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**Drowning on arrival, missing the boat and x-events:**

**How likely are sorting events?**

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One of the major goals of coevolution studies is to infer the chronicle of events that has determined the present distribution of parasites on their hosts. The reconstruction of such events is made complex by the choice of phylogenetic model (either implicit or explicit) and underlying assumptions needed for this inference. Adding further complexity are the various events that constitute coevolution; cospeciation, sorting, host switching, and intrahost speciation (duplication) events (Page, 1994; Paterson and Gray, 1997, Paterson et al., 1999) (see Fig. 1a-d). Cospeciation events occur when host and parasite species co-diverge. For example, the isolation of a host population will often result in the isolation of the parasite population and their subsequent speciation. Sorting events occur when parasite species are entirely removed from host species. Host switching events occur when a parasite species colonises a host species other than its current host. Intrahost speciation occur when a parasite lineage diverges without the stimulus of host speciation and results in multiple closely related species on the descendant host lineage. There is also a fifth kind of event which simply is the absence of the other events. Parasite ‘inertia’ will result in the same species of parasite being present on several descendant hosts (Fig. 1e). Parasite inertia implies that although the hosts are isolated from other host populations, the parasite populations on the hosts are not. Here we will argue that increasing attention should be paid to the biological likelihood of sorting events. We will demonstrate that sorting events do occur and that they are not an artefact of small sample sizes.

Several methods have been developed to make inferences about coevolutionary history using various combinations of the above coevolutionary events (see Paterson and Gray, 1997, for a review). Early methods simply compared host and parasite trees or classifications by eye to assess their congruence, and thus infer cospeciation.

Brooks (1981) termed this a narrative approach. More recently, the extent of cospeciation in host-parasite systems has been examined quantitatively using Brooks parsimony analysis (Brooks, 1981) and reconciliation analysis. Page (1990a, 1990b, 1993, 1994, 1996) has developed a method that reconstructs cospeciation, intrahost speciation, sorting and suspected host switching events from phylogenetic trees of parasites and their hosts. This method, termed reconciliation analysis, postulates the minimal numbers of intrahost speciation and sorting events needed to reconcile incongruent host and parasite trees without postulating host switching. TreeMap (Page, 1994) is a modification to reconciliation analysis that allows host switching to be addressed in a systematic manner.

TreeMap is an important advance in the cospeciation field. This method uses a host tree (Fig 2a) and a, usually incongruent, parasite tree (Fig 2b) together with the parasite distribution (Fig 2a) to make specific predictions about how these groups have coevolved. There are many scenarios which would reconcile the host and parasite trees given various combinations of the different coevolving events. Early reconciliation analyses (eg Paterson et al, 1993) used the assumption that no host switching had occurred (Fig 2c) while TreeMap now examines all possible combinations with a view to maximising cospeciation events (Fig 2d-e). Resource tracking models generally assume that parasite species are free to host switch to available host taxa (Fig 2e). More recently the program Jungle (see Page and Charleston, 1998) has allowed the differential weighting of all events.

If all coevolutionary events are accorded equal likelihood or weighting then it could be argued that those scenarios that postulate fewer events are more parsimonious.

This would imply that the Figures 2e and 2f are more parsimonious than figures 2c and 2d. It is clear, however, that the different events are not equally likely but, rather, relate directly to parasite ecology. For example, fleas are highly mobile and we would expect host switching to occur more often than cospeciation. The only precise method to use in order to discriminate between the various scenarios are molecular data that are evolving in a clock-like fashion (Hafner and Page, 1995; Page et al., 1998; Paterson et al, 2000). For example, the louse genus *Saedmundssonina* is found on the charadriiform (gulls) and procellariiform (petrels) bird orders but not on the closely related sphenisciforms (penguins) and pelecaniforms (cormorants). There are two scenarios to test (Fig 3). The first scenario postulates that *Saedmundssonina* colonised the petrels from the gulls and the second scenario postulates that the penguins and the cormorants have lost the genus. These two scenarios imply different levels of genetic divergence between the two *Saedmundssonina* lineages. If the genus has host switched from the gulls to the petrels then the genetic divergence between them will be less than between that of their hosts. If *Saedmundssonina* has been passed down through the host lineages then the level of divergence between the louse lineages will be at least as great as their hosts. Paterson et al. (2000) showed that the level of genetic divergence between the lice (corrected  $d = 0.45$ ) was considerably greater than that of their hosts ( $d = 0.22$ ) which supported the scenario of descent. The same arguments are made for testing cospeciation events (host and parasite relative genetic distances should be similar) and duplication events (parasite relative genetic distances should be at least as large as their hosts).

Sorting events, however, cannot be directly tested. How can one test for a lineage that is not there? There is nothing that can be sequenced. This is doubly unfortunate

as there are often high numbers of sorting events predicted relative to other coevolutionary events in reconciliation analyses. For example, Paterson et al. (2000) in their analysis of seabird and chewing louse cospeciation found 11 sorting events (Fig 4; relative to seven cospeciation events) and Paterson and Poulin (1999), in their analysis of parasitic copepods and teleost fish, found 9 sorting events (Fig. 5; relative to three cospeciation events).

A further complication is that there are three processes that produce the pattern of absence of parasites from their hosts (Fig. 1b). First, parasites may occur in low numbers on the extant host population but have escaped detection by sampling error (Fig. 1b: S1; X-event). Note that sampling error only generates false absence of parasites from hosts and is, therefore, only a pseudosorting event. Second, parasites may have gone extinct from a host lineage after a host speciation event (Fig. 1b: S3; extinction or “drowning on arrival [DOA]”). Third, parasites may have been absent from the host founder population at a speciation event because of the patchy distribution of a parasite throughout the range of the host or some other stochastic event (Fig. 1b: S2; “missed the boat” – [MTB], Paterson and Gray, 1997; Paterson et al., 1999).

To test the idea that sorting events are common in parasite-host coevolution we added to the data obtained by Paterson et al. (1999) and analysed Australasian bird-louse distributions where we could clearly identify a parent-daughter relationship between bird taxa (i.e., a taxon that was clearly derived from another taxon). We divided the records into three groups: human-introduced bird taxa (introduced), bird taxa with a history of repeatedly colonising an island (cosmopolitan) and closely

related taxa (such as regional subspecies). Australasia is well placed for such a study as it is relatively isolated, has an unfortunate history of successful human introductions of bird species, and has many offshore islands which have led to host differentiation.

We predicted that there would be a reduction in the louse species present on the daughter taxon relative to the parent taxon. A summary of the data is given in Table 1. A further purpose of this study was to extend that of Paterson et al. (1999) by examining the likelihood of x-events.

Sixty five bird taxa were identified as having a parent-daughter connection (Appendix 1 and Paterson et al. 1999) and of these 47 showed a reduction in louse species number. This reduction was significant (one-tailed binomial test, binomial probability = 0.5:  $P = 0.0002$ ). When partitioned into the three categories, both the introduced and closely-related taxa showed a significant reduction in louse species number ( $P < 0.0001$  and  $P = 0.0178$ , respectively), whereas the cosmopolitan species showed no significant decrease ( $P = 0.945$ ). These results are reflected in the mean decrease in louse species number from parent to daughter taxa (overall :  $1.5 \pm 1.7$  species; introduced :  $2.5 \pm 2.0$ ; closely related taxa :  $0.9 \pm 0.9$ ; cosmopolitan :  $0.3 \pm 0.5$ ).

A major issue with the interpretation of these data is the degree to which apparent sorting events are really a result of poor sampling effort (x-events). X-events will be of importance if the daughter taxon is usually sampled less well relative to the parent taxon. Is this something that we might expect in our australasian data set? Many of the daughter taxa in this study are found on small oceanic islands that are relatively inaccessible, eg Kermadec storm petrel, Bounty Island shag, Antipodes pipit, while



their parent taxa are found on the mainland, eg white-faced storm petrel, Stewart Island shag and New Zealand pipit respectively. Sampling of remote species is often a matter of brief collecting trips or occasional beach-cast specimens. Introduced taxa may be insufficiently sampled for a quite different reason as their ubiquitousness and low priority for research result in them being little studied. An additional problem is that we are only interested in positive hosts, hosts that actually have lice when sampled, because we are not interested in how the lice are distributed but rather if the species are simply present. We may sample 100 individuals from a species and find that only one host has lice. In this situation there would be a positive host sample size of one.

In order to determine whether x-events were a problem in our data we examined louse species collected from 136 New Zealand bird taxa that are held in the Museum of New Zealand Te Papa Tongarewa collection. We collected data on the number of positive individuals sampled for each host taxon and the number of louse species found on that host taxon (Appendix 2). If x-events are common in our data we would expect to see a strong positive relationship between louse species number and host sample size, that is that the more hosts searched, the greater the chance of finding louse species that are present on a host taxon. A linear regression of the data showed that there was significant positive relationship ( $P = 0.001$ ) but that it explained very little of the variation observed ( $r^2 = 0.078$ , Fig 6). It is likely that much of this signal is generated by those host taxa with only a few individuals sampled. This was confirmed by cumulatively excluding hosts by sample size and repeating the regression, eg excluding those hosts that had only been sampled once, then those that had only been sampled once or twice and so on. This analysis (Fig 7) showed that hosts that had

more than five individuals sampled, and certainly hosts that had more than seven samples, no longer showed a significant relationship between sample effort and finding louse species. What does this say about x-events in our data? Most of our samples have greater than four samples and even for those that may have had less, there is only a small chance that a louse species will be missed.

In order to examine the generality of our finding we analysed a data set of louse presence on host species collected by one of us (RLP) in the Galapagos islands in 1992. Forty seven of the island group's 58 bird species were examined and numbers of hosts sampled, positive hosts and louse species found were recorded (Appendix 3). A linear regression of positive host versus louse species number showed no significant relationship ( $P = 0.915$ ,  $r^2 < 0.001$ , Fig 8). Sampling more hosts did not equate to finding more louse species. This result agrees with the New Zealand data by showing that x-events are unlikely to be common explanations for sorting events. It appears that, in general, our identified sorting events are likely to be real. This should not be a surprise given that the distribution of parasites is patchy (Rekasi et al., 1997), and the size of host populations in speciation events are small (e.g., a small founder population).

Given that the majority of sorting events identified in our data are real, is it possible to determine which of MTB or DOA plays a greater role? The two types of sorting events predict very different affects of founding events on parasite diversity. The most important factor for DOA in reducing parasite diversity, eg louse species extinction, is time since a founding event as the likelihood of a species going extinct will increase with time. The most important factor for MTB in reducing parasite diversity is the

founding event itself. The likelihood of a species going extinct will not increase with time. On examining the louse species reduction data, the human-introduced data should provide a good test. These species have been through the greatest bottleneck event (most populations were established from only a few to a hundred individuals) but have had only about a hundred years since founding. We would predict under a DOA scenario that there will have been few sorting events in this time whereas a MTB scenario would predict large numbers of sorting events. Human-introduced hosts lost 2.4 louse species per event, whereas closely related host species, which probably better reflects the usual situation, lost about one louse species per founding event. This seems to support the idea that MTB events are important determinants of louse species diversity in daughter host taxa.

Is it possible to generalise from the louse and bird species of Australasia and the Galapagos to louse and birds (or even parasites and hosts) in general? Sorting events may be much more frequent in these areas due to high levels of isolation between islands. These conditions make the opportunities for continuing contact between founding and parent populations rare. In a continental area it may be more difficult to achieve these levels of isolation. Individuals may periodically continue to arrive in the founding population, sometimes carrying louse species that were lost after the initial founding. The cosmopolitan species that we see in the Australasian data set may illustrate this point. These species showed virtually no reduction in louse species diversity. Cosmopolitan bird species appear to have the ability to repeatedly colonise isolated island groups, that is individuals periodically arrive carrying louse species that have been lost from the founding population. A future test of this idea would be in

examining a continental bird-lice fauna in the same detail as we have done here. We would predict much lower levels of sorting events.

A further impediment to generalising further to other parasite taxa may be that lice are ideally suited to experiencing sorting events. The distribution of lice is patchy. Fowler and Price (1987) found that the distribution of the louse *Philoceanus robertsi* over a population of Wilson's Storm Petrel (*Oceanites oceanicus*) was shown to fit a negative binomial curve. This agrees with our own and other observations about the patchiness of lice on birds. Given a patchy distribution of lice on their host species then a large founding group of hosts would be required before it was likely that all louse species were present in the new population. The numbers of hosts needed to qualify as a 'large' founding group will vary with such host traits as body mass (Rozsa, 1997: larger body masses carry more lice) and coloniality (Rekasi et al., 1997: territorial species show greater variation in louse distributions). It may be that other parasite species with different life histories would be less susceptible to sorting events.

Reconciliation approaches to measuring host-parasite coevolution typically infer many sorting events. We believe that, far from representing a problem with the reconciliation approach or worldview, this reflects a more realistic view of the relative probabilities of the processes involved in host-parasite coevolution. Sorting events have the potential to be very informative about the historical ecological processes that have occurred in a particular host-parasite relationship. Most importantly, these studies will go beyond the mere chronicling of coevolutionary patterns to the testing of hypotheses about the origin of these patterns. There are several directions in which future studies of sorting events might move. First, such studies may examine whether

parasite population structure underlies the likelihood of sorting events, e.g. is population distribution more uniform on hosts with fewer sorting events? Second, it may be determined whether ecological and life history parameters of both host and parasite reflect the likelihood of sorting events occurring, e.g. are sorting events related to the number of niches present on the host? Third, studies may address the hypothesis that hosts are islands, e.g. are sorting events determined by island biogeographical theory? Fourth, and most definitely not finally, studies may reveal how real the distinction between the two forms of sorting events (MTB and DOA) is and whether it is useful to have this distinction? We look forward to sorting out these and other questions.

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Table 1. Australasian examples of parent-daughter host taxa and the status of their louse species. Same = no change in louse species composition, reduced = fewer louse species on the daughter bird taxon relative to its parent taxon.

	Human introduced	Cosmopolitan	Closely related
Same	3	7	8
Reduced	24	3	20

Figure 1. The five different types of coevolutionary events inferred in reconciliation analysis. Each figure shows a phylogeny of three host taxa (shaded line) with a parasite lineage (line) mapped upon it. (a) Cospeciation events ('C'): the parasite taxa speciate or co-diverge at the same point as their host. (b) Sorting events ('S'): parasite taxa are lost from their host lineage. There are three types of sorting events: S1 – the parasite taxa are present but have not been detected (x-events); S2 – the parasite taxa were not present on the founding host population (MTB – 'missing the boat'); S3 – the parasite taxa have gone extinct on a host lineage (DOA – 'drowning on arrival'). (c) Host switching events ('H'): a parasite taxon has colonised the host taxon from a different host lineage and then successively colonised the host's close relatives. (d) Duplication event ('D'): the parasite taxon has speciated on a host without an accompanying host speciation event and has produced multiple parasite lineages on the host's descendants. (e) Inertia ('I'): the absence of the other events where the parasite taxon does not speciate resulting in the same species being present on multiple hosts.

Figure 2. (a) The phylogeny for a group of hosts A-D and the distribution of the parasites 1-4 over these hosts. (b) The phylogeny for the parasites 1-4. Reconciliation analysis provides many different scenarios for reconciling these trees. (c) This reconciliation assumes no host switching. The lines of different widths refer to the two different lineages descending from the duplication event. (d) This reconciliation allows one host switching event. Note that the host switching event makes a prediction that the host clade (C,D) is older than the host clade (A,B). (e) This reconciliation allows two host switching events. (f) This reconciliation only allows host switching events.

Figure 3. Two possible scenarios (or reconciliations) for explaining the presence of *Saedmundssonina* lice on gulls and petrels and its absence from penguins and cormorants. (a) *Saedmundssonina* has colonised the petrels from the gulls. (b) *Saedmundssonina* has passed down the lineage from a common ancestor of gulls and petrels. The hypothesised louse phylogeny (dark lines) are mapped onto the known host phylogeny (shaded line).

Figure 4. A reconciliation tree for the coevolution of seabirds and chewing lice (after Paterson et al. 2000 Fig. 5b). The louse phylogeny (italicised taxon names and dark lines – the varying width of lines reflects lineages derived from duplication events) are mapped onto the known host phylogeny (bold names and shaded line). This reconciliation hypothesises 11 sorting, 9 cospeciation, 1 host switching and 3 duplication events.

Figure 5. A reconciliation tree for the coevolution of teleost fish and *Chondracanthus* parasitic copepods (after Paterson and Poulin, 1999 Fig. 2f). The copepod phylogeny (dark lines – the varying width of lines reflects lineages derived from duplication events) are mapped onto the known host phylogeny (bold taxon names and shaded line). This reconciliation hypothesises 9 sorting, 3 cospeciation, 1 host switching, 2 inertia and 3 duplication events.

Figure 6. The positive relationship ( $P = 0.001$ ,  $r^2 = 0.078$ ) between host sample size and numbers of louse species found for 136 New Zealand bird taxa.

Figure 7. The effect of cumulatively excluding host taxa by sample size on the significance of the relationship between host sample size and louse species number for 136 New Zealand bird taxa. There is a significant positive relationship from host species that have been sampled for lice from 1, 2 or 3 individuals. There is no significant relationship after hosts with more than three individuals samples are included. The host species sample size remaining is shown next to each bar.

Figure 8. The nonsignificant relationship ( $P = 0.915$ ,  $r^2 < 0.001$ ) between host sample size and numbers of louse species found for 47 Galapagos Islands bird taxa.

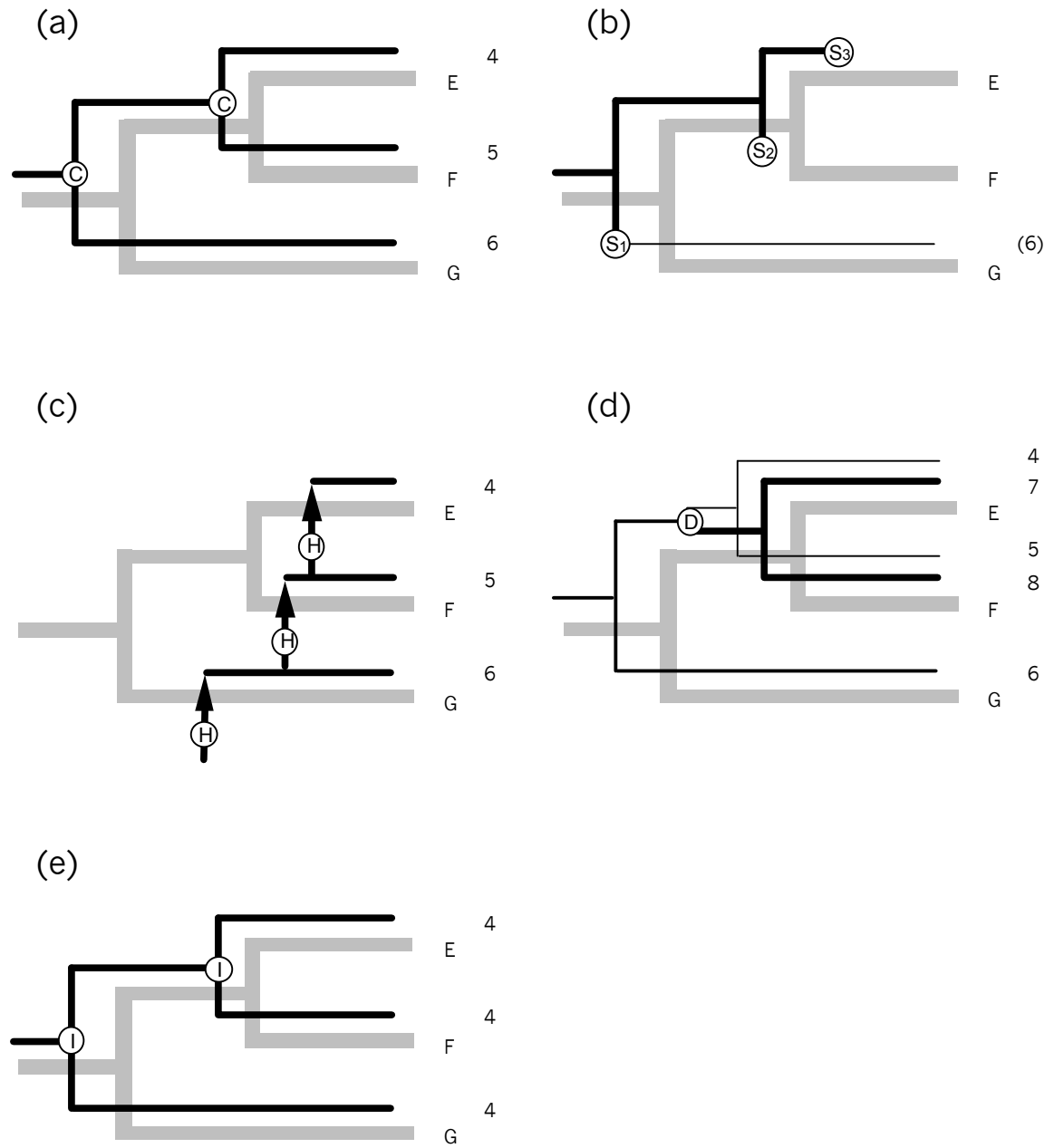


Fig. 1

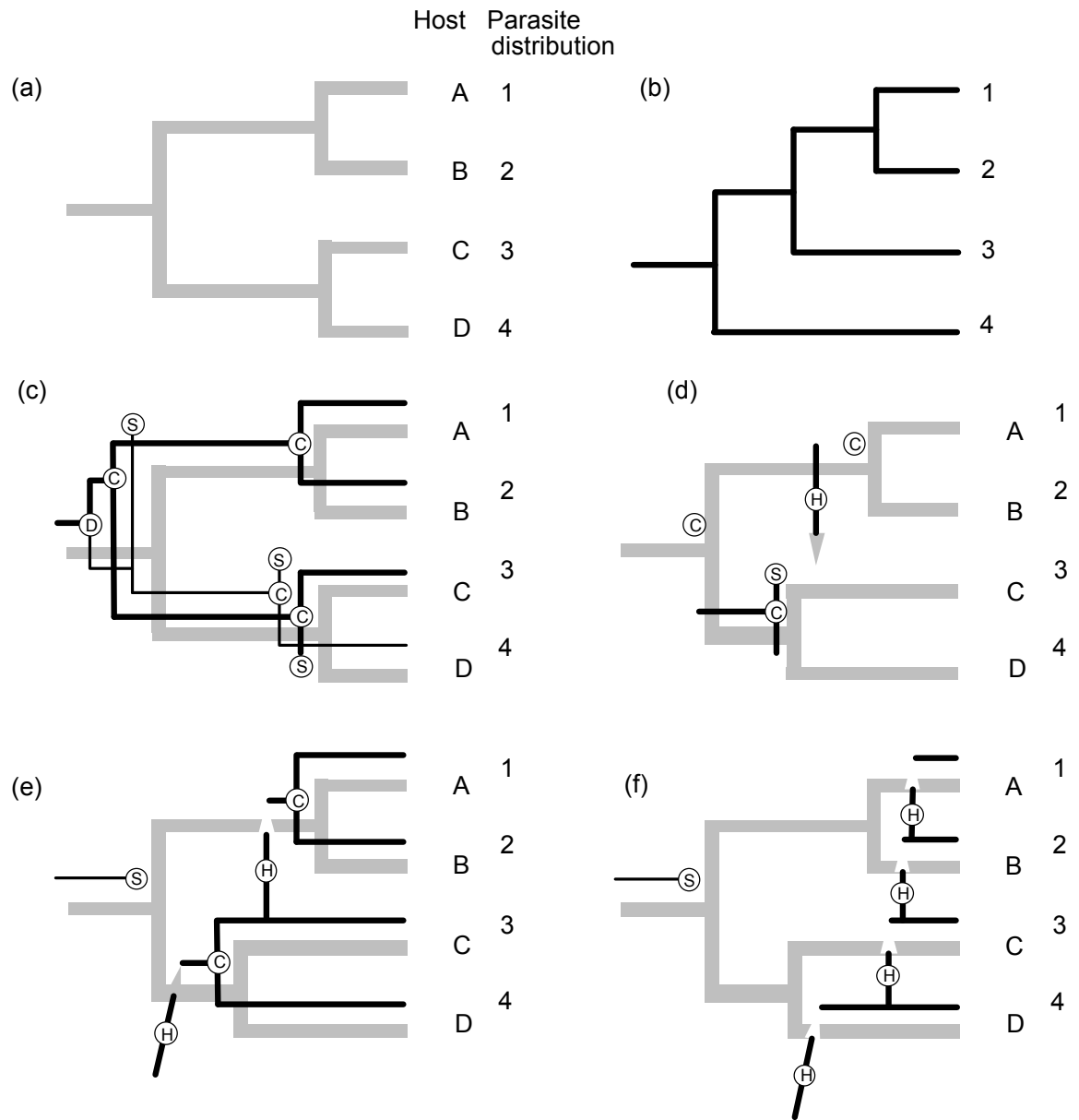


Fig. 2

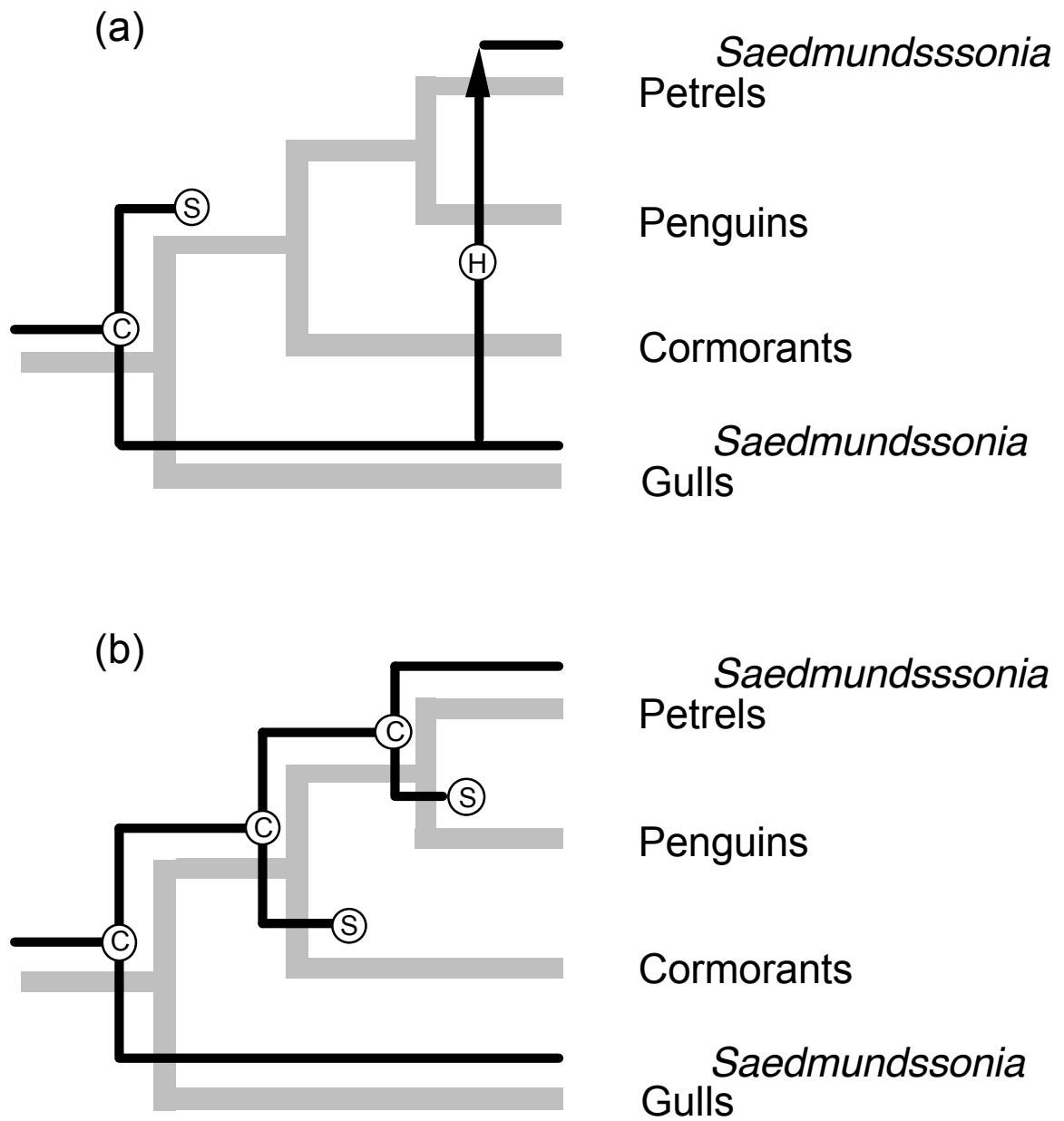
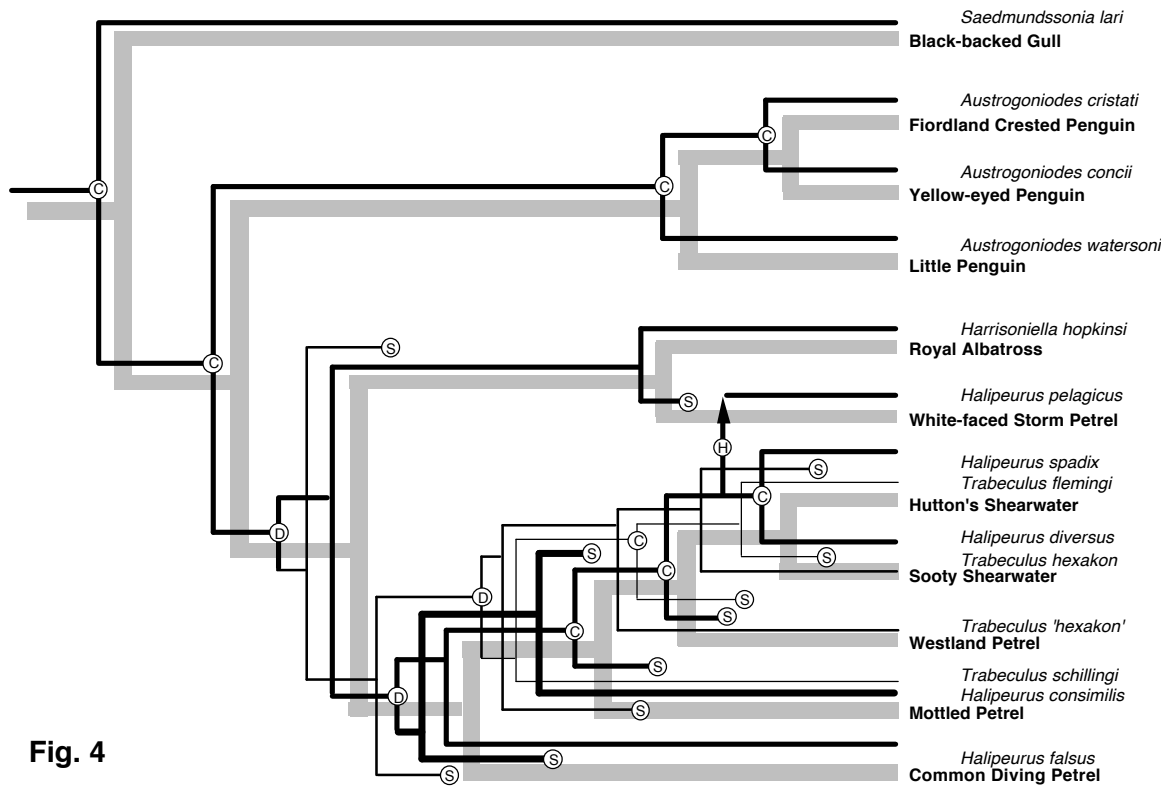


Fig. 3



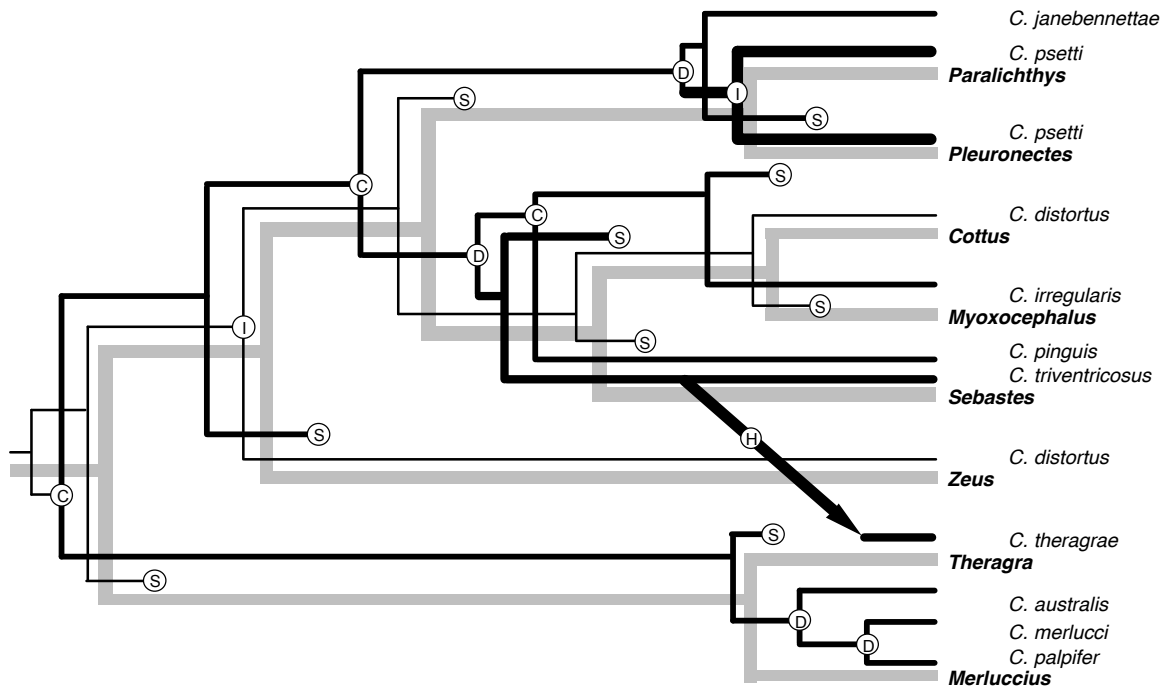


Fig. 5

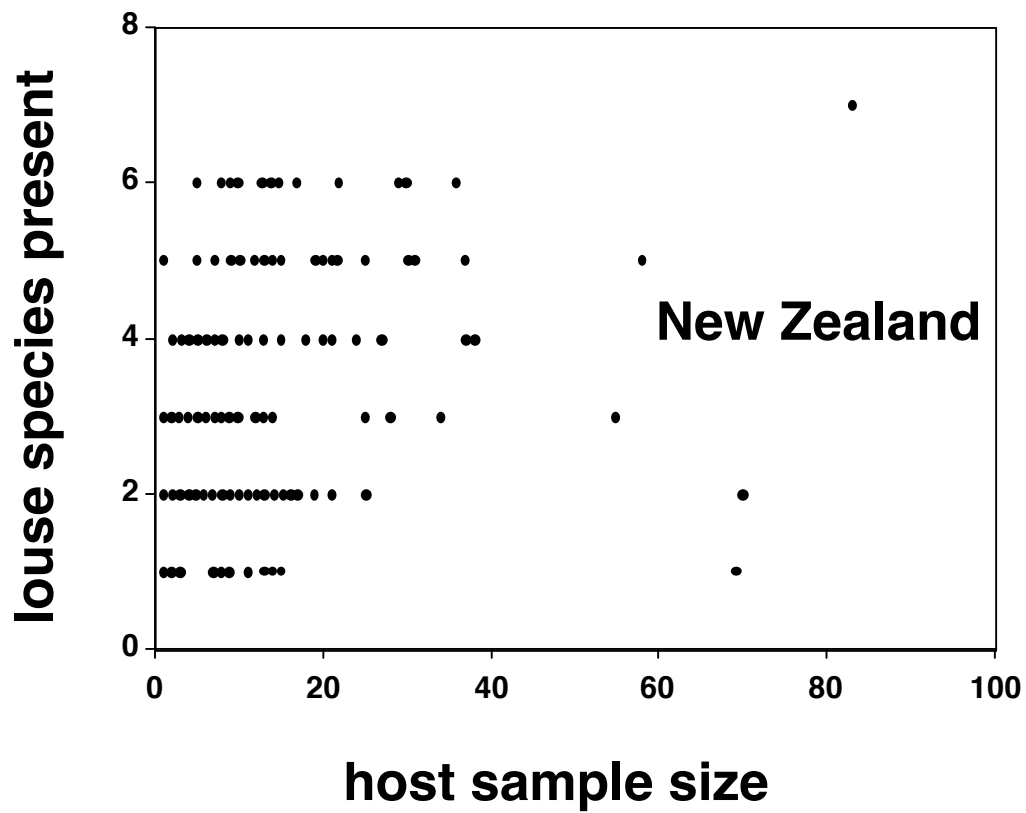


Fig. 6



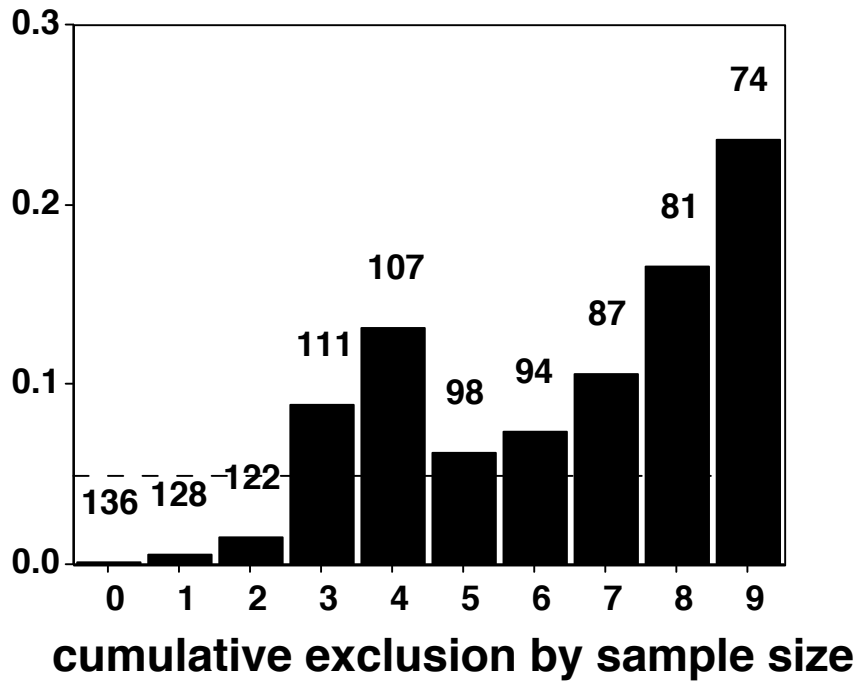


Fig. 7

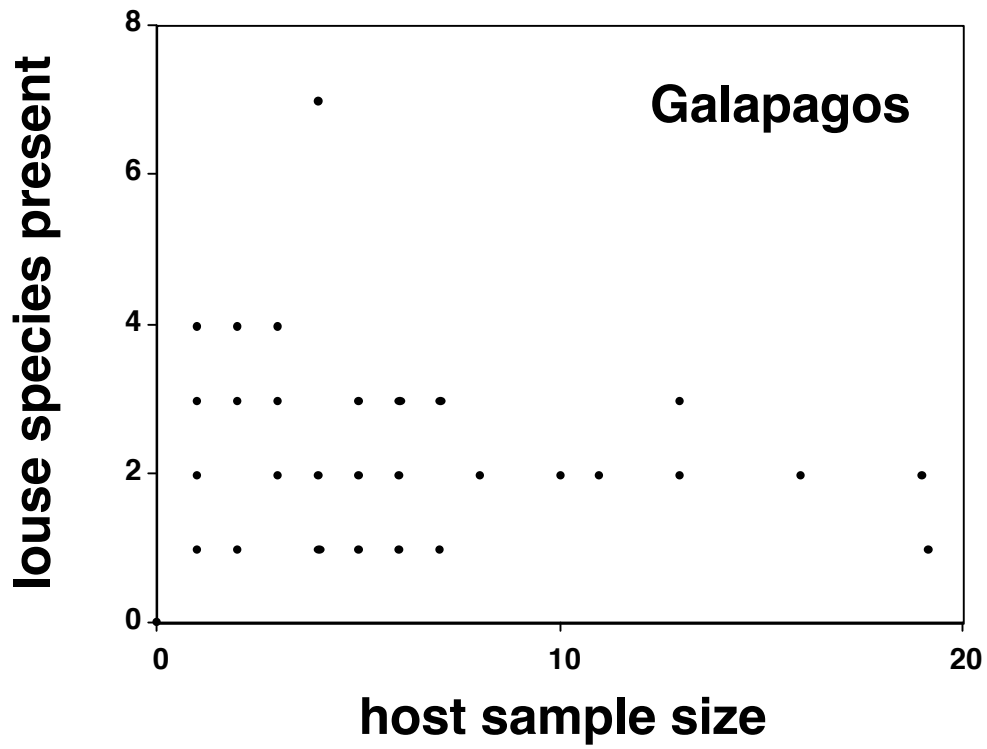


Fig. 8

Appendix 1. Louse records for 17 Australian bird parent-daughter taxa (after Palma and Barker, 1996).

Parent taxa	Daughter taxa
<b>Human introduced</b>	
Mute Swan ( <i>Cygnus olor</i> Gmelin, 1789)	
<i>Anatoecus icterodes oloris</i> Zlotorzycza, 1970	<i>Anatoecus icterodes oloris</i>
	<i>Anatoecus dentatus magnicornutus</i> Zlotorzycza, 1970
<i>Anatoecus penicillatus</i> Keler, 1960	
<i>Ciconiphilus cygni</i> Price & Beer, 1965	
<i>Ornithobius bucephalus</i> (Giebel, 1874)	<i>Ornithobius bucephalus</i>
<i>Trinoton anserinum cygni</i> Eichler, 1943	
Mallard Duck ( <i>Anas platyrhynchos platyrhynchos</i> Linnaeus, 1758)	
<i>Anaticola crassicornis</i> (Scopoli, 1763)	<i>Anaticola crassicornis</i>
<i>Anatoecus dentatus</i> (Scopoli, 1763)	<i>Anatoecus dentatus</i>
<i>Anatoecus icterodes</i> (Nitzsch, 1818)	<i>Anatoecus icterodes</i>
<i>Holomenopon leucoanthum</i> (Burmeister, 1838)	<i>Holomenopon leucoanthum</i>
<i>Holomenopon maxbeieri</i> Eichler, 1954	
<i>Trinoton querquedulae</i> (Linnaeus, 1758)	<i>Trinoton querquedulae</i>
Ring-necked Pheasant ( <i>Phasianus colchicus</i> Linnaeus, 1758)	
<i>Amyrsidea perdicis</i> (Denny, 1842)	
<i>Goniocotes chrysocephalus</i> Giebel, 1874	
<i>Goniodes colchici</i> Denny, 1842	<i>Goniodes colchici</i>
<i>Lagopoecus colchicus</i> Emerson, 1949	
<i>Lipeurus maculosus maculosus</i> Clay, 1938	
<i>Menacanthus phasiani</i> (Modrzejewska & Zlotorzycza, 1977)	
<i>Oxylipeurus mesopelios colchicus</i> Clay, 1938	
	<i>Lipeurus caponis</i> (Linnaeus, 1758)
Peafowl ( <i>Pavo cristatus</i> Linnaeus, 1758)	
<i>Amyrsidea minuta</i> Emerson, 1961	<i>Amyrsidea minuta</i>
<i>Amyrsidea phaeostoma</i> (Nitzsch (in Giebel), 1866)	
<i>Colpocephalum tausi</i> (Ansari, 1951)	
<i>Goniocotes parviceps</i> (Piaget, 1880)	
<i>Goniocotes rectangulatus</i> Nitzsch (in Giebel), 1866	
<i>Goniocotes mayuri</i> Lakshminarayana & Emerson, 1971	
<i>Goniodes meinertzhageni</i> Clay, 1940	
<i>Goniodes pavonis</i> (Linnaeus, 1778)	<i>Goniodes pavonis</i>
<i>Lipeurus pavo</i> Clay, 1938	
Wild Turkey ( <i>Meleagris gallopavo</i> Gray, 1843)	
<i>Chelopistes meleagridis</i> (Linnaeus, 1758)	<i>Chelopistes meleagridis</i>

<i>Menacanthus stramineus</i> (Nitzsch, 1818)	<i>Menacanthus stramineus</i>
<i>Oxylipeurus corpulentus</i> Clay, 1938	
<i>Oxylipeurus polytrapezius polytrapezius</i> (Burmeister, 1838)	<i>Oxylipeurus polytrapezius</i> <i>polytrapezius</i>
Rock Pigeon ( <i>Columba livia</i> Gmelin, 1789)	
<i>Bonomiella columbae</i> Emerson, 1957	
<i>Campanulotes bidentatus compar</i> (Burmeister, 1838)	<i>Campanulotes bidentatus compar</i>
<i>Coloceras aegypticum</i> (Kellogg & Paine, 1911)	
	<i>Coloceras damicorne</i> (Nitzsch, 1866)
<i>Colpocephalum turbinatum</i> Denny, 1842	<i>Colpocephalum turbinatum</i>
<i>Columbicola columbae columbae</i> (Linnaeus, 1758)	<i>Columbicola columbae columbae</i>
<i>Hohorstiella lata</i> (Piaget, 1880)	<i>Hohorstiella lata</i>
Song Thrush ( <i>Turdus philomelos</i> Brehm, 1831)	
<i>Brueelia merulensis</i> (Denny, 1842)	
<i>Brueelia turdinulae</i> Ansari, 1956	
<i>Menacanthus eurysternus</i> (Burmeister, 1838)	
<i>Myrsidea iliaci</i> Eichler, 1951	
<i>Philopterus turdi</i> (Denny, 1842)	<i>Philopterus turdi</i>
<i>Ricinus elongatus</i> (Olfers, 1816)	
<i>Sturnidoecus melodicus</i> Eichler, 1951	
Common Blackbird ( <i>Turdus merula</i> Linnaeus, 1758)	
<i>Brueelia amsel</i> (Eichler, 1951)	
<i>Brueelia merulensis</i> (Denny, 1842)	
<i>Brueelia oudhensis</i> Ansari, 1956	
<i>Menacanthus eurysternus</i> (Burmeister, 1838)	<i>Menacanthus eurysternus</i>
<i>Myrsidea thoracica</i> (Giebel, 1874)	
<i>Philopterus turdi</i> (Denny, 1842)	<i>Philopterus turdi</i>
<i>Ricinus elongatus</i> (Olfers, 1816)	
European Starling ( <i>Sturnus vulgaris</i> (Linnaeus, 1758))	
<i>Brueelia nebulosa</i> (Burmeister, 1838)	<i>Brueelia nebulosa</i>
<i>Menacanthus eurysternus</i> (Burmeister, 1838)	<i>Menacanthus eurysternus</i>
<i>Myrsidea cucullaris</i> (Nitzsch, 1818)	
<i>Sturnidoecus sturni</i> (Schrank, 1776)	<i>Sturnidoecus sturni</i>

### Closely related

Little Penguin ( <i>Eudyptula minor minor</i> (Forster, 1781))	Fairy Penguin ( <i>Eudyptula minor novaehollandiae</i> (Stephens, 1826))
<i>Austrogoniodes waterstoni</i> (Cummings, 1914)	<i>Austrogoniodes waterstoni</i>
Brown Quail ( <i>Synoicus ypsilophorus ypsilophorus</i> Bosc, 1792)	Brown Quail ( <i>Synoicus ypsilophorus australis</i> (Latham, 1801))
<i>Cuclotogaster synoicus</i> (Clay, 1938)	<i>Cuclotogaster synoicus</i>
<i>Goniodes retractus</i> Le Souef, 1902	<i>Goniodes retractus</i>

Australian Bush-Turkey ( <i>Alectura lathami lathami</i> Gray, 1831)	( <i>Alectura lathami purpureicollis</i> Le Souf, 1898))
<i>Colpocephalum alecturae</i> Price and Beer, 1964	<i>Colpocephalum alecturae</i>
<i>Colpocephalum lathami</i> Price and Beer, 1964	<i>Colpocephalum lathami</i>
<i>Goniodes fissus</i> (Rudow, 1869)	<i>Goniodes fissus</i>
<i>Oxylipeurus ischnocephalus</i> (Taschenberg, 1882)	<i>Oxylipeurus ischnocephalus</i>
Scrub Fowl ( <i>Megapodius reinwardt tumulus</i> ( <i>Megapodius reinwardt yorki</i> Mathews, 1929) Gould, 1842)	
<i>Goniodes biordinatus</i> Clay, 1940	
<i>Goniodes minor</i> (Piaget, 1880)	<i>Goniodes minor</i>
<i>Lipeurus sinuatus</i> Taschenberg, 1882	<i>Lipeurus sinuatus</i>
Brown Goshawk ( <i>Accipiter fasciatus fasciatus</i> (Vigors & Horsfield, 1827))	
<i>Degeeriella fulva</i> (Giebel, 1874)	
<i>Degeeriella fusca</i> (Denny, 1842)	<i>Degeeriella fusca</i>
Brown Goshawk ( <i>Accipiter fasciatus fasciatus</i> (Vigors & Horsfield, 1827))	
<i>Degeeriella fulva</i> (Giebel, 1874)	
<i>Degeeriella fusca</i> (Denny, 1842)	<i>Degeeriella fusca</i>
Purple Swamp Hen ( <i>Porphyrio porphyrio melanotus</i> Temminck, 1820)	
<i>Pseudomenopon concretum</i> (Piaget, 1880)	<i>Pseudomenopon concretum</i>
<i>Rallicola lugens</i> (Giebel, 1874)	<i>Rallicola lugens</i>
Common Bronzewing ( <i>Phaps chalcoptera</i> (Latham, 1790))	
<i>Campanulotes flavus flavus</i> (Rudow, 1863)	Tasmanian population
<i>Coloceras grande</i> Tendeiro, 1973	
<i>Columbicola angustus</i> (Rudow, 1869)	
	<i>Columbicola tasmaniensis</i> Tendeiro, 1967
<i>Physconelloides strangeri</i> Tendeiro, 1980	
	<i>Physconelloides australiensis</i> Tendeiro, 1969

## Appendix 2. New Zealand bird taxa sampled for louse species listed by order.

Host species name	Host individuals sampled	Louse species found
<b>Sphenisciformes</b>		
<i>Eudyptes chrysocome chrysocome</i>	13	3
<i>Eudyptes chrysocome filholi</i>	5	3
<i>Eudyptes pachyrhynchus</i>	9	2
<i>Eudyptes robustus</i>	19	2
<i>Eudyptes sclateri</i>	7	3
<i>Eudyptula minor</i>	69	1
<i>Megadyptes antipodes</i>	6	2
<b>Podicipediformes</b>		
<i>Podiceps cristatus</i>	2	1
<i>Podiceps rufopectus</i>	1	1
<b>Procellariiformes</b>		
<i>Daption capense</i>	38	4
<i>Diomedea bulleri</i>	30	6
<i>Diomedea cauta cauta</i>	22	6
<i>Diomedea cauta eremita</i>	9	5
<i>Diomedea cauta salvani</i>	14	6
<i>Diomedea chrysostoma</i>	10	6
<i>Diomedea epomophora epomophora</i>	29	6
<i>Diomedea epomophora sandfordi</i>	13	6
<i>Diomedea exulans</i>	31	5
<i>Diomedea melanophris</i>	9	6
<i>Fregretta tropica</i>	5	4
<i>Fulmaris glacialisoides</i>	15	4
<i>Garrodia nereis</i>	12	2
<i>Halobaena caerulea</i>	14	5
<i>Lugensa brevirostris</i>	19	5
<i>Macronectes giganteus</i>	30	6
<i>Macronectes halli</i>	10	5
<i>Oceanites oceanicus</i>	1	1
<i>Pachyptila belcheri</i>	20	5
<i>Pachyptila crassirostris</i>	15	4
<i>Pachyptila desolata</i>	13	5
<i>Pachyptila salvini</i>	22	5
<i>Pachyptila turtur</i>	58	5
<i>Pachyptila vittata</i>	37	5
<i>Pagodroma nivea</i>	3	2
<i>Pelagodroma marina</i>	24	4
<i>Pelecanoides urinatrix</i>	55	3
<i>Phoebetria palpebrata</i>	7	5
<i>Procellaria aequinoctialis</i>	10	4
<i>Procellaria cinerea</i>	5	4
<i>Procellaria parkinsoni</i>	13	4

<i>Procellaria westlandica</i>	27	4
<i>Pterodroma auxillaris</i>	3	2
<i>Pterodroma cookii</i>	15	6
<i>Pterodroma externa</i>	10	3
<i>Pterodroma inexpectata</i>	36	6
<i>Pterodroma leucoptera</i>	4	4
<i>Pterodroma longirostris</i>	5	5
<i>Pterodroma macroptera</i>	22	6
<i>Pterodroma magentae</i>	17	6
<i>Pterodroma mollis</i>	12	5
<i>Pterodroma neglecta</i>	6	4
<i>Pterodroma nigripennis</i>	18	4
<i>Pterodroma pycrofti</i>	6	4
<i>Puffinus assimilis elegans</i>	6	3
<i>Puffinus assimilis haurakiensis</i>	3	4
<i>Puffinus assimilis kermadecensis</i>	11	4
<i>Puffinus bulleri</i>	10	4
<i>Puffinus carneipes</i>	5	6
<i>Puffinus gavia</i>	10	3
<i>Puffinus griseus</i>	37	4
<i>Puffinus huttoni</i>	25	5
<i>Puffinus pacificus</i>	8	6
<i>Puffinus tenuirostris</i>	8	4
<i>Thalassoica antarctica</i>	7	4
Pelecaniformes		
<i>Leucocarbo campbelli campbelli</i>	3	1
<i>Leucocarbo campbelli ranfurlyi</i>	2	1
<i>Leucocarbo carunculatus chalconotus</i>	5	2
<i>Leucocarbo carunculatus onslowi</i>	3	1
<i>Pelecanus conspicillatus</i>	1	2
<i>Phalacrocorax melanoleucos brevirostris</i>	13	2
<i>Phalacrocorax sulcirostris</i>	4	2
<i>Phalacrocorax carbo novaehollandiae</i>	10	2
<i>Phalacrocorax varius varius</i>	8	2
<i>Stictocarbo punctatus</i>	25	2
<i>Sula bassana serrator</i>	70	2
<i>Sula dactylatra personata</i>	4	2
Ciconiiformes		
<i>Ardea novaehollandiae</i>	11	2
<i>Botaurus stellari</i>	15	2
<i>Egretta alba</i>	11	2
Anseriformes		
<i>Anas platyrhynchos</i>	30	5
<i>Anas rhynchotis</i>	3	4
<i>Anas superciliosa</i>	21	4
<i>Branta canadensis</i>	20	5

<i>Cygnus atratus</i>	83	7	
<i>Cygnus olor</i>	3	2	
<i>Tadorna variegata</i>	12	5	
Falconiformes			
<i>Circus approximans</i>	34	3	
<i>Falco cenchroides</i>	1	3	
<i>Falco novaeseelandiae</i>	7	2	
Galliformes			
<i>Alectoris chukar</i>	8	3	
<i>Meleagris gallopavo</i>	4	3	
<i>Pavo cristatus</i>	5	3	
<i>Perdix perdix</i>	1	2	
<i>Phasianus colchicus</i>	5	6	
<i>Synoicus ypsilophorus</i>	2	2	
Gruiformes			
<i>Gallirallus australis australis</i>	16	2	
<i>Gallirallus australis scotti</i>	11	1	
<i>Porphyrio mantelli</i>	13	1	
<i>Porphyrio porphyrio</i>	15	2	
Charadriiformes			
<i>Anarhynchus frontalis</i>	8	1	
<i>Calidris canutus</i>	5	5	
<i>Charadrius bicinctus bicinctus</i>		2	2
<i>Charadrius bicinctus exilis</i>	2	2	
<i>Charadrius obscurus</i>	28	3	
<i>Coenocorypha aucklandica</i>	9	2	
<i>Haematopus chathamensis</i>	14	2	
<i>Haematopus ostralegus</i>	20	4	
<i>Haematopus unicolor</i>	5	4	
<i>Himantopus himantopus leucocephalus</i>	7	4	
<i>Himantopus novaezealandiae</i>	3	2	
<i>Limosa lapponica</i>	13	5	
<i>Limosa limosa</i>	1	5	
<i>Pluvialis fulva</i>	3	3	
<i>Vanellus miles novaehollandiae</i>	9	3	
Columbiformes			
<i>Columba livia</i>	15	5	
<i>Hemiphaga novaeseelandiae</i>	21	2	
Psittaciformes			
<i>Cyanoramphus auriceps</i>	1	1	
<i>Cyanoramphus malherbi</i>	1	1	
<i>Cyanoramphus novaeseelandiae</i>	15	1	
<i>Cyanoramphus unicolor</i>	3	2	

<i>Nestor meridionalis</i>	9	3
<i>Nestor notabilis</i>	18	4
<i>Strigops habroptilus</i>	3	1
Strigiformes		
<i>Athene noctua</i>	7	1
<i>Ninox novaeseelandiae</i>	17	2
Coraciiformes		
<i>Halycon sancta vagans</i>	14	1
Passeriformes		
<i>Acridotheres tristis</i>	25	2
<i>Anthornis melanura melanura</i>	7	3
<i>Corvus frugilegus</i>	8	1
<i>Gymnorhina tibicen</i>	25	3
<i>Passer domesticus</i>	15	2
<i>Prunella modularis</i>	9	1
<i>Sturnus vulgaris</i>	12	3
<i>Turdus merula</i>	2	5
<i>Turdus philomelos</i>	14	3
<i>Zosterops lateralis</i>	14	1



## Appendix 3. Galapagos Islands bird taxa sampled for louse species and listed by order.

Host species species	total hosts sampled	positive hosts sampled	louse found
<b>Sphenisciformes</b>			
<i>Sphenicus mendiculus</i>	5	5	1
<b>Procellariiformes</b>			
<i>Diomedea irrorata</i>	4	4	7
<i>Oceanodroma castro</i>	6	6	3
<i>Oceanites gracilis galapagoensis</i>	is 4	4	
1			
<i>Pterodroma phaeopygia</i>	2	2	4
<i>Puffinus subalaris</i>	5	5	3
<b>Pelecaniformes</b>			
<i>Fregata magnificans</i>	3	3	3
<i>Fregata minor</i>	3	3	3
<i>Nannopterum harrisi</i>	7	7	1
<i>Pelecanus occidentalis</i>	4	4	2
<i>Phaethon aethereus</i>	3	3	2
<i>Sula dactylatra</i>	5	5	2
<i>Sula neboxii</i>	10	10	2
<i>Sula sula</i>	5	5	1
<b>Charadriiformes</b>			
<i>Anous stolidus</i>	3	3	4
<i>Arenaria interpres</i>	1	1	2
<i>Creagus furcatus</i>	7	7	3
<i>Haematopus palliatus</i>	3	3	4
<i>Larus fuliginosus</i>	9	5	1
<i>Larus pipixcan</i>	2	2	3
<i>Tringa incana</i>	1	1	3
<b>Ciconiiformes</b>			
<i>Butorides sundevalli</i>	4	2	1
<i>Nyctanassa violacea</i>	5	4	1
<i>Phoenicopterus ruber</i>	3	3	2
<b>Anseriformes</b>			
<i>Anas bahamensis</i>	2	1	4
<b>Falconiformes</b>			
<i>Buteo galapagoensis</i>	3	3	3
<b>Strigiformes</b>			
<i>Asio flammeus</i>	1	1	2

Gruiformes			
<i>Laterallus spilonotus</i>	4	2	3
Columbiformes			
<i>Zenaida galapagoensis</i>	19	19	2
Passeriformes			
<i>Camarhynchus pallidus</i>	1	1	1
<i>Camarhynchus pauper</i>	6	1	1
<i>Camarhynchus parvulus</i>	1	0	0
<i>Camarhynchus psittacula</i>	12	5	2
<i>Certhidea olivacea</i>	6	0	0
<i>Dendroica petechia</i>	8	6	2
<i>Geospiza conirostris</i>	42	8	2
<i>Geospiza difficilis</i>	47	6	2
<i>Geospiza fortis</i>	46	6	2
<i>Geospiza fuliginosus</i>	86	13	3
<i>Geospiza magnirostris</i>	7	3	2
<i>Geospiza scandens</i>	6	0	0
<i>Myarchus magnirostris</i>	65	16	2
<i>Nesomimus parvulus</i>	12	11	2
<i>Nesomimus trifasciatus</i>	6	6	1
<i>Nesomimus macdonaldi</i>	18	13	2
<i>Platyspiza crassirostris</i>	5	1	1
<i>Pyrocephalus rubinus</i>	6	2	1