RESEARCH PAPER

Tandem host-parasite dispersal inferred from similarities in phylogeographical patterns among Little Penguins and their 'terrestrial' ectoparasites

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Abstract

Aim: Organisms with poor intrinsic dispersal capacity, such as parasites, often rely entirely on transport with host species that have a greater dispersal capacity. Penguins, for example, are exploited by terrestrial ectoparasites when they come ashore to breed. Recent research indicates that Little Penguin (*Eudyptula minor* and *E. novaehollandiae*) hard ticks (*Ixodes eudyptidis* and *I. kohlsi*) may be capable of surviving short periods (days) at sea with their hosts, but their capacity to survive longer voyages (weeks) is not known. We here aimed to assess whether phylogeographical patterns in Little Penguins and their ticks indicate that the terrestrial ectoparasites are able to disperse long distances at sea with their swimming hosts.

Location: Southern Australia and New Zealand.

Taxon: *Ixodes eudyptidis* and *I. kohlsi* ticks.

Methods: We conducted a broad-scale genomic assessment of Little Penguin ticks from across their hosts' ranges in Australia and New Zealand. Using genotyping by sequencing, we generated SNP data sets from ticks from 14 penguin colonies, and analysed phylogeographical structure. We included ticks from some sympatric flighted seabirds to verify host specificity.

Results: We resolved two distinct lineages of *Ixodes* from Little Penguins, with one restricted to Australia, and the other found throughout New Zealand and in low numbers at some eastern Australian sites. Both lineages exhibited phylogeographical structure consistent with patterns observed in their hosts, with some evidence of occasional oceanic dispersal, including across the Tasman Sea between Australia and New Zealand. Ticks from sympatric short-tailed shearwaters (*Ardenna tenuirostris*), which disperse aerially, were genetically distinct from those collected from Little Penguins, supporting prior evidence of host specificity in seabird ticks.

Main conclusions: The most parsimonious explanation for our results is that ticks can travel at sea with Little Penguins. We infer that some terrestrial ectoparasites associated with aquatically dispersing hosts have evolved the capacity to survive oceanic voyages.

KEYWORDS
Eudyptula spp., *Ixodes* spp., physiological tolerance, SNPs, ticks

1 | INTRODUCTION

Trans-oceanic dispersal is emerging as an important mechanism underpinning biodiversity patterns. Long-distance dispersal has played an especially important role in structuring biodiversity across many parts of the largely oceanic Southern Hemisphere, including postglacial recolonisation of high-latitude regions such as the sub-Antarctic islands and south-western South America (Fraser, Nikula, Ruzzante, & Waters, 2012; McGlone, 2005; Moon, Chown, & Fraser, 2017). Phylogeographical analyses of plants, invertebrates, bats, birds, fish, and marine animals also indicate that post-Gondwanan (<80 Ma) movement between Australia and New Zealand has been common (Wallis & Trewick, 2009). These trans-Tasman movements have, however, usually been too rare to maintain frequent gene flow and thus panmixia among populations (Pratt, Morgan-Richards, & Trewick, 2008; Waters, Dijkstra, & Wallis, 2000).

Organisms with poor intrinsic dispersal capacity (e.g. those unable to fly, swim, or float long distances) can sometimes disperse considerable distances via transport with species that have a greater dispersal capacity. For example, entire communities of sedentary coastal invertebrates have been shown to raft hundreds of kilometres at sea associated with buoyant kelp (Fraser, Nikula, & Waters, 2011). Assisted dispersal is also common in parasites, which can depend entirely on hosts to facilitate movement (Esch & Fernández, 2013). When dispersal of one species is dependent on another, the microevolutionary expectation is for similar phylogeographical structure, as observed for crustaceans associated with rafting kelp (Nikula, Fraser, Spencer, & Waters, 2010). If the host specificity is consistently high—for example, there are no instances of host-switching or lineage sorting and parasites speciate when their hosts do (see Paterson, Palma, & Gray, 2003)—the macroevolutionary expectation is for concordant phylogenetic structure between the host-parasite groups (e.g. as observed for pocket gophers and their lice: Hafner, Demastes, Spradling, & Reed, 2003). Extensive tests of host-parasite phylogeographical concordance have been undertaken for a number of endoparasitic species and have found that parasites often show more structure than their hosts (Criscione, Cooper, & Blouin, 2006; Nieberding, Morand, Libois, & Michaux, 2004). The results of such studies have therefore enabled clarification of physical interactions for a number of host species, particularly fish (Criscione et al., 2006; Esch & Fernández, 2013). However, genetic differentiation in parasites appears to be driven by a complex interplay of life history traits (e.g. the extent of free-living stages, see Mazé-Guilmo, Blanchet, McCoy, & Loot, 2016 for a review), and in the case of ectoparasites, some of which show looser associations with host species than endoparasites (e.g. those with considerable off-host phases, and multi-host lifecycles), comparison of host-parasite phylogeographical and/or phylogenetic structure has been less commonly undertaken (but see Sands, Apanaskevich, Matthee, Horak, & Matthee, 2017; Talbot, Vonhof, Broders, Fenton, & Keyghobadi, 2016).
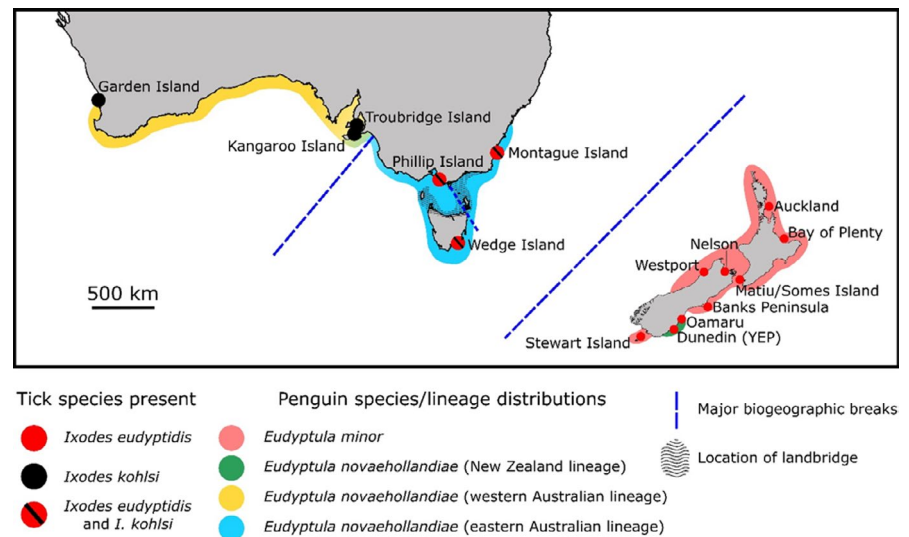
Co-diversification—whereby parasite and host diversification occur in tandem—is an important process driving parasite evolution (Morand, Krasnov, & Littlewood, 2015) including seabird ectoparasites (Paterson, Wallis, Wallis, & Gray, 2000). For co-diversification to occur at any scale, the parasite must be able to track host movements by surviving host-associated dispersal. When both host and parasite are adapted to the same environment (e.g. marine pathogens on marine kelp: Blake, Thiel, López, & Fraser, 2017), tandem dispersal is unlikely to be problematic. However, some parasites that occupy primarily terrestrial environments have biotic associations with hosts that frequent marine environments. Penguins, for example, are colonial seabirds parasitised by terrestrial ectoparasites (e.g. fleas, lice, and ticks), yet their movements are almost entirely in an aquatic environment. Although there has been some suggestion that co-diversification may be less common in penguin ectoparasites than in those that exploit other hosts (Banks, Palma, & Paterson, 2006; McCoy et al., 2012), the limitations that aquatic host dispersal might impose on terrestrial ectoparasites are poorly understood. Furthermore, genetic studies of penguin ectoparasites to date have largely focussed on interspecific phylogenetic patterns, rather than micro-evolutionary (phylogeographic) processes (e.g. Banks et al., 2006; McCoy et al., 2012). The question therefore remains: have these ectoparasites evolved the capacity to survive trips at sea with the penguins (in which case we would expect similar phylogeographical structure in the parasites as in the penguins), or do they have a more limited dispersal capacity (in which case we would expect far greater structure in the parasites than the penguins)?

Little penguins (*Eudyptula* spp.) are native to southern Australia and New Zealand, with one species present in Australia and in some parts of the south of New Zealand (*Eudyptula novaehollandiae*), and the other restricted to New Zealand (*E. minor*) (Figure 1), and exhibit a phylogenetic history consistent with multiple but infrequent trans-Tasman dispersal events (Banks, Mitchell, Waas, & Paterson, 2002; Grosser, Burridge, Peucker, & Waters, 2015). During the breeding season, Little Penguin movements are often limited to one- or two-day foraging trips, but during the winter months, individuals often travel for weeks at a time and have been known to go to sea for a month (Collins, Cullen, & Dann, 1999). Phylogeographically, Little Penguins show genetic homogeneity across large (>1,000 km) scales in Australia, with the exception of a zone of high genetic structure in South Australia (Burridge, Peucker, Valautham, Styan, & Dann, 2015; Overeem, Peucker, Austin, Dann, & Burridge, 2008). Australian lineages are also largely consistent with an east/west divide, the cause of which remains largely speculative, but which could be the result of a biogeographical break during recent glacial maxima (Burridge et al., 2015; Overeem et al., 2008).

Little penguins are parasitised by two morphologically cryptic *Ixodes* tick species, *Ixodes eudyptidis* and *I. kohlsi* (hereafter Little Penguin ticks), when they come ashore to breed and moult (Figure 1). Penguin ticks exhibit no obvious adaptations to oceanic conditions, and so long-distance dispersal in association with their penguin host is thought to present a challenge (Dietrich, Gómez-Díaz, & McCoy, 2011; Pugh, 1997), yet Little Penguin ticks are present across the entire range of their hosts in Australia and New

FIGURE 1 Figure indicating the major biogeographical breaks across Australia and New Zealand, identified in a number of phylogeographical studies of diverse taxa, as well as the landbridge that connected Tasmania to the mainland of Australia until ~13,000 years ago (Waters, 2008). Little Penguin species/lineages (Banks et al., 2002; Burridge et al., 2015; Grosser et al., 2015) and sample sites are also shown, with symbols representing the *Ixodes* tick species present at each sampled colony

Tick species present
● *Ixodes eudyptidis*
● *Ixodes kohlsi*
◑ *Ixodes eudyptidis* and *I. kohlsi*

Penguin species/lineage distributions
● *Eudyptula minor*
● *Eudyptula novaehollandiae* (New Zealand lineage)
● *Eudyptula novaehollandiae* (western Australian lineage)
● *Eudyptula novaehollandiae* (eastern Australian lineage)

╱ Major biogeographic breaks
▒ Location of landbridge

Zealand. If Little Penguin ticks are not host-species specific, their dispersal could be facilitated by flighted seabird hosts. Although some Little Penguin ticks have been recorded on non-penguin hosts (Roberts, 1970), new evidence suggests these records could be the result of poorly resolved taxonomy, and are likely to represent distinct species (Heath & Palma, 2017). *Ixodes uriae*, which parasitises diverse seabirds in the sub-Antarctic and Antarctic, has evolved host-specific races among different seabird species (McCoy et al., 2012; McCoy, Chapuis, et al., 2005) that can endure for long periods (Dietrich, Kempf, Boulinier, & McCoy, 2014), and is not found on other sympatric vertebrates such as marine mammals (Bergström, Haemig, & Olsen, 1999). Likewise, in Australia, ticks found parasitising Little Penguins at Phillip Island were genetically distinct from sympatric ticks parasitising blue-tongue lizards (*Tiliqua nigrolutea*) (which are frequently found in penguin nesting areas) (Moon, Dann, Chown, McGaughran, & Fraser, 2018). Dispersal of Little Penguin ticks is therefore most probably dependent on their swimming hosts. Although a recent physiological study of Little Penguin ticks suggests that they could be capable of surviving short periods of immersion in seawater (Moon, Aitkenhead, Fraser, & Chown, 2019), whether they could survive long journeys at sea remains unknown.

We here carried out a broad-scale phylogenomic assessment of Little Penguin ticks from throughout their range. Based on physiological analyses suggesting Little Penguin ticks can survive some time at sea (Moon et al., 2019), which would facilitate co-diversification, we hypothesised that they would show similar phylogeographic structure to their hosts, supporting their capacity to survive lengthy ocean trips. Based on previous research (as outlined above), we also hypothesised that Little Penguin ticks would be distinct from ticks on sympatric flighted seabirds. To test this hypothesis, we targeted ticks from short-tailed shearwaters (*Ardenna tenuirostris*), as they are a highly vagile flighted seabird species, have been recorded as an alternate host for Little Penguin ticks (Roberts, 1970), and are the most common flighted seabird species present at Little Penguin colonies across their range.

2 | MATERIALS AND METHODS

2.1 | Study sites and sampling

To evaluate whether Little Penguin ticks also parasitise sympatric flighted seabirds (and thus whether the latter might represent alternative dispersal vectors), 20 ticks from short-tailed shearwaters and 40 ticks from Little Penguins were removed directly from hosts at an intermingled colony on Wedge Island in Tasmania, Australia, and preserved for genetic analysis using methods described in Moon et al. (2018).

For phylogenomic analyses, ticks were obtained from 14 Little Penguin colonies (including Wedge Island) throughout the entire range of the two species in Australia and New Zealand (with the exception of the Chatham Islands: see Figure 1). A total of 166 samples were taken from six Australian colonies, and 182 samples were taken from eight colonies and one additional site in New Zealand (see Table 1).

Field collections were undertaken between November 2014 and November 2016. Sampling was conducted as per Moon et al. (2018), and yielded 328 ticks from 10 sites (see Table 1 for sample sizes). Ticks from Phillip Island comprised the same samples used in a previous study (Moon et al., 2018). No ticks were found at Penguin Island (32.3057° S, 115.6906° E) in Western Australia, despite extensive searches of over 20 burrows and birds, and although the colony at Garden Island—only 6.5 km away from Penguin Island – had ticks (K. L. Moon, pers. obs.). An additional 19 preserved Little Penguin tick samples representing a further four Little Penguin colonies were collected from the insect collection at Te Papa Museum and from Massey University, New Zealand. A single tick from a yellow-eyed penguin (*Megadyptes antipodes*), collected in Dunedin, was also taken from Te Papa Museum and included in the genetic analyses, to assess whether Little Penguin ticks exploit other penguin species within their range. DNA extractions were undertaken as per Moon et al. (2018).

TABLE 1 Sample sizes from each colony, with the number of samples yielding data for genomic analysis given in brackets

Location		N
Australia	Phillip Island (38.4899° S, 145.2038° E)	50 (12, 31)
	Montague Island (36.2510° S, 150.2270° E)	22 (1, 15)
	Wedge Island (43.1352° S, 147.6722° E)	30 (1, 26)
	Kangaroo Island (35.7752° S, 137.2142° E)	14 (13)
	Troubridge Island (35.1180° S, 137.8276° E)	23 (22)
	Garden Island (32.2043° S, 115.6776° E)	27 (23)
New Zealand	Auckland (36.8485° S, 174.7633° E)	2 (1)
	Bay of Plenty (37.6893° S, 177.1423° E)	13 (6)
	Matiu/Somes Island (41.2582° S, 174.8659° E)	40 (39)
	Nelson (41.2706° S, 173.2840° E)	1 (1)
	Westport (41.7545° S, 171.6059° E)	40 (37)
	Banks Peninsula (43.7500° S, 173.0000° E)	35 (35)
	Oamaru (45.0975° S, 170.9704° E)	47 (40)
	Dunedin (45.8788° S, 170.5028° E)*	1 (1)
	Stewart Island (46.9973° S, 167.8372° E)	3 (2)

Note: Where applicable, samples used in the *I. eudyptidis* analyses are shown first, followed by the number used in the *I. kohlsi* analysis. Sites in Australia include Garden Island in Western Australia, Troubridge Island and Kangaroo Island in South Australia, Phillip Island in Victoria, Montague Island in New South Wales and Wedge Island in Tasmania. Sites in New Zealand include Stewart Island, Oamaru, Banks Peninsula, Westport and Nelson on the South Island, and Matiu/Somes Island, Bay of Plenty and Auckland on the North Island. *Yellow-eyed penguin

2.2 | Mitochondrial genetic sequencing

Because there are two, morphologically cryptic species of Little Penguin tick in Australia (*I. kohlsi* and *I. eudyptidis*; see Figure 1), we first analysed several samples from Australian colonies (Phillip Island, Montague Island, Troubridge Island, Kangaroo Island, and Garden Island) for mitochondrial COI to assist with delineation of the species. Methods are described in Moon et al. (2018). Sequencing was undertaken by the Genetic Analysis Services at the University of Otago.

2.3 | Genotyping by sequencing library preparation

Library preparations for genotyping by sequencing (GBS) were carried out as per Moon et al. (2018) but with the following alterations: post-ligation PCRs were performed in two sets of 25 μl volumes, each containing 5 μl of purified DNA product, 12.5 μl of 1 × MyTaq™ HS Master Mix (Bioline), 6.5 μl of MilliQ H_2O, and 0.5 μM each of forward and reverse PCR primer (see Elshire et al., 2011). The products from the two PCRs were then combined equimolarly. Following quantitation and pooling, a 200-bp range (400–600 bp) was excised for paired-end sequencing, carried out on a single lane of an Illumina NextSeq500 undertaken by the Biomolecular Resource Facility

in the John Curtin School of Medical Research at the Australian National University.

2.4 | Analysis

2.4.1 | COI data

Maximum likelihood (ML) and Bayesian phylogenetic analyses were undertaken using PhyML 3.0 (Guindon et al., 2010) and MrBayes (Huelsenbeck & Ronquist, 2001) as described in Moon et al. (2018) (including the same outgroups), and included samples from Moon et al. (2018) (representing Phillip Island) and Moon, Banks, and Fraser (2015).

2.4.2 | GBS data

Raw Illumina data were processed using the *Stacks* (Catchen, Hohenlohe, Bassham, Amores, & Cresko, 2013) pipeline as described in Moon et al. (2018) with the following alterations and specifications: all fragments were trimmed to 68 bp after demultiplexing, the minimum depth of coverage required to create a stack in ustacks was set to 2, the maximum distance (in nucleotides) allowed between stacks was set to 2, the maximum distance (in nucleotides) allowed to align secondary reads to primary stacks was set to 0 and the number of mismatches allowed between sample loci when building the catalogue was set to 1. Following sstacks, rxstacks was used to correct genotype and haplotype calls made by cstacks and sstacks, before cstacks and sstacks were then rerun on the output from rxstacks. In rxstacks, the minimum log likelihood required to keep a catalogue locus was set to −15.0, the proportion of loci in a population that must be confounded relative to the catalogue locus was set to 0.25, and the prune haplotype algorithm was enabled to prune out non-biological haplotypes considered unlikely to occur in the population. The populations *Stacks* script was then used to filter the data and export loci for downstream analyses. The minimum minor allele frequency required to process a nucleotide site at a locus was set to 0.1, the minimum depth of coverage for each individual was set to 5, and the minimum percentage of individuals required to process a locus was set to 50%, meaning each SNP had to be present in at least 50% of the individuals to be called (also known as call rate). A python script was then used to prune samples that had ≥95% missing data. Loci were tested for selection as described in Moon et al. (2018).

The .plink file outputs from the *Stacks* population script were used for Principle Components Analysis (PCA) (Patterson, Price, & Reich, 2006; Price et al., 2006; R Core Team, 2014; Roshyara & Scholz, 2014), and fastSTRUCTURE analysis (Raj, Stephens, & Pritchard, 2014) for each species independently as per Moon et al. (2018). Principle Coordinate Analysis (PCoA) was also performed (on the host-species specificity data only) with the .plink outputs, but following their conversion into .raw files and imputation into R (R Core Team, 2014). PCoA analyses were undertaken using the gl.pcoa function in dartR v. 1.1.11 (Gruber, Unmack, Berry, & Georges, 2018)

and visualized with the gl.pcoa.plot function from the same package. IQ-TREE (Nguyen, Schmidt, von Haeseler, & Minh, 2014) was used to infer unrooted phylogenetic trees for each species using ML analyses. The −m MFP flag was enabled so that IQ-TREE would firstly identify the optimal model of evolution, based on the Akaike Information Criterion (AIC) score, corrected AIC score and Bayesian Information Criterion score, and would then subsequently perform the analysis with the selected model. One thousand bootstraps were used to assess node support, and trees were visualised using FigTree v.1.4.3 (Rambaut, 2009).

3 | RESULTS

3.1 | Species identification

COI data were obtained for a total of eight ticks from Kangaroo Island (SA), five ticks from Troubridge Island (SA), and six ticks from Garden Island (WA). These data were analysed with sequences from 24 ticks from Phillip Island (sequenced during Moon et al., 2018), and previously used outgroups (see Table S2 in Moon et al., 2018 for GenBank accession numbers). Two deeply divergent clades were identified using both ML and Bayesian analyses, and these were consistent with the clades found in Moon et al. (2015) and in Moon et al. (2018) (see Figure S1). Unrooted phylogenomic trees (IQ-TREE analyses) were then used to classify the remaining individuals from Australia into these two clades, using the placement of COI-barcoded individuals as a guide. The two clades likely represent the two Little Penguin species, with one present across New Zealand and in small numbers in eastern Australia (henceforth *I. eudyptidis*), and the other present across Australia (henceforth *I. kohlsi*) (see Discussion for explanation of species assignment).

3.2 | Host-species specificity

Following quality control and filtering of genomic data, 4,726 SNPs remained from 25 Little Penguin ticks and 18 short-tailed shearwater ticks from Wedge Island. Both the fastSTRUCTURE and IQ-TREE analyses of the Little Penguin and shearwater ticks provide strong evidence for host-species specificity (see Figure 2). A model complexity of $K = 1$–2 was identified, and the distruct2 plot of $K = 2$ shows that the two populations are almost entirely delineated by host species. IQ-TREE chose the K3Pu+F+R2 model of substitution and this model was subsequently used with the following rate parameters: A-C: 1.000 A-G: 3.196 A-T: 0.632 C-G: 0.632 C-T: 3.196 G-T: 1.000, and base

frequencies: A: 0.217 C: 0.280 G: 0.281 T: 0.222. IQ-TREE analyses further support host-species specificity, with two well-supported tick clades that correspond to ticks from the two different host species (see Figure 2). Due to the large amount of missing data in the dataset (likely the result of considerable divergence between the penguin and shearwater ticks), PCoA analyses were more appropriate than PCA to assess host-species specificity (Rohlf, 1972). PCoA plots show clear separation between Little Penguin ticks and short-tailed shearwater ticks (see Figure S2).

### 3.3 | Genomic structure

3.3.1 | PCA analyses

Following quality control and filtering of genomic data, a total of 60,412 SNPs were retained from 176 *I. eudyptidis* ticks, and 7,196 SNPs were retained from 130 *I. kohlsi* ticks (see Table 1 for site representation) across Australia and New Zealand. PCA plots provide evidence for population structuring in both Little Penguin tick species, but movement between some colonies is evident. In *I. eudyptidis*, the PCA plot was strongly skewed by differences between Australian and New Zealand colonies (Figure S3). A second PCA analysis was therefore performed without the Australian ticks (Figure 3). When the Australian ticks were removed, the PCA indicated similarities among tick colonies on the east coast of the South Island in New Zealand (particularly Banks Peninsula and Oamaru) (Figure 3). The yellow-eyed penguin tick grouped with Little Penguin ticks from the same area.

The *I. kohlsi* PCA plot was skewed by differences between mainland colonies and the Wedge Island (Tasmania) colony (Figure S3), so a second analysis was performed without this site, to allow differences among mainland colonies to be examined (Figure 3). In this second analysis, all sites appeared distinct except the two South Australian colonies, which were intermixed (Figure 3).

3.3.2 | fastSTRUCTURE analyses

FastSTRUCTURE analyses of *I. eudyptidis* suggested a model complexity of $K = 6$–7. The distruct2 plots show population structure among colonies, but also suggest some movement between colonies is occurring (Figure 4). In particular, Oamaru and Bay of Plenty ticks were diverse, and population assignments reflected ancestry in other populations (particularly Banks Peninsula). Inferred population membership suggested both Stewart Island and Nelson ticks may also have a mixed ancestry, but sample sizes were too small to confirm gene

FIGURE 2 Genomic results from Little Penguins (right) and short-tailed shearwaters (left), including a fastSTRUCTURE distruct2 plot ($K = 2$), and IQ-TREE results (see Figure S2 for PCoA plot)
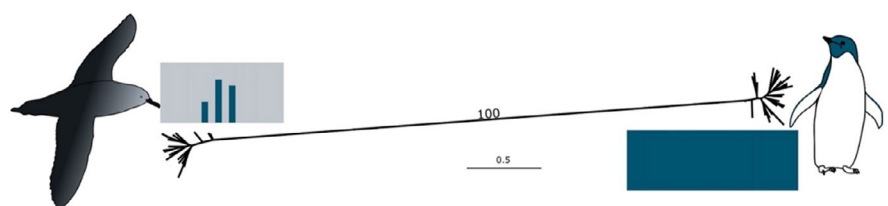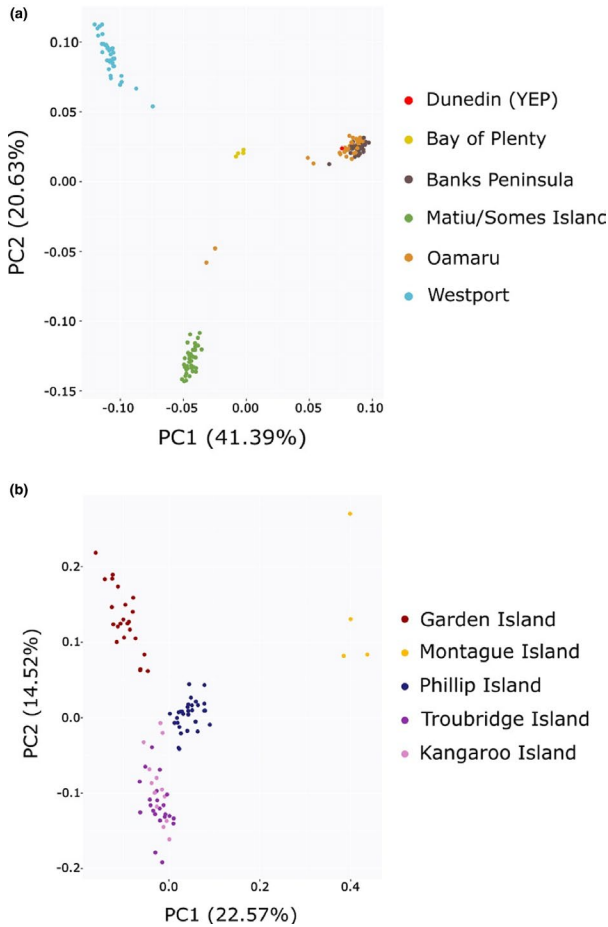
FIGURE 3 PCA plots of both (a) *Ixodes eudyptidis* (without Australian samples) and (b) *I. kohlsi* (without Wedge Island samples) Little Penguin tick samples from New Zealand and Australia. Percentage of variation explained by each PC is given in parentheses. Sites are differentiated by colour, and 'YEP' identifies the yellow-eyed penguin sample

FIGURE 4 fastSTRUCTURE distruct2 plots of both (a) *Ixodes eudyptidis* and (b) *I. kohlsi* Little Penguin tick samples

flow. A single *I. eudyptidis* tick from Wedge Island (Tasmania, Australia) grouped with New Zealand ticks (North Island or Oamaru), rather than with the Australian *I. eudyptidis* tick population. The yellow-eyed penguin tick from Dunedin grouped with the Oamaru population.

FastSTRUCTURE analyses of *I. kohlsi* inferred a model complexity of K = 2–7. Distruct2 plots suggest a division between ticks from east coast colonies (Phillip Island, Montague Island and Wedge Island) and more western colonies (Troubridge Island, Kangaroo Island and Garden Island), with little movement inferred between them, although Wedge Island appears to have mixed ancestry with some possible genetic input from western areas (see Figure 4). Movement also appears to be restricted between Garden Island and the South Australian colonies (at K > 2), but the two South Australian colonies are not genetically distinct.

3.3.3 | IQ-TREE analyses

For *I. eudyptidis*, the K3Pu+F+R5 model of substitution was chosen by IQ-TREE and subsequently used with the following rate
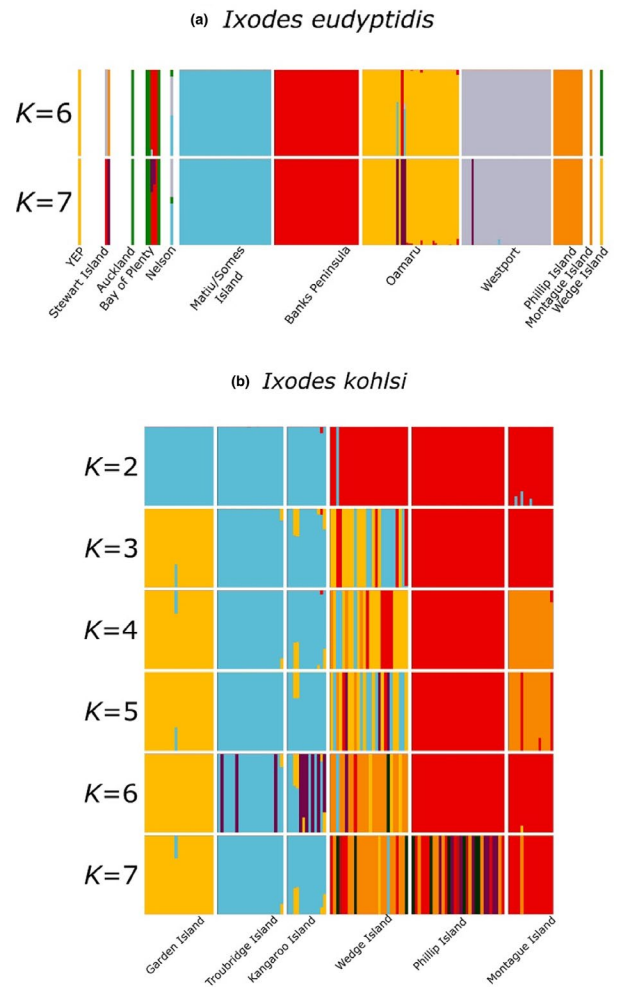
parameters: A-C: 1.000 A-G: 4.772 A-T: 0.911 C-G: 0.911 C-T: 4.772 G-T: 1.000, and base frequencies: A: 0.225 C: 0.280 G: 0.274 T: 0.221. The K3Pu+F+I+G4 model of substitution was chosen by IQ-TREE and subsequently used for *I. kohlsi* with the following rate parameters: A-C: 1.000 A-G: 2.867 A-T: 0.791 C-G: 0.791 C-T: 2.867 G-T: 1.000, base frequencies: A: 0.226 C: 0.271 G: 0.268 T: 0.235, proportion of invariable sites: 0.050, and gamma shape alpha parameter: 2.298. The phylogenetic tree for *I. eudyptidis* provided further support for the differentiation of Australian and New Zealand ticks (see Figure 5). In accordance with fastSTRUCTURE analyses, a single Wedge Island tick grouped with the New Zealand ticks suggesting recent trans-Tasman movement. Within New Zealand, IQ-TREE analysis suggests there has been some—but limited—recent movement among colonies, with a single tick from the Bay of Plenty grouping with Banks Peninsula ticks, and three ticks from Oamaru more closely related to North Island ticks than to others from the eastern South Island.

The tree for *I. kohlsi* indicated a division between colonies on the east coast of Australia and those to the west (Figure 6). The eastern colonies—including Wedge Island (Tasmania)—were not well
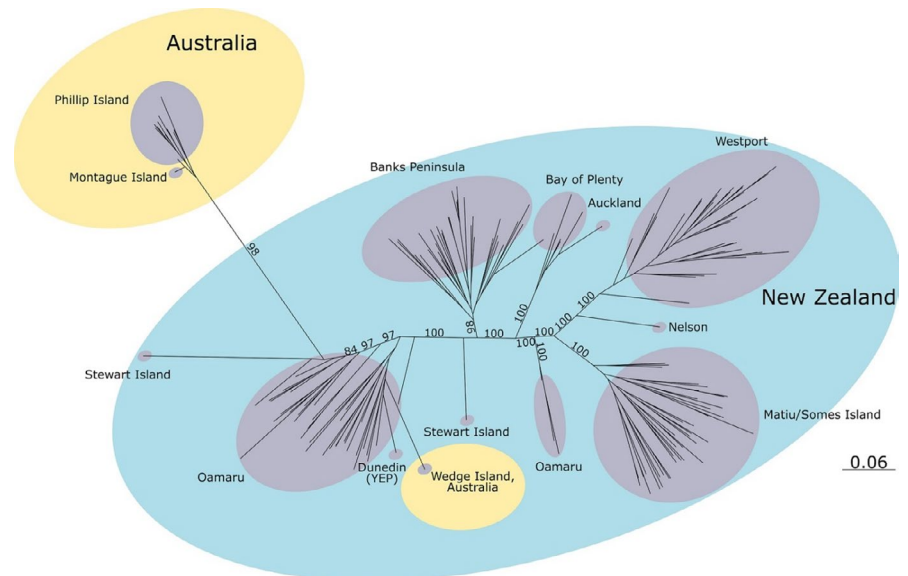
FIGURE 5 IQ-TREE results from *Ixodes eudyptidis* Little Penguin tick samples

differentiated. Ticks from the two South Australian colonies formed a single clade.

4 | DISCUSSION

Our results support our hypotheses that Little Penguin ticks are host-species specific, and that they are capable of considerable aquatic dispersal in association with their hosts. These results are consistent with previous fine-scale genetic studies (McCoy et al., 2012; McCoy, Chapuis, et al., 2005; Moon et al., 2015), and a recent study of Little Penguin tick physiological tolerances (Moon et al., 2019), but are the first to indicate penguin-associated tick movement between landmasses separated by thousands of kilometres of open ocean. Although the ticks showed greater phylogeographical structure than their hosts—which may be due, in part, to the higher-resolution markers used in this study, or as a result of the tendency of parasites to show higher levels of genetic structure than hosts (e.g. Criscione et al., 2006)—major biogeographical breaks were consistent for both hosts and parasites. We discuss our results in terms of their implications for biogeography and penguin conservation.

4.1 | Species identification

The genetic division indicating two divergent clades (one found throughout New Zealand and in low numbers on the east coast of Australia, and the other from all colonies across Australia: see Figure S1) is consistent with Moon et al. (2015) and Moon et al. (2018), and likely represents the two cryptic Little Penguin *Ixodes* species. Strong genetic differences between the lineages across both mitochondrial and SNP datasets in this study are also consistent with a lack of evidence for hybridisation between the species, even for sympatric samples (Moon et al., 2015). Species identities were assigned based on geographical patterns. Unlike *Ixodes kohlsi*, which has never been recorded from New Zealand, *I. eudyptidis* is found in both Australia

and New Zealand (Roberts, 1970). Our mitochondrial and genomic data also provide the first evidence that *I. kohlsi* is present in western Australian colonies, as the penguins in the west were thought to be exploited by *I. eudyptidis* (Heath & Palma, 2017; Roberts, 1970).

4.2 | Host-species specificity in Little Penguin ticks

Despite records of Little Penguin ticks exploiting short-tailed shearwaters (Roberts, 1970), our results suggest that the two hosts do not commonly share ticks even when they share a colony (Figure 2). In Australia, there are few flying seabird species that nest sympatrically with Little Penguins; the short-tailed shearwater is, however, commonly found close to Little Penguins colonies, and also burrow-nests, thus representing the best test of potential host specificity. Australian and New Zealand seabird tick taxonomy is poorly resolved (Heath & Palma, 2017), and so host records cannot be relied upon to resolve host range (McCoy, Léger, & Dietrich, 2013). Our results might further support a recent taxonomic revision that has described a new tick species (*I. laridis*) on flighted seabirds in New Zealand and Australia, which was erroneously recorded as *I. eudyptidis* (Heath & Palma, 2017). *Ixodes laridis* is known to occur on birds in Tasmania, and might be the species present on Wedge Island short-tailed shearwaters.

Previous studies have shown that different host races of seabird ticks can evolve in ticks on penguins and flighted birds (e.g. albatross and shags) when they breed in sympatry (McCoy et al., 2012), and that life history can influence the level of host specificity and thus dispersal of seabird parasites (Wessels, Matthee, Espinaze, & Matthee, 2019). However, host specificity was not evident between three penguin species in the western Antarctic Peninsula (McCoy et al., 2012), nor among two related species of penguin in the Crozet Archipelago (McCoy, Chapuis, et al., 2005), nor among the two recently split Little Penguin species (this study), suggesting that ticks might readily be shared among penguin species. The present study also suggests—although based on a single specimen—that
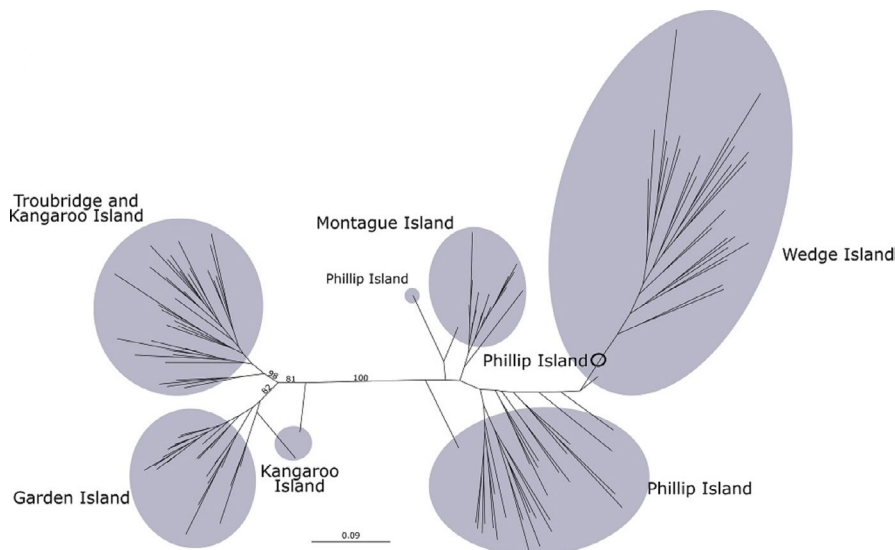
FIGURE 6 IQ-TREE results from *Ixodes kohlsi* Little Penguin tick samples

New Zealand penguin species (Little and yellow-eyed penguins) may share ticks. Our results nonetheless suggest that Little Penguin ticks (either *Ixodes eudyptidis* or *I. kohlsi*) do not exploit flighted seabirds (Figure 2). We cannot, however, completely rule out the possibility that Little Penguin ticks might occasionally parasitise nearby shearwaters, and thus be transported aerially. Regardless, such rare events seem unlikely to explain our results, as shearwaters do not normally fly directly between New Zealand and Australia, but rather fly out to sea to feed, or to the Northern Hemisphere and South America during migrations (Shaffer et al., 2006). Penguin ticks might be transported by other means, too, such as oceanic rafting (Thiel & Gutow, 2005). Such a mechanism seems considerably less plausible than transport with penguins, however, especially given evidence that these ticks can survive conditions encountered during penguin dives (Moon et al., 2019) and because the ticks do not, to our knowledge, usually occupy littoral habitats independently of their hosts. Phylogeographical patterns of penguin ticks are therefore most likely to result from penguin movements.

4.3 | Contemporary movement

Our genomic analyses indicate that movement of Little Penguin ticks may be mediated by the distance between colonies, and the quality of a colony. For example, Kangaroo and Troubridge Islands in South Australia are only separated by ~60 km of open ocean, and were found to share a single, panmictic tick population. Movement between these colonies is well-supported by the physiological capabilities of Little Penguin ticks, and, based on average swimming speeds of Little Penguins (1.8 m/sec: Bethge, Nicol, Culik, & Wilson, 1997), dispersal between them could be achieved by a swimming penguin in under an hour (Moon et al., 2019). Likewise, population assignments and phylogenetic analyses of the ticks at Oamaru (New Zealand), Wedge Island (Tasmania) and Phillip Island (Victoria) colonies also provide evidence for immigration. Phillip Island and Oamaru represent the largest and most reproductively successful colonies in Australia and New Zealand

(Agnew, Houston, Lalas, & Wright, 2014; Chiaradia, Ropert–Coudert, Kato, Mattern, & Yorke, 2007; Sutherland & Dann, 2014) and the population at Wedge Island is exhibiting considerable growth (~17% per annum) (Vertigan, 2010). A previous study of seabird ticks found that the extent of gene flow into colonies may be partially explained by quality, as larger, more productive colonies will attract more prospecting birds, facilitating long-distance gene flow in ticks (McCoy, Boulinier, Tirard, & Michalakis, 2003). Increased immigration of penguins into Oamaru, Wedge Island and Phillip Island due to their high quality may explain the phylogeographical patterns, and confirms that prospecting activities in seabirds translate into effective dispersal of their ectoparasites (Danchin, 1992; McCoy, Boulinier, & Tirard, 2005). Our results support occasional, successful long-distance dispersal and establishment of ticks across Australia and New Zealand, but probably do not show the full extent of tick movement in the region. Many dispersal events are likely to fail to result in colonisation, establishment and gene flow, for example when there is already a densely established population at the destination (Waters, Fraser, & Hewitt, 2013), or because of other factors that influence transmission efficiency upon arrival (MacLeod, Paterson, Tompkins, & Duncan, 2010).

4.4 | Biogeography

Within Australia, phylogeographical patterns of *I. kohlsi* reflected a similar phylogenetic split (see Figures 4 and 6) to that of their hosts (Burridge et al., 2015; Overeem et al., 2008). If host phylogenetic structure was related to a past bottleneck in the South Australian colonies (as suggested in Burridge et al., 2015), reduced genetic diversity would be expected in the ticks, but there was no evidence for this. Our results could, however, support the theory of secondary contact of isolated eastern and western penguin (and associated tick) lineages resulting from the historical closure of the Bass Strait via the Bassian Isthmus, as inferred for other phylogeographical studies of marine animals from the region (see Figure 1) (Burridge, 2000; Fraser, Spencer, & Waters, 2009; Waters, 2008).

Our genomic data support previous inferences of infrequent trans-Tasman movements of Little Penguins (Grosser et al., 2015; Peucker, Dann, & Burridge, 2009), with evidence for host-associated penguin tick movements between Australia and New Zealand in both directions. In addition, we found that a single *I. eudyptidis* tick from Wedge Island (Tasmania, Australia) grouped genetically with ticks from New Zealand in multiple analyses (see Figures 4 and 5), suggesting a recent dispersal event from New Zealand to Australia. However, as for the host—and a number of other organisms (Pratt et al., 2008; Wallis & Trewick, 2009; Waters et al., 2000)—trans-Tasman movements have not been frequent enough to maintain gene flow, resulting in divergence.

4.5 | Movement of terrestrial ectoparasites with aquatically dispersing hosts

A small number of terrestrial ectoparasites were able to remain associated with host groups whose ancestors returned to the oceans, but very little is known of their dispersal capacity in association with their swimming hosts. These groups are almost entirely restricted to hosts that have maintained close contact with land (e.g. pinnipeds, sea otters and seabirds), because they still rely on terrestrial environments for reproduction and transmission (Raga, Fernández, Balbuena, & Aznar, 2009). Some avoid marine conditions via microhabitat, for example the sucking lice of penguins which inhabit the layer of trapped air under the feathers of its host while it is at sea (Murray, 1967). As a result, the lice have been able to maintain considerable genetic contact across their range (Banks et al., 2006). Previous studies of terrestrial ectoparasites that are exposed to marine conditions have focussed on the sucking lice of seals and the river otter (Echinophthiriidae) and have only described parasite loads, transmission dynamics within colonies, preferred attachment locations, and morphological adaptations to marine conditions (Kim, 1971, 1975; Kim & Emerson, 1974; Leonardi & Lazzari, 2014; Leonardi & Palma, 2013; Murray & Nicholls, 1965; Murray, Smith, & Soucek, 1965). The present study therefore represents one of the first to characterise the dispersal capacity of a seemingly host-species specific terrestrial ectoparasite exposed to marine conditions on an aquatically dispersing host (but see McCoy et al., 2012; McCoy, Boulinier, et al., 2005; Wessels et al., 2019). However, such movements may be restricted by life history, including philopatry (Moon et al., 2017).

The phylogeographical structure we detected in this research highlights the importance of climatic cycles (e.g. the opening and closing of Bass Strait due to sea level changes) and occasional trans-Tasman dispersal on the evolution of biodiversity in the region. The correspondence of phylogenetic structure in Little Penguins and their host-specific ticks also provides some of the first evidence that terrestrial ectoparasites exploiting semi-aquatic hosts are capable of long-distance aquatic movements.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All genomic data generated for this study are available in FASTA format on Dryad.

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ETHICS STATEMENT

Collections were made under an Australian National University Ethics Permit (protocol number A2014/06) granted to Katherine L. Moon and valid from 10 April 2014 to 10 April 2017, a Victorian research permit (under the Wildlife Act of 1975; permit number 10007242) granted to Katherine L. Moon and valid from July 2014 to 10 April 2017, a New South Wales research permit (under the National Parks and Wildlife Act 1974; permit number SL100746) granted to Gemma Carroll and valid from 13 March 2012 to 31 December 2015, an Animal Research Authority permit (protocol number A2014/057) granted to Gemma Carroll and valid from 23 December 2014 to 23 December 2017, a Tasmanian research permit (under the Nature Conservation Act of 2002, National Parks and Reserved Land Regulations 2009 and the Crown Lands Regulations 2011; permit number FA 14314) granted to Katherine L. Moon and valid from 30 November 2014 to 29 November 2015, two Western Australian research permits (under the Wildlife Conservation Act of 1950; permit numbers SF010902 and 01-000086-1) with the former granted to Belinda Cannell, and the latter granted to Katherine L. Moon and valid from 30 October 2016 to 29 October 2017, a South Australian research permit (under the Animal Welfare Act 1985; permit number 20/2014) granted to Ceridwen Fraser and valid from 10 July 2014 to 29 February 2017, a Department of Conservation New

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BIOSKETCH

Katherine L. Moon is broadly interested in answering evolutionary questions with genomic techniques, particularly those concerning the movements of species through time. This project represents a section of her PhD at the Australian National University, which was supervised by the co-authors, and which aimed to investigate the evolution of terrestrial ectoparasites on marine hosts. Steven L. Chown has interests in macrophysiology, ecology and conservation policy and has a long-standing research programme in the Antarctic. Ceridwen Fraser is interested in understanding how, and which, species can disperse long distances, and how dispersal influences broad-scale biogeographical patterns. She has a particular focus on marine and Antarctic/sub-Antarctic ecosystems.

Author contributions: KLM, CIF, SLC conceived and designed the experiment; KLM performed all experiments; KLM analysed the data; KLM, CIF, SLC wrote the paper.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.