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Contemporary and historical separation of transequatorial migration between genetically distinct seabird populations

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1 Contemporary and historical separation of transequatorial migration between
2 two genetically-distinct seabird populations

3

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31 **Abstract**

32 Pelagic seabirds are highly mobile, reducing the likelihood of allopatric speciation
33 where disruption of gene flow between populations is caused by physically
34 insurmountable, extrinsic barriers. Segregation during the non-breeding season appears
35 to provide an intrinsic barrier to gene flow among seabird populations that otherwise
36 occupy nearby or overlapping regions during breeding, but how this is achieved remains
37 unclear. Here we show that the two genetically distinct populations of Cook's petrel
38 (*Pterodroma cookie*) exhibit transequatorial separation of non-breeding ranges at
39 contemporary (ca. 2-3 yrs) and historical (ca. 100 yrs) time scales. Segregation during
40 the non-breeding season *per se* appears an unlikely barrier gene flow. Instead we
41 provide evidence that habitat specialisation during the non-breeding season is associated
42 with breeding asynchrony which, in conjunction with philopatry, restricts gene flow.
43 Habitat specialisation during breeding and non-breeding likely promotes evolutionary
44 divergence between these two populations via local adaptation.

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56 **Introduction**

57 Divergent migratory behaviours to and from breeding sites have led to the disruption of
58 gene flow among populations in many species ^{1,2}, contributing to reproductive isolation
59 under the classic model of allopatric speciation ³. In terrestrial environments, genetic
60 differentiation among migratory populations is frequently paralleled by extrinsic (e.g.
61 mountain ranges) and intrinsic (e.g. timing of dispersal, inherited migratory direction,
62 host use by parasites) barriers that restrict gene flow and facilitate divergence via
63 genetic drift and/or selection ⁴⁻⁶. However, the nature of the extrinsic and intrinsic
64 barriers that disrupt gene flow among populations of marine animals have only recently
65 begun to be investigated ^{7,8} and remain poorly known for many highly mobile taxa ^{8,9}.

66

67 Seabirds undertake the longest known migrations on Earth, routinely crossing
68 hemispheres between breeding and non-breeding habitat within ocean basins ^{10,11}. As a
69 result of this extreme mobility, seabirds experience few apparent physical barriers to
70 dispersal. Thus, seabirds can potentially visit and ultimately breed on islands thousands
71 of kilometres from their natal colony, which may contribute to a lack of genetic
72 structure observed in several species ¹²⁻¹⁵. Yet other seabird species show surprisingly
73 high levels of population genetic structure ^{8,16-18} and intrinsic barriers to gene flow
74 appear to play an important role in the evolution of seabird diversity ^{4,18-22}. For example
75 given the strong tendency for seabirds to return to their natal site to breed, natal
76 philopatry has been proposed as such a barrier to gene flow ¹⁹. However given that not
77 all seabirds exhibit strong genetic structure it is unlikely to be the sole driver.

78

79

80 A recent meta-analysis suggests that segregation of non-breeding distributions may be a
81 key determinant of genetic structure among seabird populations ⁸, but how occupying
82 disjunct non-breeding distributions can restrict gene flow remains unclear. Although
83 advances in tracking technology have improved our ability to record the long-distance
84 movements of seabirds at sea ²⁰, few studies have examined the non-breeding
85 segregation amongst seabird populations that occupy nearby or overlapping regions
86 during the breeding season ^{11,21}. Accordingly, the role of seasonal movements in
87 shaping the genetic structure of seabird populations, and the persistence of these
88 movement patterns at the timescale of generations, remain unknown. Such information
89 is vital for providing insights into behavioural and ecological mechanisms underlying
90 the diversification of highly mobile taxa, including those within oceanic environments.

91
92 *Pterodroma cookii* (Cook's petrel; Procellariiformes: Procellariidae Gray 1843), are
93 pelagic seabirds that breed exclusively on two islands at the northern and southern
94 extremes of their prehistoric range within the New Zealand archipelago ²²: Little Barrier
95 Island (LBI) and Codfish Island (CDF), respectively ^{23,24}. When breeding, *P. cookii*
96 range within the south-west Pacific and Tasman Sea, with overlapping foraging ranges
97 centred around their respective breeding colonies ²⁵. Shipboard observations indicate
98 that after breeding, *P. cookii* are trans-equatorial and trans-Pacific migrants, with
99 sightings concentrated in the North Pacific (North-Pacific Convergence and centrally
100 along Baja California) and in the South Pacific (Humboldt Current) Oceans ²⁶. On the
101 basis of body size and plumage characteristics, in 1929 Murphy ²⁷ distinguished
102 between smaller *P. c. cookii* that were collected in the North Pacific and assigned to the
103 breeding population at LBI, and the larger *P. c. orientalis*, of unknown breeding origin,
104 collected south of the Equator, off the coast of Peru. Subsequently, Falla ²⁸ observed

105 that the plumage and morphological characteristics of *P. cookii orientalis* were
106 consistent with juveniles of *P. cookii cookii* from the breeding population at CDF that
107 was discovered in 1934²⁴. In addition to differences in body size, body mass, and the
108 potential for non-breeding birds to occupy disjunct habitats^{5,26,29}, birds on LBI and
109 CDF exhibit a one-month asynchrony in breeding phenology⁵ and are genetically
110 distinct⁶. These combined observations strongly suggest that gene flow between the
111 two extant *P. cookii* populations is highly restricted. Thus, *P. cookii* is an ideal study
112 species to explicitly examine whether and how occupying disjunct non-breeding
113 distributions can restrict gene flow among seabird populations.

114

115 Here we combined geolocator-based tracking with an isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and
116 genetic (mitochondrial cytochrome Oxidase subunit 1) comparison of modern breeding
117 birds, and historical specimens (i.e. museum skins), to test the hypothesis of
118 transequatorial separation of the two *P. cookii* breeding populations at varying temporal
119 scales. Specifically, we tested the predictions that contemporary *P. cookii* populations,
120 tracked over a complete annual cycle, would exhibit divergent non-breeding
121 distributions, habitat use, and foraging patterns; this divergence would be consistent
122 between contemporary cycles (ca. 2-3 years) as revealed by stable isotope analyses; the
123 stable isotope signatures of historical specimens of unknown breeding provenance
124 collected ca. 100 years ago from the two non-breeding oceanic regions used by
125 contemporary populations, would match those of modern samples, and that genetic
126 analysis would clearly assign origin of breeding population for these museum
127 specimens and confirm divergence in transequatorial migration of the *P. cookii*
128 populations over historical timescales. This combination of tracking, museum-based
129 investigation, and elemental and molecular analyses presents a novel opportunity to

130 evaluate how differences in contemporary and historical migratory behaviour can
131 contribute to the diversification of a highly mobile marine species.

132

133 **Results**

134 **Population movements**

135 Consistent with the prediction that contemporary tracked *P. cookii* would exhibit
136 divergent non-breeding distributions, our analysis reveals that birds tracked between
137 consecutive breeding seasons using light-based geolocation loggers (hereafter called
138 loggers) between 2007 and 2009 from LBI (n = 11: female (♀) = 5, male (♂) = 6) and
139 CDF (n = 11: ♀ = 6, ♂ = 5) exhibited transequatorial separation of their non-breeding
140 habitats within the Pacific Ocean (Fig. 1, Supplementary Fig. S1). This contrasts with
141 previous studies of other transequatorial migrants, including related Procellariiform
142 seabirds, which showed substantial overlaps in space use and mixing during the
143 nonbreeding period of individuals that originated from different breeding populations
144 ^{10,11,29}. Post-breeding LBI *P. cookii* (tracked for 389 ± 49 SD days) completed an anti-
145 clockwise migration of $48,037 \pm 7953$ SD km within the North and South Pacific
146 Ocean. Birds tracked from LBI moved east, then north across the equator to reach core
147 non-breeding distributions within the California and North-Pacific currents
148 (approximately 35°N) in 34 ± 8 SD days. Pre-breeding migration returning to New
149 Zealand waters was completed in 20 ± 5 SD days (Fig. 1) on a direct southwest route.
150 In contrast, post-breeding CDF *P. cookii* (tracked for 450 ± 3 SD days) migrated within
151 the South Pacific Ocean ($37,813 \pm 6920$ SD km) moving east then north within the
152 Humboldt Current to reach core non-breeding distributions off the Peruvian Coast
153 (approximately 15° S) in 19 ± 5 SD days. Pre-breeding migration returning to New
154 Zealand was again completed in 20 ± 5 SD days through a south-western corridor, north

155 of the region traversed during post-breeding movements. Consistent with their breeding
156 timetables, the migration schedule of both *P. cookii* populations was asynchronous; LBI
157 birds commenced post- and pre-breeding migrations approximately 1 month before
158 CDF birds (post-breeding 11 March \pm 12 SD days vs. 8 April \pm 15 SD days ($t_{(18)} = -$
159 4.67, $p < 0.0001$) ; pre-breeding 5 Sept \pm 10 SD days vs. 20 Oct \pm 6 SD days ($t_{(15)} = -$
160 11.85, $p < 0.0001$)).

161

162 During initial migration east towards South America, the routes taken by *P. cookii* from
163 LBI and CDF overlapped, followed a similar direction to those of post-breeding sooty
164 shearwaters (*Puffinus griseus*)¹¹ and Westland petrels (*Procellaria westlandica*)³⁰, but
165 not Australasian gannets (*Morus serrator*), departing from New Zealand nesting
166 colonies³¹. Subsequently, LBI birds moved north-west across the equator and
167 eventually returned on south-westerly trajectories to New Zealand along routes that
168 were directionally similar to sooty shearwaters¹¹, flesh-footed shearwaters (*Puffinus*
169 *carneipes*)³² and bar-tailed godwits (*Limosa lapponica baueri*) departing from on or off
170 North America³³. These observations highlight the existence of an important cross-taxa
171 avian migration corridor within the Pacific Ocean between approximately 170° E and
172 160° W.

173

174 **Isotopic and habitat segregation**

175 *P. cookii* moult during the non-breeding period^{26,34}, and hence incorporate local
176 isotopic dietary signals in their new plumage³⁵. Stable isotope ratios of C ($\delta^{13}\text{C}$) and N
177 ($\delta^{15}\text{N}$) in particular provide an indication of carbon source (benthic vs. pelagic, inshore
178 vs. offshore, and information on water mass) and trophic level of prey, respectively³⁵,
179 and comparisons thus can indicate geographic and/or dietary segregation^{36,37}.

180 Consistent with the prediction that geographic divergence would be consistent between
181 the *P. cookii* populations at a contemporary timescale (ca. 2-3 years), there was no
182 significant difference in the isotope signatures of *P. cookii* body feathers collected in
183 2006 and 2008 from LBI (2006 untracked n = 20, 2008 tracked n = 11)($\delta^{13}\text{C}$: Z = 0.83,
184 p = 0.41; $\delta^{15}\text{N}$: Z = 1.70, p = 0.10) or CDF (2006 untracked n = 20, 2008 tracked n = 9)(
185 $\delta^{13}\text{C}$: Z = 1.34, p = 0.19; $\delta^{15}\text{N}$: Z = 1.79, p = 0.07)(Fig. 2) suggesting that, currently,
186 within each breeding population, birds forage within similar oceanic regions and on
187 prey of a similar trophic level in successive years.

188

189 In support of the prediction of a match between the stable isotope signatures of
190 historical and contemporary samples sharing the same non-breeding provenance,
191 variation in the $\delta^{13}\text{C}$ signatures of feathers from modern (LBI: 2006 and 2008
192 combined; CDF: 2006 and 2008 combined) and historical specimens collected within
193 the core non-breeding habitats of birds tracked from LBI and CDF, respectively
194 (samples collected in 1905 at 22.42°N, 112.67°W, North Pacific Ocean, in the
195 California Current region off Baja California, hereafter called BC, and in 1913 at ca.
196 11°S, 79°W, South Pacific Ocean, in the Humboldt Current, hereafter called HC;
197 Supplementary Tables S1 and S2) suggest that birds have used population-specific
198 oceanic regions, with similar carbon signatures, at historical time scales (Fig. 1) (F =
199 81.32, df = 2, p < 0.001). The mean $\delta^{13}\text{C}$ value of LBI *P. cookii* (-17.18 ± 0.70 SD ‰)
200 was not significantly different from that of historical samples from BC (-16.72 ± 0.51
201 SD ‰) (t = 2.085, p = 0.250), but was significantly lower than that of modern samples
202 from CDF (-14.69 ± 0.58 ‰) (t = 14.92, p < 0.01), and historical samples from HC ($-$
203 14.79 ± 0.73 ‰) (t = 9.292, p < 0.001) (Fig. 2). The mean $\delta^{13}\text{C}$ value of modern CDF
204 samples was not significantly different from that of historical samples collected within

205 the HC ($t = 0.42$ $p = 1.00$) but was significantly higher than historical samples collected
206 from BC ($t = 8.94$ $p < 0.001$) (Fig. 2). These results suggest consistent differences in
207 carbon isotopic signals between the North Pacific Convergence and South Pacific
208 Humboldt Current systems, and support our initial prediction.

209

210 The mean $\delta^{15}\text{N}$ value of modern LBI *P. cookii* feathers ($15.37 \pm 0.95\text{‰}$) was not
211 significantly different from modern CDF feathers ($16.05 \pm 1.29\text{‰}$) ($t = 3.69$, $p = 0.16$)
212 and the only difference in mean $\delta^{15}\text{N}$ value between modern and historical feathers was
213 observed in modern samples from LBI ($15.37 \pm 0.95\text{‰}$) and historical samples from HC
214 ($16.76 \pm 1.42\text{‰}$) ($t = 3.53$, $p < 0.01$) (Fig. 2). The most likely explanation for these
215 results is that modern *P. cookii* feed on prey at similar trophic levels, despite occupying
216 different oceanic regions (as suggested by tracking and carbon isotope data).
217 Accordingly, the environmental characteristics of core non-breeding habitats exploited
218 by modern LBI and CDF *P. cookii* were significantly different, with LBI *P. cookii*
219 foraging over deeper (4930 ± 581 SD m vs. 3330 ± 314 SD m, $Z = -3.97$, $p < 0.0001$),
220 warmer (20.11 ± 1.97 SD °C vs. 17.29 ± 1.59 SD °C, $Z = 3.12$, $p < 0.01$) and less
221 productive waters (0.16 ± 0.10 SD mg Chl *a* m⁻³ vs. 0.73 ± 0.18 SD mg Chl *a* m⁻³, $Z = -$
222 3.91 , $p < 0.0001$) than their CDF conspecifics (Fig. 3). At the intrapopulation level,
223 comparisons of environmental characteristics for presence and absence data indicated
224 that LBI *P. cookii* occupied less productive waters (0.16 ± 0.10 mg Chl *a* m⁻³ vs. $0.28 \pm$
225 0.17 mg Chl *a* m⁻³, $Z = -2.20$, $p = 0.03$) and CDF *P. cookii* more productive waters (0.73
226 ± 0.18 mg Chl *a* m⁻³ vs. 0.47 ± 0.12 mg Chl *a* m⁻³, $Z = 2.79$, $p < 0.01$) than those
227 available within their respective non-breeding core habitats (Fig. 3).

228

229

230 **Genetic divergence**

231 Consistent with prediction that genetic analysis would confirm divergence in
232 transequatorial migration of the *P. cookii* populations over historical timescales, all nine
233 historical BC *P. cookii* skins had mitochondrial *cytochrome c oxidase subunit 1* (COI)
234 haplotypes that were identical to those of the modern LBI population³⁸ (Fig. 1). Seven
235 of ten historical HC *P. cookii* skins shared the same haplotype as that of modern CDF *P.*
236 *cookii*³⁸ and each of the three remaining skins had a novel haplotype (Fig. 1). We
237 previously identified a single nucleotide polymorphism (SNP; at site 156) that
238 differentiates modern LBI and CDF *P. cookii*³⁸. All haplotypes sequenced from
239 historical HC *P. cookii* skins in this study share the same diagnostic SNP as modern
240 CDF birds, including the three novel haplotypes (Fig. 1, Supplementary Figure S2,
241 Supplementary Tables S1, S2 and S3). These results support the previous predictions of
242 contemporary and historical transequatorial separation of the extant *P. cookii*
243 populations, revealed by our tracking and isotopic analyses, and suggests that these two
244 populations have been genetically structured for a minimum of 100 years.

245

246 **Discussion**

247 Intrinsic factors argued to restrict gene flow between seabird populations include natal
248 philopatry¹⁹, divergent breeding timetables^{39,40} and differences in breeding and non-
249 breeding distributions^{8,12,17}, though how these interact is poorly understood. Our
250 combined results suggest that the use of population specific non-breeding habitats plays
251 an interactive role in the restriction of gene flow, as both a pre-mating and post-mating
252 barrier. In regards to the former, migration routes of differing lengths or directions, are
253 widely recognised pre-mating barriers in migrant terrestrial bird species^{5,41,42}. In *P.*
254 *cookii* differences in the duration of migratory movement or non-breeding distribution

255 seem to underlie the pronounced breeding asynchrony between the populations.
256 Moreover, regional differences in the timing of peak primary productivity, or the onset
257 of gonad development based upon differences in day length and temperature shifts ⁴³,
258 could amplify asynchronies in breeding timetables beyond those mediated by
259 differences in route or non-breeding residency times alone. Thus, it is not segregation
260 during the non-breeding season *per se*. that represents a pre-mating barrier to gene flow.
261 Rather, it is the interaction between differing non-breeding distributions and divergent
262 breeding timetables, combined with high natal philopatry, which restricts gene flow.

263

264 In regards to the latter, adult Cook's petrel desert their chicks up to two weeks prior to
265 fledging and, as seen in many migratory species ^{5,41}, chicks presumably follow an
266 inherited migratory direction and timing ^{5,42}. Studies of migrant terrestrial bird species
267 indicate that the inheritance of suboptimal migration routes during secondary contact
268 represents a post-mating barrier to gene flow ^{10, 40}. Although secondary contact is
269 presumably rare in *P. cookii*, the inheritance of an alternative or intermediate migratory
270 strategy would place individuals at a selective disadvantage if it led to the occupancy of
271 suboptimal non-breeding grounds or breeding timetables that were out of synchrony
272 with the rest of the population ^{10, 40}.

273

274 Habitat specialisation during both the breeding and non-breeding season is also likely to
275 promote divergence among the two extant *P. cookii* populations via local adaptation.
276 For example, when breeding, *P. cookii* exhibit divergent, although overlapping
277 distributions and diets in response to regional differences in oceanography ^{25 (current study)}.
278 Moreover, the populations differ in body mass ²² with smaller LBI birds foraging in
279 warmer low-latitude waters compared to larger CDF conspecifics ²⁵. That individuals

280 from these two populations also occupy oceanic waters with similarly divergent
281 characteristics during the non-breeding period (i.e., LBI birds occupy warmer less
282 productive waters than CDF birds; Fig. 1) suggests population-specific adaptation to
283 differing marine habitats, possibly linked to body size. Indeed, differences in seabird
284 habitat use related to body size have been observed in other studies, particularly in
285 species with pronounced sexual size dimorphism⁴⁴⁻⁴⁶. It remains uncertain whether
286 body size differences between populations of *P. cookii* are a cause or consequence of
287 divergent habitat use. Regardless, our data support and extend local adaptation
288 hypotheses by suggesting that conspecific seabird populations can become tied to
289 particular marine habitats during the breeding^{18,39,47} and non-breeding periods (current
290 study), presenting opportunities for population divergence.

291

292 Overall, this study demonstrates the use of integrative techniques to track space use,
293 behaviour, foraging, and breeding to demonstrate clear spatial segregation of non-
294 breeding distribution between two populations which, mediated by its influence on
295 breeding phenology, appears to represent an intrinsic barrier to gene flow, and has lead
296 to local adaptation in a highly mobile seabird.

297

298 **Methods**

299 **Tracking and environmental data**

300 *P. cookii* breeding on LBI and CDF were equipped with light-based geolocation loggers
301 (British Antarctic Survey, Mk14) in November-December 2007 (LBI, 36° 11'S, 175°
302 04'E, n = 13; CDF, 46° 11'S, 167° 38'E, n = 14) during early incubation. Loggers were
303 deployed on birds of known breeding history using published²⁵ with the total package
304 weighing < 1% of body mass. The sex of all birds were previously determined using

305 molecular methods ^{25,48}. The following breeding season, 24 (89%) birds (LBI n = 12
306 and CDF n = 12) returned to breed and were recaptured in January - March 2009 at their
307 same breeding burrows, and loggers were removed. Two loggers (LBI n =1 and CDF n
308 = 1) failed to download resulting in 11 datasets from each population for processing and
309 analyses.

310

311 Light data from the loggers were processed using Multitrace software (Jensen Software
312 Systems) and locations (2 d^{-1}) were estimated with an expected mean accuracy \pm SD of
313 $186 \pm 114 \text{ km}$ ⁴⁹. Sunrise and sunset times were identified based on light curve
314 thresholds, with latitude calculated from day/night length and longitude calculated from
315 the time of local midday/midnight relative to Greenwich Mean Time. As a result of day
316 length uniformity around the equinoxes, clearly erroneous locations occurring 3-4
317 weeks either side of the equinox were excluded. Furthermore, points that involved
318 movements of $> 1600 \text{ km}$ in one day ⁵⁰, those with interruptions to light curves around
319 sunset and sunrise, or that were clearly outside of the known or possible range for *P.*
320 *cookii*, were removed from the data set.

321

322 Totals of 7,886 and 9,082 locations were obtained for LBI and CDF *P. cookii*
323 respectively, of which 9.7% and 10.6% were excluded after filtering. Filtered locations
324 were then used to estimate year-round utilisation distribution (UD) kernels for each
325 population following methods detailed in ref ⁵¹. In brief, 2-D Gaussian kernel densities
326 were estimated using custom routines created in MatLab ⁵¹ (The Mathworks, Natick,
327 MA, USA). Kernels were calculated using a Lambert Cylindrical Equal Area projection
328 on an 80 km grid with grid cells normalized for bird effort by dividing each cell by the
329 number of birds contributing the locations within a cell. The kernel smoothing

330 parameter (h) was estimated using an adaptive method ⁵² to estimate an optimal local
331 value, following ref. ⁵³. Based published methods ²⁵, a 1,000 km buffer was used
332 around each colony to define breeding habitat, and the 80% contour of UD kernels,
333 calculated individually, were used to define the core non-breeding distributions for each
334 bird ⁵⁰. Dates of the first and last locations to enter and exit the core non-breeding
335 habitats were used to define migration timing for each individual. Individuals' migration
336 distances were calculated by summing the point to point distances travelled during post-
337 breeding and pre-breeding movements between these core areas.

338

339 Satellite-derived remotely-sensed environmental data were used to contrast the core
340 habitats of *P. cookii* from LBI and CDF during the non-breeding period (presence
341 dataset) as well as those available, but not used, within each population-specific region
342 (absence dataset). For the presence dataset, environmental data were extracted for
343 logger locations falling within the 20% UD for each tracked bird using a 1° longitude by
344 2° latitude grid centred (the approximate error of geolocation estimates) on the date and
345 coordinates of the location ⁵¹. For the absence dataset, environmental data were
346 extracted from ten randomly selected locations, derived within a 1,000 km radius buffer
347 of each logger location and centred on the corresponding logger location date.
348 Environmental data extracted for the random locations were averaged to give a mean
349 absence estimate to contrast presence values. Remotely-sensed environmental data
350 were obtained from NOAA's Environmental Research Division
351 (<http://coastwatch.pfel.noaa.gov/thredds/catalog.html>) including 5-day composites of
352 chlorophyll *a* (Chl *a*) concentration (mg Chl m⁻³) at a spatial resolution of 0.1°
353 resolution ⁵⁴ and 8-day composites sea surface temperature (SST) in °C with a spatial
354 resolution of 0.1° ⁵⁵. Bathymetric data were obtained from the ETOPO2 dataset ⁵⁶.

355

356 **Stable isotopes**

357 To contrast population-specific dietary signals during the non-breeding period, we
358 conducted stable isotope analyses of C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) ratios in body feathers
359 collected from modern LBI and CDF *P. cookii* and museum specimens held at the
360 Californian Academy of Sciences (n = 9) and American Museum of Natural History (n
361 = 10). Single body feathers were collected from breeding *P. cookii* in 2006 and from
362 tracked birds upon their recapture in 2009, with no resampling of birds between years.
363 Modern and historical feathers were cleaned with 70% ethanol, then washed in distilled
364 water to remove contaminants, dried in at 50°C and cut into fine fragments using
365 scissors. Stable isotope analyses of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, using a subsample (approximately
366 0.7 mg) of each homogenised feather, were carried out on a DeltaPlus (Thermo-
367 Finnigan) continuous flow isotope ratio mass spectrometer using protocols outlined by
368 ref²⁵. Measurement precision of the isotope analysis was 0.29‰ for $\delta^{15}\text{N}$ and 0.24‰
369 for $\delta^{13}\text{C}$. To account for the Seuss effect, the temporal biasing of the atmospheric CO₂
370 pool to more negative $\delta^{13}\text{C}$ values as a result of the burning of fossil CO₂, $\delta^{13}\text{C}$ data
371 from historical feathers were normalised by subtracting a year-specific factor $\delta^{13}\text{C} = -1$
372 $+ 1.1^{(2009-\text{year} (1905 \text{ or } 1913)) \cdot 0.027}$ following ref⁵⁷.

373

374 **Genetic analyses**

375 Toe pad skin samples were collected from the same historical Cook's petrel specimens
376 from which feathers were sampled for stable isotope analyses (Supplementary Table S1
377 and S2). DNA extraction and polymerase chain reaction (PCR) set up was performed in
378 a physically isolated dedicated ancient DNA laboratory. Contamination was monitored
379 using extraction and PCR negative controls and genomic DNA was isolated as per ref

380 ⁵⁸. A 375 base pair (bp) region of the mitochondrial *cytochrome c oxidase subunit 1*
381 gene (COI) was amplified using two sets of primers that amplified two overlapping
382 fragments: AWCF1 and AWCintR2 ⁵⁸; LCRintF2 5'-TCATAATTGGGGGATTTGGA-
383 3' (designed using Primer3 software ⁵⁹) and AWCintR3 ⁵⁸. This region corresponds to
384 the first 375 bp of the 677 bp fragment sequenced by ref ³⁸. PCR products were purified
385 using a QIAquick PCR Purification kit (Qiagen) then sequenced bidirectionally from
386 independent PCRs ⁵⁸. Sequences were concatenated and aligned using Sequencher
387 version 4.8 (Gene Codes), deposited in NCBI GenBank (accession numbers HQ263645
388 to HQ263663) and compared with those in ref ³⁸.

389

390 **Statistical analyses**

391 Habitat data extractions, processing and analyses, were conducted using Matlab. Non-
392 parametric Mann-Whitney U tests were used to test for differences between presence
393 and absence habitat data for the extracted environmental parameters at an intra-
394 population level, and for the presence data at an inter-population level. Mean
395 environmental parameter values for individual birds were used as the sampling unit.
396 Mann-Whitney U tests were initially used to compare stable isotope values between
397 years (2006 and 2009) for LBI and CDF. Isotope data ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) were
398 subsequently pooled for each population and permutation-based non-parametric
399 ANOVA, with pair-wise comparisons using the Bonferroni correction method,
400 conducted to compare isotope values between individuals from the breeding
401 populations (LBI and CDF) and museum skin specimens (CAS 1905 and AMNH 1913)
402 using the programme PERMANOVA. Sex was initially included as a factor in all
403 analyses, but excluded as a result of non-significant differences.

404

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416

417 **Author Contributions**

418 M.J.R, D.R.T, P.M.S, M.E.H, S.A.S, and T.E.S designed the research. M.J.R, T.J.L,
419 R.A.P., L.R and S.A.S processed and analysed spatial data. M.J.R., H.A.L, and T. E. S
420 conducted genetic analyses, and S.J.B, M.E.H and M.J.R processed and analysed
421 isotope data. M.J.R wrote paper and all authors discussed the results and contributed to
422 the manuscript.

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424 **Competing financial interests:** The authors declare no competing financial interests.

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436 **Figure legends**

437 **Fig. 1. Pacific migrations of tracked *P. cookii***

438 Movements of *P. cookii* breeding on Little Barrier Island (red circle, North Island) and
439 Codfish Island (purple circle, South Island), New Zealand. Approximate post-breeding
440 and pre-breeding migration routes of tracked LBI (red dashed lines) and CDF (purple
441 dashed lines) birds begin and end with mean migration departure and arrival dates
442 (white text). Red and purple tones, and associated contour lines, represent the 95%,
443 75%, 50%, and 25% kernel estimates for LBI and CDF birds respectively. Pie charts
444 show the geographic distribution of cytochrome *c* oxidase subunit 1 mtDNA haplotypes
445 sequenced from modern *P. cookii* populations (charts attached to LBI and CDF colony
446 locations) and historical *P. cookii* skins collected in the North (BC) and South Pacific
447 (HC) Ocean in 1905 and 1913 respectively (charts attached to white circles showing
448 approximate collection location). Pie chart size reflects genetic analysis sample size:
449 modern *P. cookii* LBI $n = 26$ and CDF $n = 19$; historical *P. cookii* BC $n = 9$ and HC $n =$
450 10.

451

452 **Fig. 2 Isotope ratios of contemporary and historic *P. cookii* feathers**

453 Feather isotope signatures of *P. cookii* (\pm SD) from LBI (red circle, 2006 (untracked)
454 and 2008 (tracked) combined, $n = 31$) and CDF (purple circle, 2006 (untracked) and

455 2008 (tracked) combined, $n = 29$) and from historical skins collected in the North
456 Pacific (BC) (black circle, 1905, $n = 9$) and South Pacific Ocean (HC) (clear circle,
457 1913, $n = 10$).

458

459 **Fig. 3 Characteristics of selected oceanic habitats**

460 Box plots of median values for remotely sensed environmental data (a. water depth, b.
461 sea surface temperature, c. chlorophyll *a* concentration) from logger locations of *P.*
462 *cooki* tracked from Little Barrier Island (LBI, $n = 11$) and Codfish Island (CDF, $n = 11$)
463 during occupancy of core non-breeding habitats (LBI Pres. and CDF Pres., 20% UD)
464 and in randomly selected proximate locations (LBI Abs. and CDF Abs.) see Methods.
465 Asterisks represent significance of difference for group comparisons: * $p = 0.05$, ** $p =$
466 0.01 , *** $p = 0.001$, - = not significant. Box plots illustrate 25th, 50th (median), and
467 75th percentiles, error bars represent minimum and maximum values falling within 1.5
468 Inter Quartile Range, and crosses plot the outliers.

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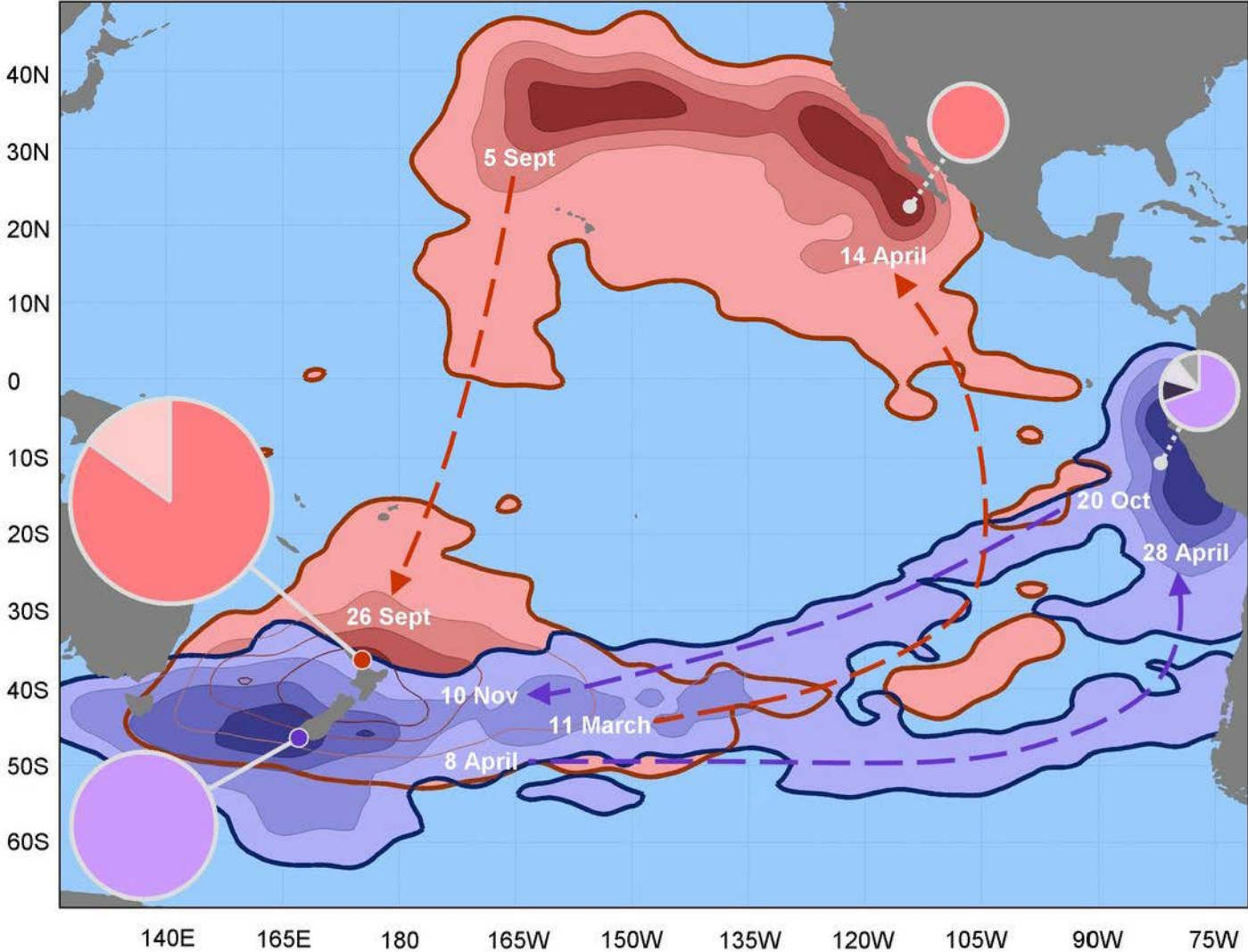
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