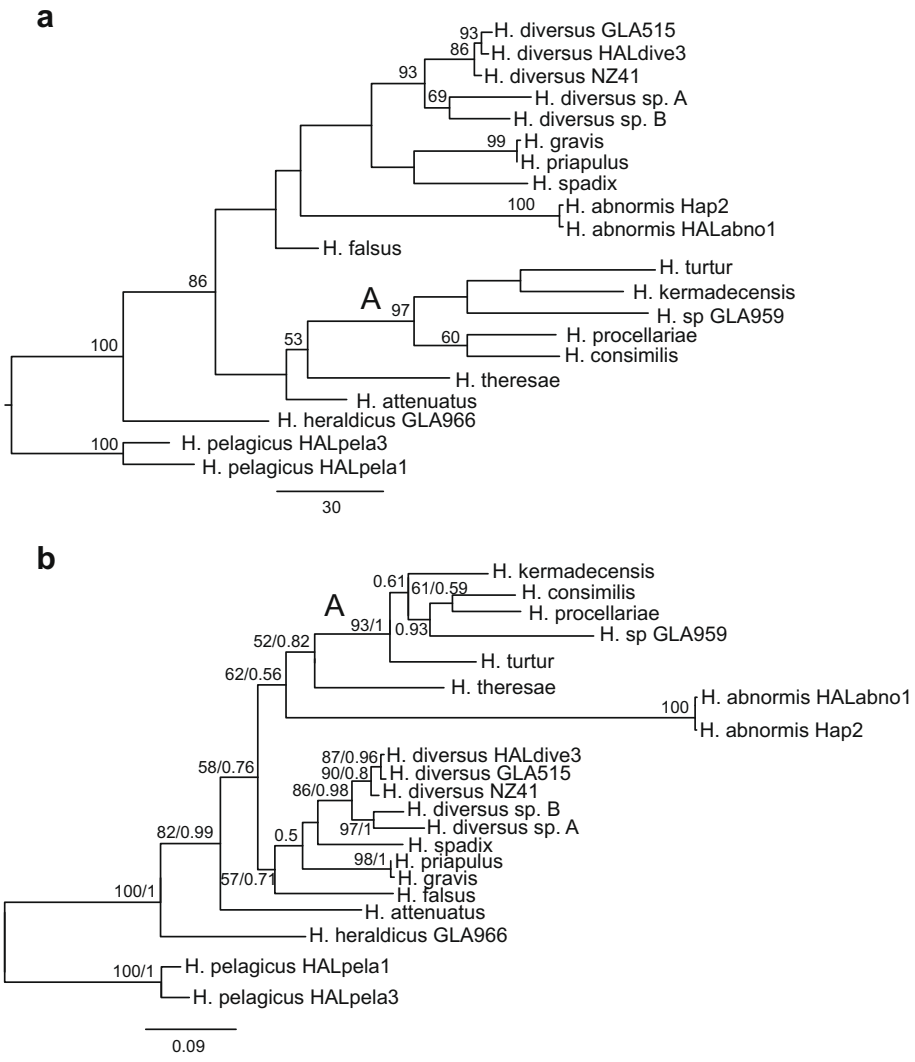

Fig. 2. Phylogenetic reconstruction of the *Halipeurus* lice genus using COI and 12S rRNA: (a) 1 of 6 maximum parsimony trees (length 780, CI = 0.574, RI = 0.603), bootstrap support is shown at the node and (b) maximum likelihood reconstruction (Phyml loglk = −4317.42, MrBayes best state = −4245.47), bootstrap support and posterior probability are shown at each node.

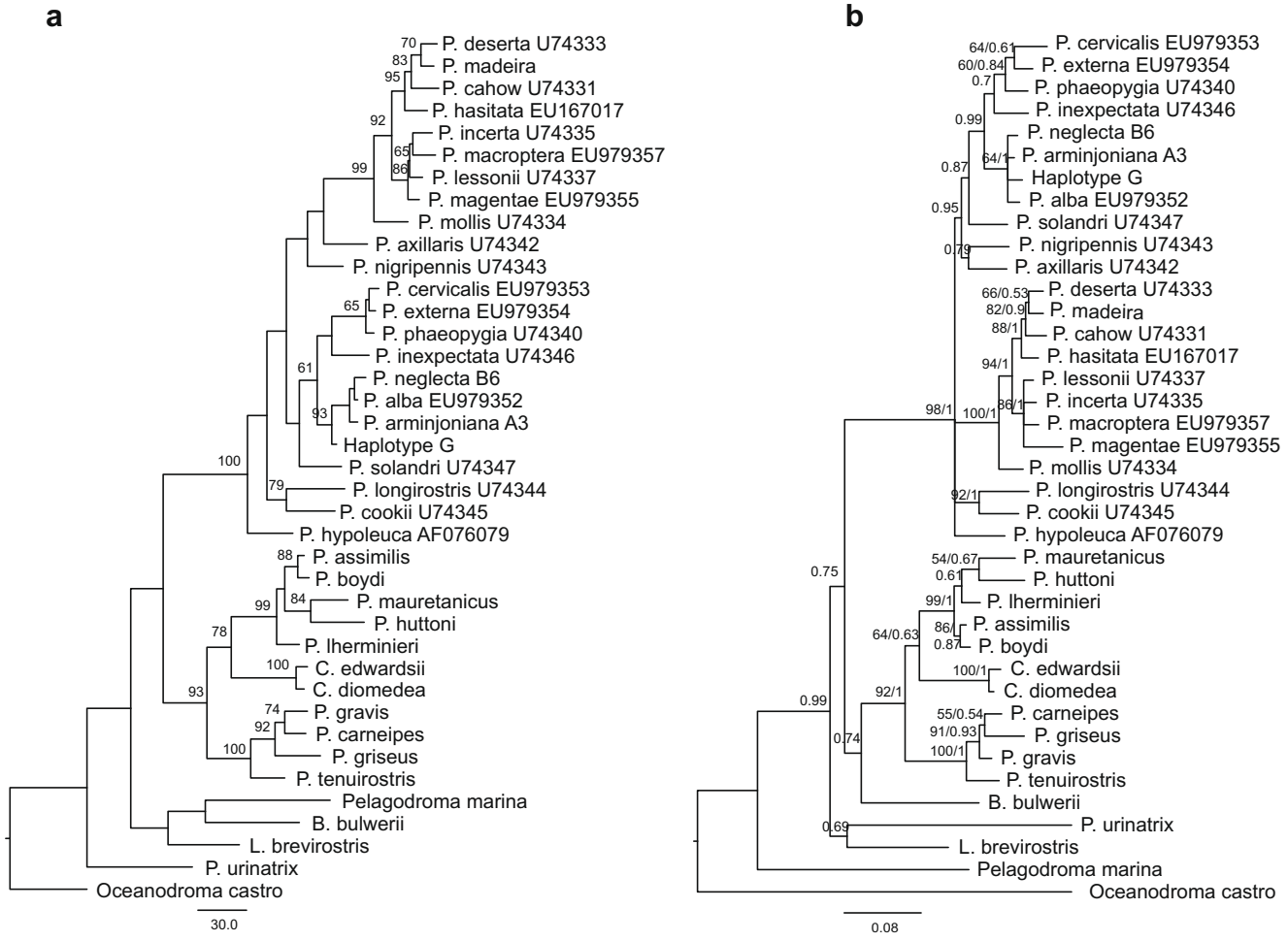

Fig. 3. Phylogenetic reconstruction of the petrels and relatives based on CytB: (a) 1 of 10 maximum parsimony trees (length 1381, CI = 0.418, RI = 0.634), bootstrap support is shown at the node and (b) maximum likelihood reconstruction (Phyml loglk = −7689.63, MrBayes best state = −7660.27), bootstrap support and posterior probability are shown at the node.

Table 1
The result of the ParaFit analyses conducted using patristic distances from 10,000 trees generated during the Bayesian analysis and based on the host information the lice specimens were collected on. The results show the proportion of host–parasite associations that were significant tested at $\alpha = 0.05$ and based on 999 permutations.

Halipeurus species	Host	Proportion of sig. links
Halipeurus abnormis Hap 1	*Calonectris diomedea*	0.5863
Halipeurus abnormis Hap 2	*Calonectris edwardsii*	0.5743
Halipeurus pelagicus Hap 1	*Oceanodroma castro*	0.5982
Halipeurus pelagicus Hap 3	*Pelagodroma marina*	0.3678
Halipeurus falsus	*Pelecanoides urinatrix*	0.3449
Halipeurus kermadecensis	*Pterodroma arminjoniana*	0.8624
Halipeurus turtur	*Pterodroma cookii*	0.5877
Halipeurus theresae	*Pterodroma hypoleuca*	0.3342
Halipeurus consimilis	*Pterodroma inexpectata*	0.7941
Halipeurus procellariae	*Pterodroma lessonii*	0.8462
Halipeurus sp. GLA959	*Pterodroma madeira*	0.7351
Halipeurus heraldicus	*Pterodroma arminjoniana*	0.0301
Halipeurus heraldicus	*Pterodroma heraldica*	0.0438
Halipeurus heraldicus	*Pterodroma neglecta*	0.0584
Halipeurus spadix	*Puffinus huttoni*	1
Halipeurus attenuatus	*Puffinus lherminieri subalaris*	0.0554
Halipeurus priapulus	*Puffinus carneipes*	0.9994
Halipeurus gravis	*Puffinus gravis*	0.9994
Halipeurus diversus GLA515	*Puffinus griseus*	1
Halipeurus diversus Hap A	*Puffinus assimilis baroli*	1
Halipeurus diversus Hap B	*Puffinus boydi*	1
Halipeurus diversus NZ41	*Puffinus mauretanicus*	1
Halipeurus diversus Hap 3	*Puffinus tenuirostris*	0.9997

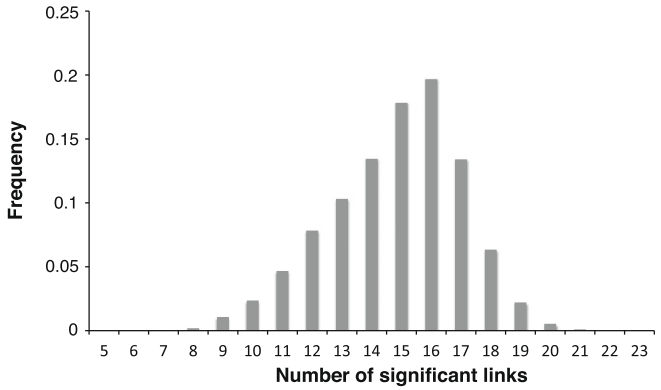

Fig. 4. Distribution of the number of significant associations from 10,000 ParaFit analyses using the parasite and host topologies generated in the Bayesian analyses and the host species the parasite specimens where collected on.

ities for all genes as well as the combined genes with the DNA model previously selected. For the louse combined genes, a partitioned Bayesian analysis was performed with unlinked model parameters across the two data partitions. The Markov chain Monte Carlo search was run twice with four chains for 1,000,000 generations with trees being sampled every 100 generations (the first 2500 trees [250,000 generations] were discarded as burn-in). A plot of generation versus the log probability was used to check for stationarity and the partition probabilities were compared in different runs to ensure convergence. This was used to check that similar likelihood values were sampled in independent runs and that a good sample from the posterior probability distribution was produced.

2.3. Analysis of cospeciation

To test for significant associations between the louse and the host phylogenies, we used ParaFit with patristic distances, i.e. summed branch lengths along a phylogenetic tree. The significance of the association was determined using 999 permutations (Legendre et al., 2002). To account for phylogenetic uncertainty, we automated the analysis across 10,000 host and 10,000 parasite phylogenies generated during the Bayesian analysis using a Perl script. We first carried out the later analysis using the host collection information for each parasite specimen and repeated the anal-

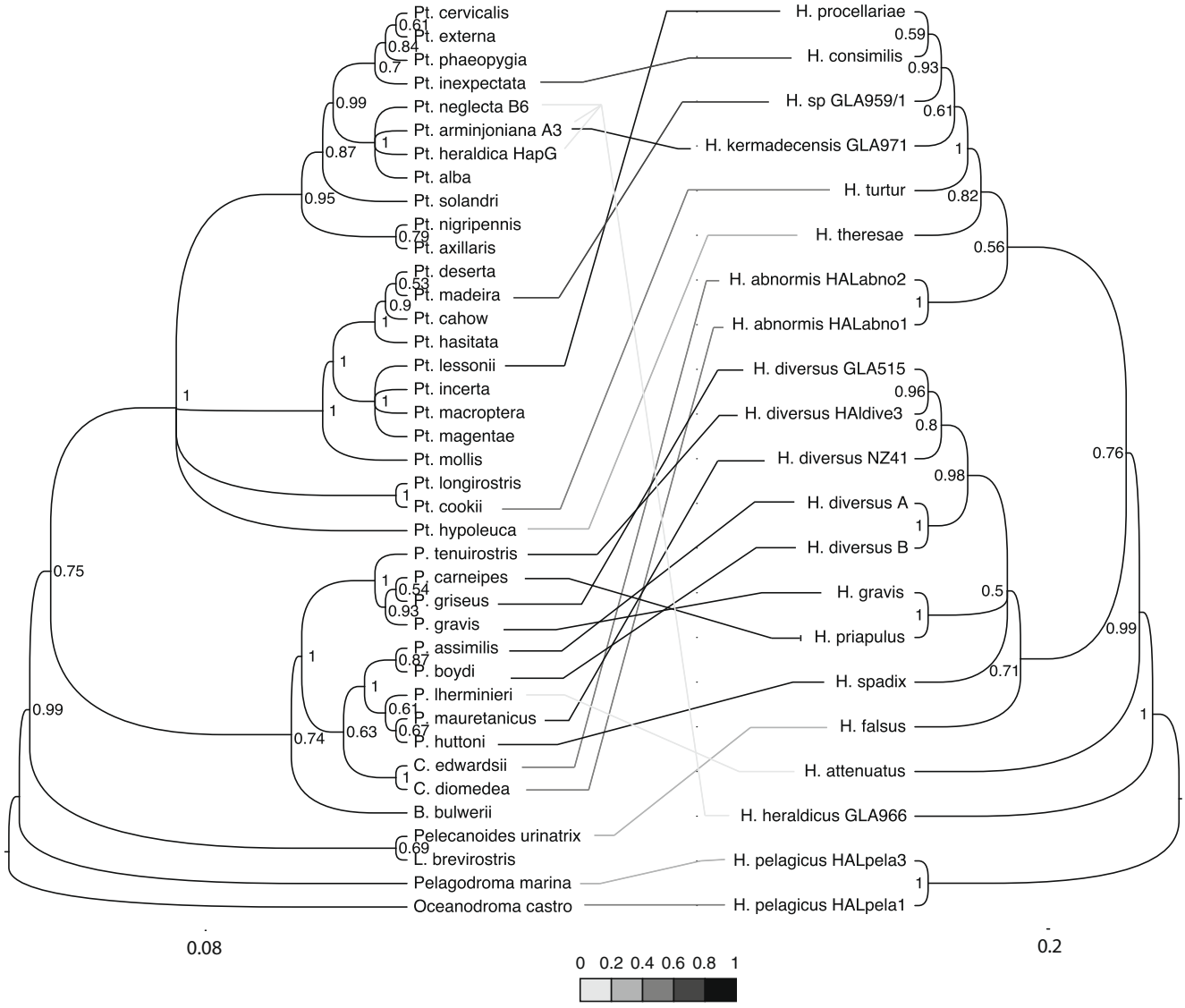

Fig. 5. Tanglegram for *Halipeurus* and its hosts (gadfly petrels, storm petrels and shearwaters). The darkness of the link between host and parasite corresponds to the proportion of time the association was found to be significant in the 10,000 ParaFit analyses.

yses for multi-host/multi-parasite associations according to the checklist information (Price et al., 2003).

3. Results

3.1. Phylogenetic analyses

Sequences from specimens of the same *Halipeurus* species did not show any differentiation for COI and 12S rRNA. Therefore, isolate GLA971 and GLA966 were used in all further analyses as representative sequences for *H. kermadecensis* and *H. heraldicus*, respectively. All sequences have been deposited in GenBank (Table A2) and the data matrix for the lice has been deposited in TreeBase (study S2601).

The louse phylogenies for COI and 12S rRNA with the different reconstruction methods did not show significant differences (Fig. A1) and the ILD found no significant difference in phylogenetic signal between the two data partitions (12S rRNA and COI, $p = 0.508$). The combined dataset of lice included 693 base pairs, and out of the 316 variable sites, 248 of the characters were parsimony informative. The MP analysis of the louse data led to 6 equally most parsimonious trees (tree length 780, CI = 0.574, RI = 0.603, Fig. 2a). The ML and Bayesian analyses trees from the combined dataset produced similar topologies (Fig. 2b).

Analyses of the petrel dataset showed that *Pt. neglecta*, *Pt. arminjoniana* and *Pt. heraldica* share cytochrome b haplotypes and that haplotypes are shared between *Pt. arminjoniana* on Round Island and Trindade Island. The phylogenies from the different reconstruction methods were similar (Fig. A2). In all further analyses, we only used Haplotype G, A3 and B6 as representatives of the *Pt. heraldica, Pt. arminjoniana* and *Pt. neglecta* as well as a single representative sequence for all other *Pterodroma* species that had more than one sequence in the database. The maximum parsimony reconstruction of petrels and their relatives yielded 10 equally most parsimonious trees (tree length 1381, CI = 0.418, RI = 0.634, Fig. 3a) and the phylogeny was similar to the maximum likelihood and bayesian reconstructions (Fig. 3b).

3.2. Cospeciation analyses

The results of the 10,000 ParaFit tests suggest an important amount of cospeciation between *Halipeurus* lice and petrels and their relatives (Table 1). Using the ParafitLink1 statistic (tested at $\alpha = 0.05$), we found 6–22 of the host–parasite (H–P) links were significant out of a total of 23 possible associations with most tests showing 16 significant H–P links (Figs. 4 and 5) and a significant GlobalFit in all 10,000 analyses (ParaFitGlobal = 0.0004–0.0016, $p < 0.05$). The significant links suggest extensive coevolution between the hosts and parasites (Fig. 5). *Halipeurus* species that showed non-significant links in more than 75% of analyses were *H. attenuatus* and *H. heraldicus*. The link between *H. abnormis* with *Calonectris diomedea* and *Calonectris edwardsii* was non-significant in more than 40% of cases. When multi-host/multi-parasite associations were used in the analysis (Table 2), 15–32 links were significant with most analyses suggesting 26 significant links out of a total of 32 possible associations (Fig. 6). The GlobalFit was significant in all 10,000 analyses (ParafitGlobal = 0.0008–0.0037, $p < 0.05$). The lice with non-significant links were similar to those found in the first analysis.

4. Discussion

The phylogenetic reconstruction of *Halipeurus* lice is broadly congruent with the morphology of the species (Edwards, 1961; Timmermann, 1965). *Halipeurus heraldicus* is more basal in the molecular phylogenies and this is supported by its very distinct morphology compared to all the other species in our analyses. Additionally, the maximum likelihood phylogeny using 12S rRNA is broadly in agreement with morphology, in particular the male genitalia, except for the grouping of *H. procellariae* with *H. consimilis* as *H. sp.* GLA959 is almost identical morphologically to *H. procellariae*.

Table 2
The result of the ParaFit analyses conducted using patristic distances from 10,000 trees generated during the Bayesian analysis and based on all known host species for each louse species according to Price et al. (2003). The results show the proportion of host–parasite associations that were significant tested at $\alpha = 0.05$ and based on 999 permutations.

Halipeurus species	Host	Proportion of sig. links
Halipeurus abnormis	*Calonectris diomedea*	0.4112
Halipeurus pelagicus	*Oceanodroma castro*	0.6884
Halipeurus pelagicus	*Pelagodroma marina*	0.5074
Halipeurus falsus	*Pelecanoides urinatrix*	0.8480
Halipeurus heraldicus	*Pterodroma neglecta*	0.1106
Halipeurus heraldicus	*Pterodroma heraldica*	0.0858
Halipeurus heraldicus	*Pterodroma alba*	0.0896
Halipeurus heraldicus	*Pterodroma arminjoniana*	0.0900
Halipeurus kermadecensis	*Pterodroma arminjoniana*	0.9735
Halipeurus kermadecensis	*Pterodroma externa*	0.9803
Halipeurus theresae	*Pterodroma hypoleuca*	0.5707
Halipeurus theresae	*Pterodroma hypoleuca*	0.5256
Halipeurus theresae	*Pterodroma magentae*	0.9108
Halipeurus theresae	*Pterodroma hasitata*	0.9171
Halipeurus consimilis	*Pterodroma inexpectata*	0.9364
Halipeurus procellariae	*Pterodroma incerta*	1.0000
Halipeurus procellariae	*Pterodroma lessonii*	1.0000
Halipeurus procellariae	*Pterodroma macroptera*	1.0000
Halipeurus procellariae	*Pterodroma magentae*	0.9999
Halipeurus procellariae	*Pterodroma mollis*	0.9862
Halipeurus sp. GLA959	*Pterodroma madeira*	0.9990
Halipeurus turtur	*Pterodroma cookii*	0.7380
Halipeurus attenuatus	*Puffinus lherminieri subalaris*	0.3508
Halipeurus diversus	*Puffinus assimilis baroli*	1.0000
Halipeurus diversus	*Puffinus boydi*	1.0000
Halipeurus diversus	*Puffinus griseus*	1.0000
Halipeurus diversus	*Puffinus mauretanicus*	1.0000
Halipeurus diversus	*Puffinus tenuirostris*	1.0000
Halipeurus gravis	*Puffinus gravis*	1.0000
Halipeurus priapulus	*Puffinus carneipes*	1.0000
Halipeurus spadix	*Puffinus huttoni*	1.0000
Halipeurus spadix	*Puffinus lherminieri*	1.0000

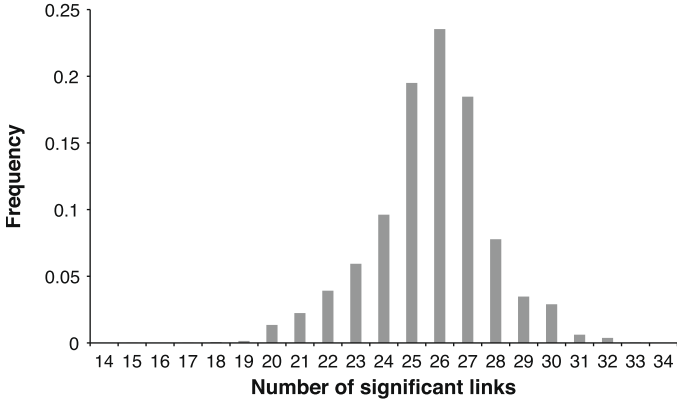

Fig. 6. Distribution of the number of significant associations from 10,000 ParaFit analyses using the parasite and host topologies generated in the Bayesian analyses and the host–parasite association according to the known host range in the checklist (Price et al., 2003).

Petrel phylogenies are similar to previous studies based on morphology and life history (Imber, 1985; modified by Brooke, 2004), DNA–DNA hybridization (Sibley and Ahlquist, 1990), cytochrome b (Nunn and Stanley, 1998) and a comprehensive supertree of the Procellariiformes (Kennedy and Page, 2002). As suggested previously (Austin et al., 2004; Nunn and Stanley, 1998), *Calonectris* and *Puffinus* are monophyletic with *Calonectris* and the small *Puffinus*, like *P. huttoni* and *P. mauretanicus* (called group A or the "Puffinus" group (Brooke, 2004)), more closely related to one another than to the larger *Puffinus* species ("Neonectris" group). *Lugensa brevirostris* is confirmed as a distinct form more closely related to *Bulweria* than *Pterodroma* (see Nunn and Stanley, 1998) although branch support at the deeper nodes are low in the maximum parsimony reconstruction.

Regarding gadfly petrels (*Pterodroma*), all north Atlantic species are in a clade (*Pt. madeira/cahow/hasitata*), partially agreeing with morphological data in Imber (1985), and excluding the south Atlantic species (*Pt. mollis*) from this group. Thus early arrangements considering northeastern Atlantic forms as subspecies of *Pt. mollis* (*Pt. feae* and *Pt. deserta*) is not supported in a range of recent genetic and morphological studies (Lawrence et al., 2009; Zino et al., 2008, and this study). On the other hand, the phylogenies presented here disagree with the four subgenera proposed by Imber (1985) and modified by Brooke (2004). We also confirm the close relationship of petrels breeding on Round Island (*Pt. arminjoniana/neglecta/heraldica*) with *Pt. alba* from the Pacific Ocean. Despite recent advances in understanding the relationships within the large and complex gadfly petrel group, further sampling is required, and additional molecular sequences are required, for example the nuclear gene RAG-1 could be useful to resolve relationships within the group.

Analysis of microsatellite genotype data from populations of *Pt. arminjoniana* on Trindade and Round Island shows significant population structure between them, in the form of a significant F_{ST} value (Brown et al., submitted for publication-b). However, this structure is weak when compared with other Procellariiform species which have populations in different ocean basins (Friesen et al., 2007), supporting the theory that the two populations of *Pt. arminjoniana* have recently split from one another (Brown et al., submitted for publication-b). The two populations also share mitochondrial DNA haplotypes, indicating that lineage sorting has not occurred. All three petrel species present on Round Island (*Pt. arminjoniana*, *Pt. neglecta* and *Pt. heraldica*) share at least some mtDNA haplotypes, possibly as a result of hybridization between them (Brown et al., submitted for publication-a). This may explain the apparent ubiquity of the louse *H. heraldicus* in the Round Island populations of at least two of the hosts.

The results from the cophylogenetic analyses taking into account the uncertainties in phylogenetic reconstruction support cospeciation between *Halipeurus* lice and their petrel hosts unlike the previous study based on a smaller number of lice–host associations (Page et al., 2004). However, the same cospeciating patterns are not found in the lice of the gadfly petrel. The widespread association of *H. heraldicus* with *Pt. heraldica* in the Pacific Ocean suggest that the association of *H. heraldicus* with *Pt. neglecta* and *Pt. arminjoniana* on Round Island and *Pt. heraldica* on Gambier Island is likely to be the result of a host switch. Further sampling of the genus *Halipeurus* on a broader diversity of hosts might enable us to detect the ancestral host of *H. heraldicus*. On the other hand, the association of *H. kermadecensis* with *Pt. arminjoniana* on Trindade Island is probably the result of an ancestral cospeciation event. The association of *H. heraldicus* with the petrels of Round Island and Gambier Islands is likely to be recent as there were no base differences in the parasite sequences of COI and 12S rRNA (total of 693 bases) between the specimens from both islands and between the specimens from different hosts. In addition to *Pt. arminjoniana* in Trindade Island, *H. kermadecensis* parasitizes *Pt. neglecta* and *Pt. externa* in the Pacific Ocean (Price et al., 2003). However, only *H. heraldicus* was found on *Pt. neglecta* and *Pt. arminjoniana* on Round Island, not *H. kermadecensis*, which would imply a loss of this parasite during or after colonisation of Round Island by *Pt. arminjoniana* and *Pt. neglecta*. Despite all the available samples in our study, our combined experience in sampling from *Pterodroma* species and other petrels, and previous records (Price et al., 2003), we consider that we have sampled *Halipeurus* from a sufficient number of birds to be confident that *H. heraldicus* does not live on Trindade *Pterodroma* species and that *H. kermadecensis* does not live on Round Island *Pterodroma* species. Thus, two scenarios are possible, one where birds colonizing Round Island arrived without *H. kermadecensis* ("missing the boat", Paterson et al., 2003), or that *H. kermadecensis* arrived at Round Island but subsequently became extinct ("drowning on arrival", Paterson et al., 2003) and was replaced by *H. heraldicus* on *Pt. arminjoniana* and *Pt. neglecta*.

Whilst it has been shown that the rates of molecular evolution are higher at a species level for the lice than their host (estimates vary from 1.53–5.5, e.g. Page et al., 1998; Paterson and Banks, 2001; Paterson et al., 2000), the lack of genetic differentiation in *H. heraldicus* on three different hosts, which do show genetic differentiation on Round Island and Gambier Island, would suggest that the population genetic processes acting on the lice are slower than those of the host. Although caution should be taken when comparing the genetic differentiation in *Halipeurus* and its hosts as the same genes were not amplified in the host and the parasite (cytb in the host, COI and 12S rRNA in the lice). Thus, despite both host and parasite genes in this study being mitochondrial, they might not have comparable evolutionary rates and histories. Nonetheless, these results mirror those found for *H. abnormis* from *Calonectris diomedea diomedea*, *C. d. borealis* and *C. edwardsii*, which showed no geographic or host-specific structuring when comparing cytochrome b in both hosts and parasites (Gómez-Díaz et al., 2007) and the association of *H. abnormis* and *Calonectris* spp. is likely to be the result of a host switch (Page et al., 2004). It is interesting to note that the presence of *H. abnormis* and *H. heraldicus* on their respective hosts is probably the result of host switching in both cases. Thus, a more likely scenario for the lack of genetic diversity of the parasite could be the more recent arrival of *H. heraldicus* on Round Island compared to its host. It is also possible that the host switch during or after colonisation resulted in a bottleneck in the louse population and was followed by the rapid spreading of *H. heraldicus* on its new hosts. However, we still lack a comprehensive understanding of the population genetic processes of lice and lack population level sampling in our study to be able to support this suggestion.

To our knowledge, this study is the first pragmatic solution to dealing with uncertainties in phylogenetic reconstruction in cophylogenetic analyses and although the approach does not enable historical reconstructions like TreeMap, it provides statistical information to exclude some of the host–parasite associations as resulting from cospeciation. The results of the cophylogenetic analyses varied slightly depending on the topologies and whether multi-host/multi-parasite associations were used but certain links in the ParaFit analyses were consistently non-significant (e.g. *H. heraldicus* and *Pt. arminjoniana/neglecta/heraldica*). Similarly to Page et al. (2004), we found that the links between *Calonectris* and *H. abnormis* and between *Pelagodroma marina* and *H. pelagicus* were not significant in a large number of cases. In this study, we have sampled 14 of the 30 known louse species in the genus and the cophylogenetic analyses provide evidence for cospeciation unlike the study of Page et al. (2004). Although the results are not directly comparable due to the different methodology used here, the increased number of species in this study probably plays an important part in the significant result found in our study.

The evidence for coevolution between *Halipeurus* lice and their hosts allows inferences about the age of the genus. The first fossil of the Procellariidae family was discovered in Belgium in 1871 in the Middle Oligocene strata (approx 30 mya) (Fisher, 1967). This would suggest that the ancestor of the genus *Halipeurus* could be approximately 30 million years old (during the Oligocene) but recent dating of diversification of the Neoaves would place the diversification of petrel lice later than 20 mya, i.e. during Miocene (Ericson et al., 2006).

More sampling would undoubtedly clarify the picture further, in particular sampling of lice from *Pt. heraldica* from Round Island and other populations from the Pacific Ocean, as well as from *Pt. alba* and other sympatrically distributed species of the Procellariidae, Hydrobatidae and Pelecanoididae. Specimens from basal host species are required to elucidate the ancestral host of *H. heraldicus*. Additionally, it would be interesting to sequence more *H. procellariae* from a greater diversity of hosts as they show strong morphological convergence on *Pt. madeira* and *Pt. lessonii* and yet are genetically distinct. Thus, the populations of *H. procellariae* on five different hosts (Price et al., 2003) may include cryptic species.

Whilst host–louse associations can be used to support the identification of a host and its distribution, they can also confound rela-

Table A1
Halipeurus species, voucher code, location, collector, date and host species for each sequenced sample. All specimens were identified by R. Palma. The DNA extractions are stored in the Lousebase collection at the University of Glasgow, UK.

Halipeurus species	Voucher and extraction code	Collection location	Collector	Date	Host (ring number)
Halipeurus heraldicus	GLA966	Below summit N, Round Island	R. Brown	14-Sep-05	*Pterodroma arminjoniana* (5H 30433)
Halipeurus heraldicus (adult)	GLA969	Big slab W, Round Island	R. Brown	28-Sep-05	*Pterodroma arminjoniana* (5H 33648)
Halipeurus heraldicus	GLA979	Gambier Islands, Tuamotu Archipelago	J.C. Thibault	1-Jul-96	*Pterodroma heraldica*
Halipeurus heraldicus (adult)	GLA965	SW Coast upper, Round Island	R. Brown	11-Sep-05	*Pterodroma neglecta* (5H 33452)
Halipeurus kermadecensis	GLA970	Morro do Paredão, Trindade Island	L. Bugoni	27-Dec-06	*Pterodroma arminjoniana* (N07378)
Halipeurus kermadecensis	GLA971	Farilhões, Trindade Island	L. Bugoni	16-Jan-07	*Pterodroma arminjoniana* (N00761)
Halipeurus kermadecensis	GLA974	Ilha do Sul, Trindade Island	L. Bugoni	17-Jan-07	*Pterodroma arminjoniana* (N00768)
Halipeurus kermadecensis	GLA976	Pico do Vigia, Trindade Island	L. Bugoni	01-Apr-07	*Pterodroma arminjoniana* (N00793)
Halipeurus kermadecensis	GLA972	Pico do Monumento, Trindade Island	L. Bugoni	08-Mar-07	*Pterodroma arminjoniana* (N07398)
Halipeurus kermadecensis	GLA975	Pico do Monumento, Trindade Island	L. Bugoni	07-Mar-07	*Pterodroma arminjoniana* (N00779)
Halipeurus kermadecensis	GLA978	Pico do Monumento, Trindade Island	L. Bugoni	30-Dec-06	*Pterodroma arminjoniana* (N00709)

Table A2
Accession numbers for the genes sequenced from *Halipeurus* lice.

Halipeurus species	Voucher and extraction code	Host	COI	12S
Halipeurus heraldicus	GLA979	*Pterodroma heraldica*	GQ507770	GQ507760
Halipeurus heraldicus (adult)	GLA965	*Pterodroma neglecta* (5H 33452)		GQ507754
Halipeurus heraldicus	GLA966	*Pterodroma arminjoniana* (5H 30433)	GQ507761	GQ507755
Halipeurus heraldicus (adult)	GLA969	*Pterodroma arminjoniana* (5H 33648)	GQ507762	GQ507756
Halipeurus kermadecensis	GLA970	*Pterodroma arminjoniana* (N07378)	GQ507763	GQ507757
Halipeurus kermadecensis	GLA971	*Pterodroma arminjoniana* (N00761)	GQ507764	GQ507758
Halipeurus kermadecensis	GLA972	*Pterodroma arminjoniana* (N07398)	GQ507767	GQ507759
Halipeurus kermadecensis	GLA974	*Pterodroma arminjoniana* (N00768)	GQ507765	
Halipeurus kermadecensis	GLA975	*Pterodroma arminjoniana* (N00779)	GQ507766	
Halipeurus kermadecensis	GLA976	*Pterodroma arminjoniana* (N00793)	GQ507768	
Halipeurus kermadecensis	GLA978	*Pterodroma arminjoniana* (N00709)	GQ507769	
Halipeurus consimilis		*Pterodroma inexpectata*	AF396556	Y14914
Halipeurus procellariae	GLA517	*Pterodroma lessonii*	AY160051	AY160061
Halipeurus sp.	GLA959/1	*Pterodroma madeira*	DQ202720	DQ20271
Halipeurus theresae	HALthere	*Pterodroma hypoleuca*	AF396565	AF396499
Halipeurus turtur	HALturtu	*Pterodroma cookii*	AF396566	AF396500
Halipeurus attenuatus	GLA906	*Puffinus lherminieri subalaris*		AY160079
Halipeurus diversus	GLA515	*Puffinus griseus*	AY160052	AY160060
Halipeurus diversus	HALdive3	*Puffinus tenuirostris*	AF396557	AF396494
Halipeurus diversus	N.Z. 41	*Puffinus mauretanicus*		AY160059
Halipeurus sp. A	HALooooA	*Puffinus assimilis baroli*	AF396563	AF396497
Halipeurus sp. B	HALooooB	*Puffinus boydi*	AF396564	AF396498
Halipeurus gravis	HALgravi	*Puffinus gravis*	AF396558	AF396495
Halipeurus priapulus	HALpriap	*Puffinus carneipes*		AF396496
Halipeurus spadix		*Puffinus huttoni*	AF396562	Y14916
Halipeurus abnormis	HALabno2	*Calonectris edwardsii*	AF396555	AF396493
Halipeurus abnormis	HALabno1	*Calonectris diomedea*	AF396554	AF396492
Halipeurus falsus pacificus		*Pelecanoides urinatrix*		Y14913
Halipeurus pelagicus	HALpela3	*Pelagodroma marina*	AF396561	Y14915
Halipeurus pelagicus	HALpela1	*Oceanodroma castro*	AF396559	AF189137

tionships and biogeographical patterns if cophylogenetic studies are not carried out. For example, prior to this study, the presence of *H. kermadecensis* on *Pt. arminjoniana* from Trindade Island was used to suggest the breeding of *Pt. neglecta* on Trindade Island and the close affinity of *Pt. neglecta* and *Pt. arminjoniana* (Imber, 2004), whilst the presence of *H. heraldicus* on *Pt. arminjoniana* and *Pt. heraldica* suggested the close affinities between these petrels on Round Island (Brooke et al., 2000). Here, we used cophylogenetic analyses taking into account the uncertainties in host and parasite phylogenetic relationships to show that although cospeciation has occurred between the lice in the genus *Halipeurus* and heir hosts, the presence of *H. heraldicus* on *Pt. neglecta*, *Pt. arminjoniana* and *Pt. heraldica* is most likely the result of a host switch whereas *H. kermadecensis* has historically been associated with *Pt. arminjoniana*.

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Table A3
Accession numbers for all bird sequences used in this study.

Host	Haplotype	Cyt b	Location
Pterodroma heraldica	G	Brooke and Rowe (1996)	Henderson Island
Pterodroma heraldica	D	Brooke and Rowe (1996)	Henderson Island
Pterodroma arminjoniana	B7	GQ328984	Round Island
Pterodroma arminjoniana	B3	GQ328979	Round Island
Pterodroma arminjoniana	A5	GQ328973	Round Island
Pterodroma arminjoniana	A4	GQ328972	Round Island
Pterodroma arminjoniana/heraldica/neglecta	C1	GQ328986/GQ328987/GQ328988	Round Island
Pterodroma arminjoniana/neglecta	B4	GQ328980/GQ328981	Round Island
Pterodroma arminjoniana/neglecta	B2	GQ328977/GQ328978	Round Island
Pterodroma arminjoniana/neglecta	B1	GQ328975/GQ328976	Round Island
Pterodroma neglecta	B6	GQ328983	Round Island
Pterodroma neglecta	B5	GQ328982	Round Island
Pterodroma neglecta	B8	GQ328985	Round Island
Pterodroma arminjoniana	A3	GQ328971	Trindade Island
Pterodroma arminjoniana	A6	GQ328974	Trindade Island
Pterodroma arminjoniana	A2	GQ328970	Trindade Island and Round Island
Pterodroma arminjoniana	A1	GQ328969	Trindade Island and Round Island
Pterodroma neglecta		U74341	Masatierra I., Juan Fernandez Islands
Pterodroma alba		EU979352	
Pterodroma axillaris		U74342	
Pterodroma cahow		U74331	
Pterodroma cervicalis		EU979353	
Pterodroma cookii		U74345	
Pterodroma deserta		U74333	
Pterodroma externa		EU979354	
Pterodroma externa		U74339	
Pterodroma hasitata		U74332	
Pterodroma hasitata		EU1670717	
Pterodroma hypoleuca		AF076079	
Pterodroma incerta		U74335	
Pterodroma inexpectata		U74346	
Pterodroma lessonii		U74337	
Pterodroma longirostris		U74344	
Pterodroma macroptera		EU979357	
Pterodroma macroptera		U74336	
Pterodroma madeira		EF537884	
Pterodroma magentae		EU979355	
Pterodroma magentae		FJ463404	
Pterodroma magentae		U74338	
Pterodroma mollis		U74334	
Pterodroma nigripennis		U74343	
Pterodroma phaeopygia		U74340	
Pterodroma solandri		U74347	
Puffinus assimilis		AF076080	
Puffinus boydi		AY219937	
Puffinus carneipes		AF076082	
Puffinus gravis		U74354	
Puffinus griseus		U74353	
Puffinus huttoni		AF076084	
Puffinus lherminieri		AF076085	
Puffinus mauretanicus		AJ004212	
Puffinus tenuirostris		U74352	
Bulweria bulwerii		U74351	
Calonectris diomedea		U74356	
Calonectris edwardsii		DQ372047	
Lugensa brevirostris		AY158678	
Oceanodroma castro		AJ004203	
Pelagodroma marina		AF076072	
Pelecanoides urinatrix		AF076076	

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Appendix A

See Tables A1–A3.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2010.01.013.

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