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Authors
Moon, Katherine L.
Chown, Steven L.
Fraser, Ceridwen I.

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Local, but not long-distance dispersal of penguin ticks between two sub-Antarctic islands

Katherine L. Moon[1,2]* , Steven L. Chown[2] , Ceridwen I. Fraser[1,3]

[1] Fenner School of Environment and Society, Australian National University, Acton, ACT 2601, Australia; [2] School of Biological Sciences, Monash University, Clayton, VIC 3800, Australia; [3] Department of Marine Science, University of Otago, PO Box 56, Dunedin 9054, New Zealand. *Corresponding author: Katherine L. Moon. University of California, Santa Cruz, Santa Cruz, California, USA 95060. Ph: +1 (831) 346 9742. E-mail: katielouisemoon@gmail.com

Abstract

Advances in high throughput genomic approaches are enabling the accurate appraisal of movements of diverse species, previously considered intractable. The impact of long-distance dispersal and distribution changes on species interactions (such as host-parasite interactions) is of particular importance as attempts are made to project how ecosystems will shift under environmental change. The sub-Antarctic region, comprising isolated islands separated by hundreds to thousands of kilometres of open ocean, presents an ideal model system for studying long-distance dispersal, distribution, and ecosystem change. Here we used genomic methods to determine the extent of movement of penguin ticks (*Ixodes uriae*) among different host species, and among penguin colonies at small (within an island) and large (among islands separated by >6000 km) scales, in the sub-Antarctic region. Our results suggest that *I. uriae* ticks may be readily shared between distantly related penguin species with similar phenology, but indicate that – as inferred by previous research – ticks are less likely to be shared between flighted and non-flighted seabirds. We also find evidence for small-scale movements of penguin ticks with their hosts, but no evidence for movements between islands separated by thousands of kilometers of open ocean. These inferred limitations to penguin tick movement could be the result of restricted host movements or the inability of penguin ticks to survive extended trips at sea. Our findings help elucidate parasite-host dynamics, with implications for host health and persistence in a region experiencing rapid environmental change.

Highlights

- Genomic data suggests *Ixodes uriae* ticks from penguin colonies are locally adapted to their hosts and are genetically differentiated from ticks removed from albatross in the sub-Antarctic.

- Penguin ticks appear to disperse with their hosts at sea over small scales (between colonies on an island).

- Penguin tick dispersal is limited over long distances (between colonies separated by thousands of kilometers), which may be the result of host movement restrictions or the inability of ticks to survive at sea for extended periods.

- Genomic data, therefore, suggest there are current limitations to the connectivity of penguin tick populations in the sub-Antarctic, with implications for parasite-host dynamics in a region where warming may require range movements from all species.

Introduction

As the climate warms, many species' distributions are changing, with general trends showing shifts toward the poles and uphill (Chen et al. 2011). Human activity is also leading to intense habitat fragmentation, with detrimental impacts on biodiversity (Haddad et al. 2015). The capacity to disperse long distances, to

maintain connectivity among populations and/or achieve range expansions into more favourable environments (Waters and Fraser 2016), is therefore likely to play an increasingly critical role in the survival of diverse plants and animals in the near future. Some species seem ill-suited to long-distance dispersal, with limited autonomous movement of adults or propagules (Gillespie et al. 2012). Yet in many cases long-distance

dispersal can still be achieved, for example through transport with wind, oceanic rafting on buoyant material, or through zoochory, with for instance migrating animals (Gillespie et al. 2012, Waters and Fraser 2016). Understanding which taxa will be well-placed to disperse to new environments is an important aspect of predicting future ecosystem changes.

The sub-Antarctic, generally comprising small islands separated by several thousands of kilometres of open ocean, represents an excellent model system for testing hypotheses about long-distance dispersal and connectivity (Moon et al. 2017). Despite the large distances among many sub-Antarctic islands, molecular studies indicate that dispersal has played, and continues to play, a key role in structuring biodiversity patterns in the region (González-Wevar et al. 2018). Some sub-Antarctic taxa – including iconic penguins (Cristofari et al. 2018) – are predicted to shift their distributions in response to environmental change. However, inferred vagility of sub-Antarctic species is not a good proxy for effective movement (Moon et al. 2017), complicating predictions. Even movement in highly vagile penguins is variably restricted by behaviour (e.g., natal philopatry, foraging), oceanographic features (e.g., temperature and salinity gradients), and in some species (e.g., gentoo penguins – *Pygoscelis papua*) long distances (Banks et al. 2006; Jouventin et al. 2006; Clucas et al. 2014; Levy et al. 2016; Vianna et al. 2017), with implications for range shifts.

Shifting distributions also threaten ecosystem structure by disrupting biotic interactions. Though studies have acknowledged the importance of maintaining some interactions as species move in response to climate change (particularly predator-prey; Aryal et al. 2016), comparatively few have investigated interactions with commensal, mutualist, or parasitic species (Carlson et al. 2013, 2017). Parasites must disperse with hosts on the move if they are to maintain populations. This may be particularly difficult for host-specific ectoparasites with considerable off-host periods, as these species will have fewer opportunities for host-associated movement to new habitat. Given the role parasites play in regulating host populations (Anderson and May 1978) and their influence on ecosystems (e.g. through food webs; Lafferty et al. 2006), the alteration of host-parasite interactions due to climate change has the potential to further destabilise systems already under pressure (Carlson et al. 2017).

Seabird ticks, *Ixodes uriae*, are present in colonies throughout the high latitudes of both hemispheres and are host generalists at global scales (>60 species). However, considerable variation in host biology has encouraged local adaptation within colonies (Dietrich et al. 2011, McCoy et al. 2013). As a result, host race formation – but not always speciation – is the norm in seabird ticks (McCoy et al. 2013), except when hosts exhibit similar breeding biology or are closely related phylogenetically (McCoy et al. 2005, 2012). Host species movement directly influences the extent of ectoparasite dispersal (McCoy et al. 2003b), so host race formation in seabird ticks has important

implications for host-parasite dynamics with shifting host distributions.

Sub-Antarctic penguins, like other seabirds, are parasitised by *I. uriae* ticks when they come ashore to breed. Little penguin (*Eudyptula novaehollandiae* and *E. minor*) ticks (*I. eudyptidis* and *I. kohlsi*) appear to travel easily with hosts on land; a recent genomic study within a single, large penguin colony found almost no spatial structure in penguin ticks over the scale of a few kilometers (Moon et al. 2018). Dispersal of penguins among colonies, however, necessarily involves aquatic movement, which may restrict tick dispersal (Pugh 1997, Dietrich et al. 2011); ticks are generally not found on penguins returning from foraging trips (Pugh 1997). A recent physiological study has found that little penguin ticks *I. eudyptidis* and *I. kohlsi* around Australasia can tolerate some conditions faced at sea (e.g., immersion in seawater for a few days and to penguin dive depths; Moon et al. 2019a), and phylogeographic work suggests at-sea movement is occurring occasionally at the scale of 10s to 100s of kilometers (Moon et al. 2019b). The capacity of the more generalist and widespread *Ixodes uriae* ticks to disperse with penguin hosts over short or long distances remains, however, largely unknown.

Only four published phylogeographic studies to date have included penguin ticks (McCoy et al. 2005, 2012, Moon et al. 2018, 2019b), and one investigated only intra-colonial (terrestrial) movements (Moon et al. 2018). Genetic differences between *I. uriae* removed from penguins compared to those removed from sympatric flighted seabirds suggest that host-specific lineages have evolved (McCoy et al. 2005, 2012, Moon et al. 2018). In contrast, host-race formation is not always observed among different penguin species: those that share similar breeding biology (e.g. timing of breeding; McCoy et al. 2005, 2012) can be parasitised by ticks of the same lineage. Penguin distributions are predicted to shift as the climate warms (Cristofari et al. 2018), but with uncertainties around penguin tick dispersal capacity we do not yet know if their ectoparasites are likely to travel with them. This prediction is of important conservation concern for penguins as high tick loads can negatively impact breeding success (Mangin et al. 2003), cause death in cases of hyperinfestation (Gauthier-Clerc et al. 1998), and have been implicated in the outright desertion of colonies by penguins (see Lynch et al. 2010), and seabirds more generally (Duffy 1983).

We used genomic approaches to assess penguin tick population structure within and among distant regions, and thus infer the extent of dispersal. Specifically, we tested i) whether tick lineages are shared between penguin species and nearby flighted bird species, ii) whether tick lineages are shared between different penguin species, and iii) whether penguin ticks show evidence of movement within and between sub-Antarctic islands. Based on previous findings (McCoy et al. 2005, 2012), we expected that ticks on penguins would be genetically distinct from those on flighted birds but shared between penguin host species that are sympatric and exhibit similar breeding characteristics (e.g., timing

of breeding). We also hypothesised that ticks would be genetically distinct on penguins – even those of the same species – occupying geographically distant islands, either because of movement limitation in the penguins (Banks et al. 2006, Vianna et al. 2017), inability of the ticks to survive very long journeys at sea (e.g., due to attachment duration limitations; Dietrich et al. 2011), or some combination thereof. With growing evidence that penguin ticks can survive at least short periods at sea (up to a few days; Moon et al. 2019a) and less commonly long periods (possibly for the length of their attachment which is ~6-12 days; Moon et al. 2019b, Murray and Vestjens 1967), we nonetheless also expected to find evidence for movement among colonies on smaller scales (among colonies within islands). We analysed 50,245 SNPs from *I. uriae* ticks collected from rockhopper (*Eudyptes chrysocome*) colonies and from nearby grey-headed (*Thalassarche chrysostoma*) and light-mantled albatross (*Phoebetria palpebrata*) colonies, on Marion Island (southern Indian Ocean); and from rockhopper, king (*Aptenodytes patagonicus*), and gentoo penguin (*Pygoscelis papua*) colonies across the Falkland Islands, (southern Atlantic Ocean), see Fig. 1. To our knowledge, this study represents the first genomic assessment of sub-Antarctic penguin ticks and the largest scale phylogeographic study of penguin ticks to date.

Methods

Sampling

A total of 73 *Ixodes uriae* ticks was collected from under rocks across two discrete rockhopper penguin colonies at Murrell (east Falkland Islands) and two sites across a small area of Pebble Island (west Falkland Islands), and from gentoo and king penguin sites at Volunteer Point (east Falkland Islands), in January of 2015, (see Fig. 1 for sample sizes). Ticks were also removed directly from rockhopper penguins, grey-headed albatross and light-mantled albatross on Marion Island (see Fig. 1) in April of 2016. Ticks (whole for Falkland Island specimens; legs only for Marion Island specimens) were preserved in 96% ethanol prior to genomic analysis.

DNA extraction and genomic analyses

DNA extractions were undertaken for tick legs only (to avoid host contamination via blood meals) using a Qiagen (Qiagen, Valencia, California, USA) QIAmp DNA Micro Kit using the Isolation of Genomic DNA from Tissues protocol as per the method outlined in Moon et al. (2018).

Library preparations were carried out as per Elshire et al. (2011) with minor modifications. Specifically, unique *Pst*I adapter barcodes (2.25 ng) were added to each sample, and DNA was digested at 37°C for 2-hours using *Pst*I-HF (New England Biolabs, Ipswich, MA) in 10 x NEBbuffer 4 (New England Biolabs, Ipswich, MA). Adapter ligation was carried out using T4 DNA Ligase and 10 x ligation buffer (New England Biolabs, Ipswich, MA), incubated at 16°C for 90 min and 80°C for 30 min, followed by a purification step using a MinElute 96-well PCR Purification Kit (Qiagen, Valencia, CA) and eluted in 25 μL of 1 x TE Buffer. PCRs were carried out in 50 μL volumes, each containing 10 μL of purified DNA product, 25 μL of 1 x MyTaqTM HS Master Mix (Bioline), 13 μL of MilliQ H_2O, and 1 μM each of forward and reverse PCR primer (see Elshire et al. 2011), in an Eppendorf
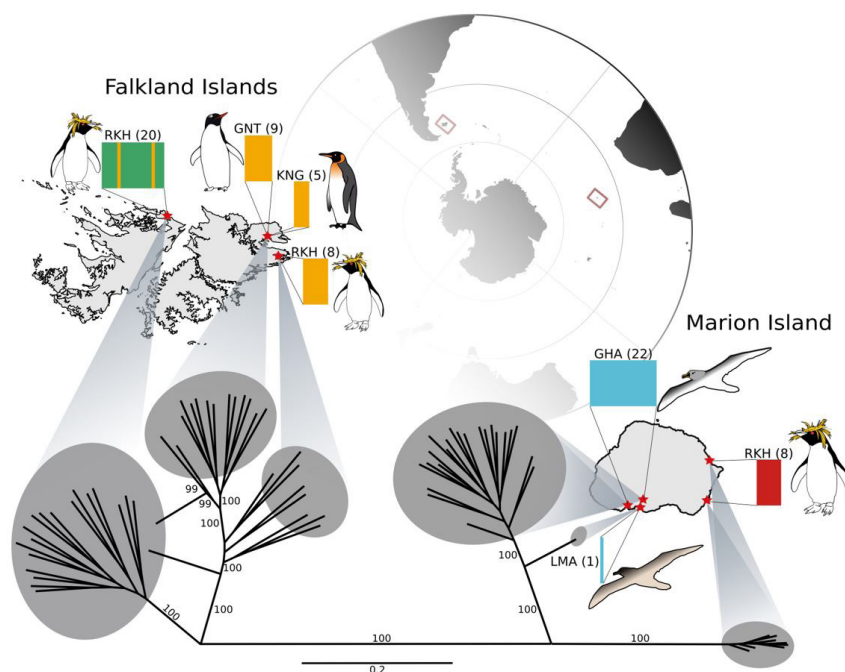

Figure 1. Sample sites across the Falkland Islands and Marion Island. Host species are depicted as images; RKH = rockhopper penguin, GNT = gentoo penguin; KNG = king penguin; LMA = light-mantled albatross; GHA = grey-headed albatross. Sample sizes for each site are shown in parentheses. Coloured plots depict the results of fastSTRUCTURE analyses, and the IQ-TREE phylogeny (including bootstrap values) is also shown.

Mastercycler Nexus under the following conditions: 72°C for 5 min, 95°C for 60 s, and 24 cycles of 95°C for 30 s, 65°C for 30 s, and 72°C for 30 s, and 72°C for 5 min. DNA concentration was assessed using a LabChip GXII (Caliper Life Sciences), samples were pooled equimolarly, and a 200-bp range (400-600 bp fragments) was sent for paired-end sequencing on a single lane of an Illumina NextSeq500. Sequencing was undertaken by the Biomolecular Resource Facility in the John Curtin School of Medical Research at the Australian National University.

Using the process_radtags script of the *Stacks* 1.35 pipeline (Catchen et al. 2011), raw Illumina sequences with ligated combinatorial barcodes were demultiplexed. Reads were then discarded if their quality dropped below a 90% probability of being correct (a raw phred score of 10), before being trimmed to 93 bp. The ustacks, cstacks, sstacks and rxstacks scripts of *Stacks* were then used to align reads (using the de novo method) into stacks (minimum stack depth of 5, maximum distance between stacks of 2), call SNPs (with secondary reads discarded), build a catalogue of SNPs (with 0 mismatches allowed), and correct genotype and haplotype calls (minimum log likelihood of -15.0, proportion of loci of 0.25 and the prune haplotype algorithm enabled). SNPs were only retained if they were present in at least 20% of individuals, and the minimum minor allele frequency required to process a nucleotide site at a locus was set to 0.1. Final filters were chosen to maximise SNP numbers, as long as results from data sets produced using a number of parameters (e.g., 50% and 80% call rate filters, missing data cut-off of >50%, and minor allele frequency cut-off of 0.01) were largely congruent (see Supplementary Materials Fig. S1). A custom python script was then used to remove samples that had >95% missing data in the final data set. Once these filters were applied, a total of 50,245 SNPs and 73 individuals remained in the data set (see Supplementary Materials Table S1).

SmartPCA analyses were subsequently conducted as outlined in Moon et al. (2018), using fcgene 1.0.7 (Roshyara and Scholz 2014) to convert Stacks output files, EIGENSOFT 6.1.2 (Price et al. 2006) to convert input files and run the script, and R 3.1.2 (R Core Team 2014) to visualise the output. fastSTRUCTURE analyses were also conducted as outlined in Moon et al. (2018), using fastSTRUCTURE 1.0 (Raj et al. 2014) to run the analysis, the choosek script to choose the optimal K, and Distruct 2.3[1] to visualise the inferred population assignments. IQ-TREE (Nguyen et al. 2014) was used to infer an unrooted maximum likelihood phylogenetic tree. The –m MFP flag was enabled allowing IQ-TREE to identify the optimal evolutionary model – based on the Akaike Information Criterion (AIC) score, corrected AIC score, and Bayesian Information Criterion (BIC) score – before performing the analysis with the selected model. Node supports were estimated based on 1000 bootstraps, and the resulting tree was visualised using FigTree v.1.4.3 (Rambaut 2016).

Results

Whereas ticks from the two Marion Island albatross species represented a single intermixed population, ticks from nearby rockhopper penguins (at least ~12 km from the albatross colony) were genetically distinct, supporting specificity among ticks on flighted seabirds versus those parasitising penguins (Fig. 1). King, gentoo, and rockhopper penguins on the east coast of the Falkland Islands supported a single population of ticks, with fastSTRUCTURE showing no evidence of genetic structure among ticks from different, sympatric penguin hosts (Fig. 1). IQ-TREE (Fig. 1) and PCA (Fig. 2, Table 1) analyses did, however, indicate some slight differentiation among rockhopper penguin ticks from the eastern Falkland Islands versus nearby gentoo and king penguin ticks. Rockhopper ticks from the western Falkland Islands population were genetically distinct from those on the east, but some
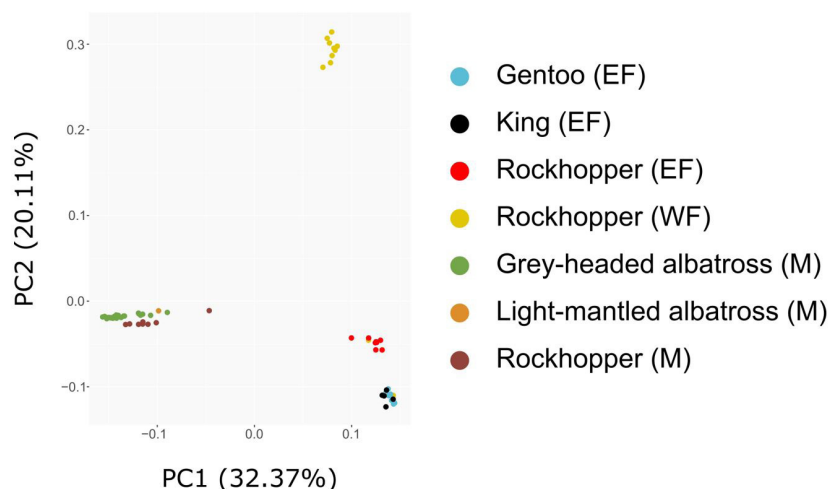

Figure 2: PCA plot of *Ixodes uriae* ticks from Marion Island (M), the east Falkland Islands (EF), and west Falkland Islands (WF). Percentage of variation explained by each PC is given in brackets, and sites and hosts are differentiated by colour.

[1] available at http://www.crypticlineage.net/pages/distruct.html, accessed on 02/08/2019

Table 1: Full results of the PCA analysis including eigenvalues, Tracy-Widom (TW) statistics, P-values and percentage of variation explained for each of the first 10 principal components (PCs). Tracy-Widom P-values that were found to be significant (p < 0.01; the first three PCs) are in italics.

PC	Eigenvalue	TW statistic	p	% Variation explained
1	*8.909*	*16.234*	*0.000*	*32.37*
2	*5.535*	*19.987*	*0.000*	*20.11*
3	*4.089*	*27.436*	*0.000*	*14.86*
4	1.564	0.085	0.153	5.68
5	1.302	-5.975	1.000	4.73
6	1.253	-6.718	1.000	4.55
7	1.243	-6.383	1.000	4.52
8	1.216	-6.534	1.000	4.42
9	1.213	-5.997	1.000	4.41
10	1.202	-5.644	1.000	4.37

movement among western and eastern colonies was inferred (Fig. 1, Fig. 2). Rockhopper ticks on Marion Island were genetically distinct from those on the Falkland Islands (Fig. 1, Fig. 2).

Discussion

Our genomic results indicate that penguin ticks can move among penguin colonies within islands and are therefore capable of some aquatic dispersal, but – based on differences between Marion and Falkland Island rockhopper ticks – movements of ticks between sub-Antarctic islands is less common. Although rockhopper penguins are capable of dispersing between Marion and the Falkland Islands (separated by >6000 km), phylogenetic studies suggest they rarely make the voyage (Banks et al. 2006). Oceanographic features – such as the Sub-Antarctic Front – might act as an effective barrier to rockhopper movement as is the case for other species (Vianna et al. 2017). Despite evidence for shared ticks among rockhopper and king penguins (this study) and for considerable movement of king penguins among colonies across the sub-Antarctic region (Clucas et al. 2016), penguin ticks do not appear to be dispersing between Marion and the Falkland Islands. Our results therefore suggest either that host movements between the islands are restricted or that penguin ticks cannot survive the journey. Furthermore, although genetic studies of grey-headed albatross suggest frequent movement around the region (Burg and Croxall 2001), we infer that host-specificity of *I. uriae* lineages (McCoy et al. 2005, 2012, this study) limits the capacity of penguin ticks to disperse with flying hosts.

A phylogenetic study of seabird ticks in the Crozet Archipelago found different lineages exploiting king and rockhopper penguins, even when they shared a colony, which the authors attributed to large differences in breeding biology and phenology (McCoy et al. 2005). Conversely, our results suggest the two species can share tick lineages, even when colonies are physically separated. Importantly, however, the king

penguin colony in the Falkland Islands represents the temperate limit of its range, and the birds exhibit behaviour that differs from those in the Crozet Archipelago (e.g., significantly shorter winter foraging trips: Baylis et al. 2015). The phenology of Falkland Islands king penguins may therefore be similar enough to gentoo and rockhopper penguins to allow tick exchange. Previously, sharing of ticks between penguin species had only been noted between sister species (e.g., between rockhopper (*Eudyptes chrysocome*) and macaroni (*Eudyptes chrysolophus*) penguins in the sub-Antarctic (McCoy et al. 2005)).

Marion and the Falkland Islands are separated by vast oceanic distances (>6000 km), and by a major frontal zone. The Sub-Antarctic Front, lying to the north of Marion Island but the south of the Falkland Islands, is characterised by convergence of cold sub-Antarctic water and warmer northern waters. Southern Ocean fronts have long been considered biogeographic barriers, although there is growing evidence for the occasional permeability of such fronts for dispersing organisms (e.g., Fach et al. 2006, Garden et al. 2014, Chown et al. 2015, Fraser et al. 2016, Moon et al. 2017, Fraser et al. 2018). Some penguin species forage around frontal zones, but fronts also represent approximate distributional boundaries for many seabirds (Bost et al. 2009). Available genetic evidence from rockhopper penguins suggests long-distance movements may be limited by the front, as well as by natal philopatry whereby penguins tend to return to their birthplace to breed (Banks et al. 2006, Vianna et al. 2017). Thus, the highly philopatric nature of penguins, oceanographic features, and the considerable distance separating the locations might all contribute to reducing transport of ticks with their penguin hosts between Marion and the Falkland Islands.

Broadly, our findings suggest that penguin tick movement is extremely limited. Despite our previous research showing that some *Ixodes* tick species are physiologically capable of periods of immersion in seawater (Moon et al. 2019a), that inter-colony movement is occurring over 10s of kilometers more frequently than

over 100s of kilometers (Moon et al. 2019b), and that intra-colony movement is high (Moon et al. 2018), our genomic data indicate that long-distance movement of penguin ticks among islands is rare. Intriguingly, our IQ-TREE results suggest that penguin ticks on Marion Island are more closely related to ticks from albatrosses on the same island than to rockhopper penguin ticks on distant islands (Fig. 1). Thus, although our expectation of detecting genomic differences among ticks from flighted seabirds and nearby penguins was met, we cannot take this as an indication that the present distribution of penguin ticks is a result of penguin movements alone. Instead, long-distance dispersal events in *I. uriae* in the sub-Antarctic could have been facilitated by flying seabirds, with host-race divergence occurring subsequently, and evolution of penguin-specific tick lineages that now have restricted dispersal capacity. Likewise, loss of (or a reduction in) dispersal capacity has been inferred for diverse taxa following colonisation and diversification into new habitats, for example plants, insects and birds (Carlquist 1966, Ikeda et al. 2012, Mitchell et al. 2014). Whether these penguin-specialised lineages could switch back to flighted hosts, and thus regain long-distance dispersal potential, is an intriguing question that future research could explore.

High-resolution genomic data have greatly improved our ability to track dispersal events (e.g., Fraser et al. 2018, Peters et al. 2019) and infer population connectivity (e.g., Fountain et al. 2018). In regions with isolated habitats, such as the sub-Antarctic, molecular studies are increasingly demonstrating the ongoing importance of dispersal for biodiversity (Moon et al. 2017). Wider sampling in future genomic studies, including more host species and colonies, are now required to clarify movements and host-switching across the region. Coupled with improved understanding of tick survival capability at sea on different hosts, such knowledge would improve understanding of what the future holds for these host-parasite interactions, which have the potential to modify seabird population dynamics directly and/or through disease transmission (Mangin et al. 2003, Grimaldi et al. 2015).

Acknowledgements

Supplementary Materials

The following materials are available as part of the online article from https://escholarship.org/uc/fb:

Figure S1. fastSTRUCTURE analysis of strict filtered data set where SNPs had to be present in at least 80% of samples to be called (call rate of 80%) and each individual had to have at least 50% data to remain in the analysis (>50% missing data cut-off).

Table S1. Raw read counts for each sample that was retained following quality control, including minimum, maximum, average, and standard deviation of the raw reads. Sample removed during stricter filtering is indicated with an *.

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