

1 Wintering in the sun: niche partitioning by three nonbreeding *Pterodroma* petrel  
2 species in the equatorial Pacific Ocean

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4 Running head: Niche partitioning by nonbreeding *Pterodroma* petrels

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6 M. J. Rayner<sup>1,2</sup> \*, N. Carlile<sup>3</sup>, D. Priddel<sup>3</sup>, V. Bretagnolle<sup>4</sup>, M. G. R. Miller<sup>5</sup>, R. A. Phillips<sup>6</sup>, L.  
7 Ranjard<sup>7</sup>, S.J. Bury<sup>8</sup> & L. G. Torres<sup>9</sup>

8

9 <sup>1</sup> Auckland Museum, Private Bag 92018, Auckland, 1141, New Zealand.

10 <sup>2</sup> School of Biological Sciences, University of Auckland, 3A Symonds Street, Auckland, PB 92019,  
11 New Zealand.

12 <sup>3</sup> Office of Environment and Heritage, PO Box 1967, Hurstville, NSW 2220, Australia.

13

14 <sup>4</sup> Centre National de la Recherche Scientifique, Centre d'Etudes Biologiques de Chizé,  
15 F-79360 Beauvoir-sur-Niort, France.

16

17 <sup>5</sup> Centre for Tropical Environmental and Sustainability Science, James Cook University, PO Box  
18 6811, Cairns, Queensland, 4870, Australia.

19

20 <sup>6</sup> British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road,  
21 Cambridge CB3 0ET, UK

22

23 <sup>7</sup> Research School of Biology, The Australian National University, Canberra, ACT 0200, Australia

24

25 <sup>8</sup> National Institute of Water and Atmospheric Research, PO Box 14-901, Kilbernie, Wellington 6011,  
26 New Zealand

27

28 <sup>9</sup> Marine Mammal Institute and Department of Fisheries and Wildlife, Hatfield Marine Science Center,  
29 Oregon State University, Newport, Oregon, United States of America.

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32 \*mrayner@aucklandmuseum.com

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43 **Abstract**

44 Niche divergence is expected for species that compete for shared resources, including migrants that  
45 occupy similar regions during the non-breeding season. Studies of temperate seabirds indicate that  
46 both spatial and behavioural segregation can be important mechanisms for reducing competition, but  
47 there have been few investigations of resource partitioning by closely-related taxa in low productivity,  
48 tropical environments. We investigated niche partitioning in three gadfly petrel taxa, *Pterodroma*  
49 *leucoptera leucoptera* (n = 22), *P. leucoptera caledonica* (n = 7) and *P. pycrofti* (n = 12) during their  
50 non-breeding season in the eastern tropical Pacific Ocean by combining tracking data from  
51 geolocator-immersion loggers with remotely-sensed environmental data in species distribution models  
52 (SDMs), and by comparing feather stable isotope ratios. The three taxa showed spatial partitioning;  
53 two foraged in the North Equatorial Counter Current and one in the South Equatorial Current. This  
54 reflected differences in their realised habitat niches, with significant taxon-specific responses to  
55 thermocline depth, sea surface temperature and bathymetry. There were also differences among taxa  
56 in activity patterns, and all birds spent a much larger proportion of time in flight at night than during  
57 the day, suggesting predominance of nocturnal foraging behaviour. Comparison of stable isotope  
58 ratios in feathers suggests that *P. leucoptera leucoptera* and *P. pycrofti* mainly consume vertically-  
59 migrating mesopelagic fishes, whereas the diet of *P. leucoptera caledonica* also include some lower  
60 trophic level including crustaceans and squid. Unique insights can be gained from studies of the  
61 foraging ecology of tropical pelagic seabirds, in comparison with temperate and polar waters, and are  
62 urgently required for understanding and protecting tropical avifauna in key marine habitats

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## 70 **Introduction**

71 The distribution of top predators in the marine environment is frequently linked to physical  
72 oceanographic processes that govern spatial and temporal variation in primary productivity and  
73 associated prey availability (Block et al. 2011). In particular, physical forcing in marine boundary  
74 currents creates convergence and upwelling zones known as some of the most productive marine  
75 environments on earth, where predators target and compete for prey concentrations that can be  
76 predictable at meso to large spatial scales (Belkin et al. 2009, Bost et al. 2009). Studies of seabird  
77 distribution during the breeding season demonstrate that populations minimise interspecific  
78 competition in such foraging zones through a variety of mechanisms including segregation in space  
79 and time, behaviour and diet (Phalan et al. 2007, Navarro et al. 2013, Moreno et al. in press). During  
80 the nonbreeding season, when seabirds are free from central-place foraging constraints, studies  
81 highlight the importance of spatial and dietary segregation, frequently across ecological gradients  
82 related to ocean temperature, reflecting the location of boundary systems (Spear et al. 2007, Thiebot  
83 et al. 2012, Cherel et al. 2013, Navarro et al. 2015, Quillfeldt et al. 2015).

84 Small gadfly *Pterodroma* petrels within the subgenus *cookilaria* (~ 10 species) are a group of seabirds  
85 that usually make long distance migrations during the non-breeding season to productive boundary  
86 systems in the temperate northern and southern Pacific Ocean where they exhibit both spatial and  
87 temporal resource partitioning (Rayner et al. 2011, Rayner et al. 2012, Priddel et al. 2014). However,  
88 not all *cookilaria* migrate to temperate habitats, with some species occupying tropical non-breeding  
89 habitats such as the eastern tropical Pacific Ocean (ETPO) (Kessler 2006), where they are part of a  
90 diverse seabird community (Au & Pitman 1986, Ballance et al. 1997, Spear et al. 2007, Priddel et al.  
91 2014). Both theoretical (Pianka 1974) and empirical data (Torres 2009, Young et al. 2010) suggest  
92 that in such low productivity tropical habitats, competitors will increase niche separation to avoid  
93 competition. Accordingly, the community of *cookilaria* in the ETPO represents a distinctive  
94 ecological system for investigating niche partitioning in small Procellariiformes, providing a useful  
95 comparison with studies in temperate systems (Ainley et al. 1992, Navarro et al. 2015)

96 A number of gadfly petrels endemic to breeding sites in temperate Australasia are known, or  
97 considered likely, to occupy the ETPO during part of their seasonal cycle. Gould's Petrel  
98 (*Pterodroma leucoptera*; ~200–250 g) occurs as two subspecies with low levels of gene flow between  
99 populations breeding on islands off the coast of New South Wales, Australia (*P. leucoptera*  
100 *leucoptera*, hereafter *leucoptera*) and on the main island of New Caledonia (*P. leucoptera caledonica*,  
101 hereafter *caledonica*)(de Naurois 1978, Priddel et al. 1995, Gangloff 2010). During the nonbreeding  
102 season, both subspecies migrate to the ETPO (Priddel et al. 2014). Pycroft's petrel (*Pterodroma*  
103 *pycrofti*, hereafter *pycrofti*) is endemic to islands off the northeast coast of New Zealand (~130 –200 g  
104 (Marchant & Higgins 1990) but has a poorly known nonbreeding distribution that likely extends, in  
105 part, to the tropical Pacific (Spear et al. 1992). Recent genetic research indicates that *pycrofti* is a  
106 sister taxon to *leucoptera* and *caledonica* (Steeves et al in prep) presenting an opportunity for  
107 comparative analysis of foraging ecology in these morphologically and genetically similar taxa.

108 We investigated niche separation in *leucoptera*, *caledonica* and *pycrofti* during the nonbreeding  
109 season by combining tracking data from geolocator-immersion loggers with remotely-sensed  
110 environmental data in species distribution models (SDM), and by comparing stable isotope ratios in  
111 feathers grown by tracked individuals during the same period. Our aims were to present the first  
112 detailed analysis of the nonbreeding movements of individual *pycrofti* and to highlight differences in  
113 habitat use and foraging ecology indicative of niche partitioning among these three closely-related  
114 taxa.

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117 **Materials and Methods**

118 Tracking data

119 Tracking methods for *leucoptera* and *caledonica* are provided by Priddel *et al.* (2014). In summary,  
120 combined geolocator-immersion loggers (MK14, British Antarctic Survey, Cambridge, UK and  
121 NanoLAT2900, Lotek, Ontario, Canada) were deployed on adult *leucoptera* (subspecies population  
122 size 800 – 1000 breeding pairs (Priddel & Carlile 2007)) at Cabbage Tree Island (Australia) on March  
123 2010 and *caledonica* (subspecies population size 1000 – 10000 breeding pairs (Brooke 2004)) at  
124 Grande Terre (the main island of New Caledonia) in January 2010. Loggers were retrieved at both  
125 sites between November 2010 and January 2011 providing data on the entire nonbreeding period for  
126 22 *leucoptera* and 7 *caledonica* respectively. Similar loggers (MK18, British Antarctic Survey,  
127 Cambridge, UK, 2g) were attached to twelve *pycrofti* (subspecies population size 2500 – 4000  
128 breeding pairs (Brooke 2004)) at Red Mercury Island (New Zealand) in December 2009, and 10  
129 (83%) were retrieved in January 2011, of which two failed to provide data. All loggers were attached  
130 using the methods described by Rayner *et al.* (2008) and weighed < 1.5% of adult body mass.

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132 Light data from the loggers were processed following the methods of Rayner *et al.* (2012). The  
133 nonbreeding phase was defined according to Priddel *et al.* (2014) based on the first location outside or  
134 inside a 1000 km buffer (an arbitrary but standardised measure) around the colony at the end or start,  
135 respectively, of the breeding season. The loggers tested for saltwater immersion data every 3 s, with  
136 the data binned into ten minute intervals, resulting in values ranging from 0 (dry) to 200 (immersed  
137 for whole period). These data were analysed using the methods of Rayner *et al.* (2012), providing  
138 temporal data on percent of time immersed, flight bouts greater than 10 minutes, and duration of flight  
139 bouts during daylight and darkness (based on the timing of civil twilight) for each species.

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141 Construction of species distribution models (SDM)

142 Post-processed geolocation data from each species during the nonbreeding season were included in  
143 binomial species distribution models (SDM) following methods presented in Torres et al. (2015). In  
144 brief, locations from tracked individuals of each species (*leucoptera* n = 22, *caledonica* n = 7, *pycrofti*  
145 n = 8) were used to construct monthly kernel density estimates (search radius 200 km) during the non-  
146 breeding season for all three species between April and October. Presence data for each SDM were  
147 those locations that fell within the 50% density contour for each of those months, which was  
148 considered to represent core habitat. Background data (otherwise known as pseudo-absences)  
149 implemented in the SDM for each month were uniformly-spaced locations (every 100 km<sup>2</sup>) falling  
150 within the 90% density contour for all species locations (April through October; n = 6245). This  
151 method was based on the assumption that all habitat was equally available to the three taxa within the  
152 timeframe of their non-breeding phase. Background locations were randomly assigned dates between  
153 the date of arrival and departure for each species, and bird identity in proportion to the number of  
154 presence points from each bird. Using these background and presence data we produced binomial  
155 boosted regression tree (BRT)(Freidman 2001) models of presence-availability (Boyce et al. 2002,  
156 Torres et al. 2015) that describe the distribution of each *cookilaria* petrel relative to the available  
157 habitat across the entire tropical pacific region exploited by all species.

158 For each species model of presence-availability, a range of static and remotely-sensed environmental  
159 data were used to describe habitat use. Depth values at each presence and background point were  
160 extracted from the 30 arc-second General Bathymetric Chart of the World (<http://www.gebco.net/>;  
161 GEBCO). Seabed slope angle and minimum distance to land were derived from the GEBCO  
162 bathymetry data using the package 'raster' in R 3.1.1 (R Core Team 2014). Several dynamic  
163 oceanographic variables (Table 1) were obtained from NOAA ERDDAP web servers using the  
164 Xtractomatic routines in R (<http://coastwatch.pfel.noaa.gov/xtracto/>): Chlorophyll-a concentration  
165 (CHL; 8-day), Sea surface temperature (SST; 8-day), sea surface height deviation (SSH; 1-day),  
166 Ekman upwelling (EKM; 3-day) and wind speed (WIND; 3-day). We obtained gridded, annual  
167 climatology data (12 month) for top of thermocline depth from IFREMER  
168 (<http://www.ifremer.fr/cerweb/deboyer/mld>); selecting the appropriate monthly grids for the non-

169 breeding period. The median values obtained for these environmental variables were those within a  
170 200km radius of each location. This extraction technique accounted for the potential 200+ km spatial  
171 error in geolocation data (Phillips et al. 2004). The absolute deviation of the dynamic variables were  
172 also included in the models to assess how environmental variability may influence petrel habitat and  
173 log transformations of slope, WIND, CHL and EKM were implemented in the models to account for  
174 skewed distributions.

175 SDMs of each petrel species were generated using BRT models, which has demonstrated strong  
176 predictive performance and model parsimony, including for another pelagic petrel species (Elith et al.  
177 2006, Buston & Elith 2011, Torres et al. 2013, Torres et al. 2015). BRT is a machine learning method  
178 that can handle correlated, interacting and non-linear data, all of which are common in ecological  
179 studies (Leathwick et al. 2006, Elith et al. 2008). Two algorithms are applied in BRT modelling: the  
180 first partitions the predictor space into homogeneous response groups using decision trees, and the  
181 second boosts this process to iteratively optimize the predictive performance of the model (Elith et al.  
182 2008). The process combines a large number of individual decision trees to generate a BRT model.

183 The contribution of each predictor variable to a BRT model is determined by the number of times it is  
184 used to split a tree branch. If a predictor variable contributed less than 5% to the model, the model  
185 was re-run without that variable (Buston & Elith 2011). The learning rate ( $lr$ ) of a BRT determines the  
186 contribution of each fitted tree to the final model and was set at 0.0025, while the bag fraction, which  
187 is the proportion of samples used at each tree from the whole dataset, was set at 0.5. Tree complexity  
188 ( $tc$ ), which represents the number of nodes on each tree and determines the number of interactions  
189 between predictors, was allowed to vary between 1 and 4 so that the number of boosting iterations,  
190 known as the number of trees ( $nt$ ), was greater than 1000, as recommended by Elith et al. (2008).

191 Each model dataset included multiple presence and background points from the same bird track, and  
192 with varying sample sizes; to account for this internal structure in the datasets, CV-folds were  
193 specified (De'ath 2007) as all presence and background locations from an individual bird. CV-folds  
194 withhold subsets of data from the model at each tree that are subsequently used to test model fit.

195 While generating each BRT, 10% of presence and 10% of background locations were withheld from  
196 model calibration for external validation to assess predictive performance and select optimal model  
197 parameters. Four metrics were used to select the optimal model and evaluate predictive performance:  
198 cross-validation deviance explained and area under the receiver operator curve (AUC) calculated  
199 during the modelling procedure, and by external validation metrics of deviance between observed and  
200 predicted values (validation deviance) and AUC (validation AUC) calculated using the withheld data.  
201 Due to the presence *vs.* availability design of the BRT models, k-fold cross validations (Boyce et al.  
202 2002) were also conducted on the optimal models to assess the predictive capacity of ‘used’ locations,  
203 while ignoring the predictability of absence locations because these are less certain when working  
204 with background or pseudo-absence data (Torres et al. 2015). The k-fold cross validation binned the  
205 predicted habitat suitability of each presence and absence location into equal-interval groups between  
206 0 and 1 (0-0.1, 0.1-0.2, 0.2-0.3, etc.), and the proportion of presence locations in each bin was  
207 determined. A Spearman-rank correlation ( $r_s$ ) was calculated between bin rank (0, 0.1, 0.2, 0.3, etc.)  
208 and the proportion of presence locations to assess whether the latter increased with increasing  
209 suitability of predicted habitat, indicating good predictive performance (Torres et al. 2015).

## 210 Stable isotope ratios

211 Observations of our study taxa indicate worn and fresh plumage at the end and beginning of each  
212 breeding season, consistent with previous research indicating that *cookilaria* moult occurs during  
213 nonbreeding when dietary signals are incorporated into new plumage (Marchant & Higgins 1990,  
214 Spear et al. 1992) (Hobson 1999). Stable isotope ratios of N ( $\delta^{15}\text{N}$ ) and C ( $\delta^{13}\text{C}$ ) provide an indication  
215 of both the trophic level and carbon source (benthic versus pelagic, inshore versus offshore, and  
216 information on water mass) of prey ingested during the time of tissue formation, which in the case of  
217 feathers from adult seabirds typically allows comparisons between trophic level and geographic  
218 segregation during the nonbreeding period (Hobson 1999, Phillips et al. 2009). To enable a  
219 comparison between stable isotope ratios and distribution from tracking data, a single body feather  
220 was collected from each *leucoptera* (n = 10), *caledonica* (n = 8) and *pycrofti* (n = 10) upon geolocator  
221 retrieval. Feathers were stored in plastic bags in the field. Once in the lab, feathers were cleaned with



222 70% ethanol, rinsed in distilled water to remove contaminants, dried in at 50°C and cut into very fine  
223 fragments. Stable isotope analyses of a subsample (~0.7 mg) of each homogenized feather were  
224 carried out at National Institute of Water & Atmospheric Research (NIWA) using an AS200\_LS  
225 autosampler and NA 1500N (Fisons Instruments, Rodano, Italy) elemental analyser combustion  
226 furnace connected to a Delta<sup>Plus</sup> continuous flow, IRMS (Thermo-Fischer Scientific, Bremen,  
227 Germany). Operational details are outlined in (Rayner et al. 2008) with the exception that  $\delta^{13}\text{C}$  values  
228 were calibrated against CO<sub>2</sub> reference gas, relative to the international standard Carrara Marble NSB-  
229 19 (National Institute of Standards and Technology (NIST), Gaithersberg, MD, USA). This, in turn,  
230 was calibrated against the original Pee Dee Belemnite (PDB) limestone standard and was then  
231 corrected for <sup>17</sup>O. A two-point normalisation process using NIST 8573 (USGS40 L-glutamic acid;  
232 certified  $\delta^{15}\text{N} = -4.52 \pm 0.12$  ‰) and IAEA-N-2 (ammonium sulphate: certified  $\delta^{15}\text{N} = +20.41 \pm 0.2$  ‰)  
233 was applied to  $\delta^{15}\text{N}$  data. Carbon isotope data were corrected via a two-point normalisation process  
234 using NIST 8573 (USGS40 L-glutamic acid; certified  $\delta^{13}\text{C} = -26.39 \pm 0.09$  ‰) and NIST 8542  
235 (IAEA-CH-6 Sucrose; certified  $\delta^{13}\text{C} = -10.45 \pm 0.07$  ‰). DL-Leucine (DL-2-Amino-4-  
236 methylpentanoic acid, C<sub>6</sub>H<sub>13</sub>NO<sub>2</sub>, Lot 127H1084, Sigma, Australia) was run every 10 samples to  
237 check analytical precision and enable drift corrections to be made if necessary. Additional  
238 international standards NIST 8574 (USGS41 L-glutamic acid; certified  $\delta^{13}\text{C} = +37.63 \pm 0.10$  ‰ and  
239  $\delta^{15}\text{N} = +47.57 \pm 0.22$  ‰), NIST 8547 (IAEA-N1 ammonium sulphate; certified  $\delta^{15}\text{N} = +0.43 \pm 0.04$ )  
240 were run daily to check isotopic accuracy. Repeat analysis of standards produced data accurate to  
241 within 0.25 ‰ for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , and a precision of better than 0.32 ‰, for  $\delta^{15}\text{N}$  and 0.24 ‰  
242  $\delta^{13}\text{C}$ .

### 243 Statistical analyses

244 Migration arrival and departure dates were compared between species using contingency analysis.  
245 Following tests for normality, a combination of non-parametric tests (Kruskall Wallace tests) and  
246 parametric tests (ANOVA) were used to test for differences among species in time spent within the  
247 non-breeding core range (50% kernel), activity parameters (based on the immersion data), and stable  
248 isotope ratios, respectively. Parametric and non-parametric multiple comparisons were used to test

249 for pairwise differences (Wilcoxon matched pairs and Tukey's pairwise comparisons) between  
250 species. Analyses were conducted using JMP 11.2.0 (©SAS Institute 2013) with a threshold of  
251 significance at  $\alpha = 0.05$ . Unless indicated otherwise, data are presented as mean  $\pm$  SD. Geospatial  
252 processing of geolocation data was conducted using ArcGIS v10.3 (ESRI, CA, USA). Extraction of  
253 remote-sensing data, creation of static environmental variables and BRT modelling were conducted in  
254 R 3.1.1 (R Development Core Team 2013) using the packages dismo (Hijmans et al. 2012), Raster  
255 (Hijmans & van Etten 2012), Gbm, PresenceAbsence (Freeman 2007), and with custom code by Elith  
256 et al. (2008).

257 **Results**

258 Processing of light data from *leucoptera* (n = 22 adults), *caledonica* (n = 7 adults) and *pycrofti* (n = 8  
259 adults), provided a total of 5287, 2330 and 2965 locations, respectively, for SDM analyses.

260 *Leucoptera*, *caledonica* and *pycrofti* exhibited spatial segregation in their core distributions within the  
261 central and eastern tropical Pacific Ocean, but there were no significant differences in migration  
262 timetables, including the time spent in core areas (Table 2). The core region used by *leucoptera* was  
263 from 10°N–5°S, 150–165°W, encompassing the eastern sector of the Republic of Kiribati (Line  
264 Islands), whereas that used by *caledonica* was 3000–6000 km southeast in the region of the East  
265 Pacific Rise (0 – 15°S, 135°- 100°W) (Figs. 1 and 2). Core areas of *pycrofti* were from 0-10°N, 140°-  
266 135°W in the eastern equatorial Pacific, and situated between those of *leucoptera* and *caledonica*  
267 (Fig. 1 and 2). The migration routes of *pycrofti* were similar to those of *leucoptera* and *caledonica*  
268 (Priddel et al 2014); all birds first migrated east from New Zealand (at approximately 40°S) and then  
269 north to reach their nonbreeding range, and the return (pre-breeding) migration was southwest through  
270 Melanesia to reach waters around their respective colony (Fig. 1).

271 Species distribution models

272 Optimal BRT models for each petrel species performed well according to internal validation metrics  
273 and external measures of predictive performance using the withheld data (Table 3). Four predictor  
274 variables were common to all three models: Thermocline, Depth, SST and Chl collectively  
275 contributed 79%, 74%, 68%, and 39%, respectively, to all three models (total contribution of 87%:  
276 261/300% for all three models). All models had a tree complexity of two, allowing one interaction  
277 between terms. Species-environment response plots for these four variables indicate that each species  
278 used different habitats (Fig. 3). Intra-species comparisons showed that presence of *leucoptera* and  
279 *caledonica* peaked in habitats where the thermocline was reached at > 100 m, and both species  
280 exhibited a positive response to a deeper thermocline. Conversely, *pycrofti* showed a negative  
281 response to a deeper thermocline, with presence peaking in habitats with the thermocline at ~ 25 m  
282 (Fig. 3). Niche separation by depth was also evident, with *leucoptera* presence peaking in the deepest

283 regions (> 5000 m), *pycrofti* in habitats with water depths of 4-5,000 m, and *caledonica* in shallower  
284 habitats (< 4000 m) (Fig. 3). *Leucoptera* presence peaked in habitats with the highest SST (27-29 °C),  
285 *pycrofti* at mid-temperatures (25-28 °C), and *caledonica* in cooler waters (20 - 26 °C) (Fig. 3). Overlap  
286 in habitat preferences relative to Chl was apparent between *caledonica* and *pycrofti*, with both taxa  
287 showing increased presence in waters with low Chl, whereas *leucoptera* avoided that habitat (Fig 3).

#### 288 At-sea activity patterns

289 There were significant differences in flight activity between daylight and darkness in all three species;  
290 tracked birds spent less time on the water and made more, and longer flight bouts in darkness (Table  
291 5; pairwise tests at 0.01). There was no significant difference in the daylight activity patterns between  
292 species; all three taxa spent a similar amount of time on the water ( $F_{2, 20} = 2.16$ ,  $P = 0.14$ ), and the  
293 number of flight bouts ( $P = 0.34$ ), and flight bout duration ( $P = 0.42$ ) were comparable (Fig. 4). In  
294 contrast, during darkness, the time spent on the water by *pycrofti* was greater than in *leucoptera* and  
295 *caledonica* (Pairwise Tukey tests  $P < 0.05$  and  $P < 0.001$ ), and by *leucoptera* was greater than in  
296 *caledonica* (Tukey HSD  $P < 0.05$ ) (Table 4, Fig. 4). The trend of higher night time activity by  
297 *caledonica* was consistent with the significantly higher number of flight bouts and longer duration of  
298 flight bouts during darkness than in *leucoptera* and *pycrofti* ( $F_{2, 20} = 8.61$ ,  $P < 0.01$ ;  $F_{2, 20} = 13.31$ ,  $P <$   
299  $0.001$ ); these last two taxa did not differ significantly in the number ( $P = 0.18$ ) or duration of flight  
300 bouts ( $P = 0.06$ ).

301 *Leucoptera* and *pycrofti* exhibited higher flight activity during daylight and darkness at the beginning  
302 and ending of the nonbreeding period, with a reduction in activity in June to August (Fig. 4).

303 *Caledonica* showed similar activity patterns across the nonbreeding season during daylight hours,  
304 whereas night time activity remained high from April to October (Fig. 4).

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308 Isotopic niche

309 Nitrogen isotope ratios differed significantly between the three species (Fig. 5;  $F_{2,27} = 19.52$ ,  $P <$   
310  $0.001$ ).  $\delta^{15}\text{N}$  in feathers of *pycrofti* ( $16.91 \pm 1.67$ ) and *leucoptera* ( $15.22 \pm 1.67$ ) did not differ  
311 significantly ( $\delta^{15}\text{N}$   $16.91 \pm 1.67$  and  $\delta^{15}\text{N}$   $15.22 \pm 1.67$  respectively; pairwise tukey test,  $p = 0.09$ ), but  
312 were higher than that in *caledonica* ( $12.45 \pm 0.93$ , Pairwise Tukey tests both  $p < 0.01$ ) (Fig. 5).  $\delta^{13}\text{C}$   
313 in feathers of *caledonica* ( $-15.72 \pm 0.55$ ) were higher than in *leucoptera* ( $-16.43 \pm 0.60$ ) but not  
314 *pycrofti* ( $-16.04 \pm 0.28$ ) (Fig. 5,  $F_{2,27} = 4.93$ ,  $P < 0.01$ , Pairwise Tukey tests: *caledonica* - *leucoptera*  
315 ( $p < 0.01$ ), *caledonica* - *pycrofti* ( $P = 0.38$ ), *leucoptera* - *pycrofti* ( $p = 0.18$ )).

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317 **Discussion:**

318 *Pterodroma* petrels are among the most wide-ranging of all birds, and capable of traversing >1,000  
319 km within a single day (Pinet et al. 2011, Rayner et al. 2011, Rayner et al. 2012). Despite this  
320 capacity for long-distance travel and thus shared habitat use, our three study taxa showed clear  
321 differences in distribution and habitat use during the non-breeding season but not in the timing of  
322 movements to and from these habitats. The core distributions of *leucoptera* and *pycrofti* were  
323 separated longitudinally - west of ~ 158° W, and east of 133° W, respectively - within the North  
324 Equatorial Counter Current (NECC) (Fig. 2, C), extending south to the edge of the cooler South  
325 Equatorial Current (SEC)(2-5°N) and north to the North Equatorial Current (NEC)(12-14°N), whereas  
326 *caledonica* was distributed mainly in the South Equatorial Current (SEC) (0 - 15°S) between 135°W  
327 and 95°W. The preference of *pycrofti* and *leucoptera* for the waters of the NECC is consistent with  
328 at-sea observations of a range of procellariiform species in this region, including *Puffinus newelli*,  
329 *Puffinus pacificus*, *Pseudobulweria rostrata* and other gadfly petrels, *Pterodroma cervicalis*,  
330 *Pterodroma externa* and *Pterodroma sandwichensis*, (Ballance et al. 1997, Spear et al. 2001).  
331 Previous studies have suggested that *leucoptera* associates with the SEC (Ribic et al. 1997).  
332 However, this previous supposition is inconsistent with our data, which indicated that the tracked  
333 *leucoptera* occupied strikingly different habitats to its sister taxon in the western NECC. This result  
334 reaffirms the utility of tracking studies for revealing population-specific foraging ranges for taxa that  
335 are similar morphologically, and therefore difficult to distinguish at sea (Rayner et al. 2011).  
336 Moreover, this utility is particularly relevant for *caledonica* and *leucoptera* with significantly different  
337 populations sizes (*caledonica* ~ 10 000 breeding pairs, *leucoptera* ~ 1000 breeding pairs; (Brooke  
338 2004, Priddel & Carlile 2007), making it particularly important to determine foraging areas and  
339 ensure a balanced assessment of at-sea threats.

340 Large scale spatial segregation is an important component of resource partitioning by small  
341 procellariiform seabirds at high latitudes, as demonstrated by recent studies linking divergent  
342 distributions with species-specific preferences for particular sea surface temperature regimes,  
343 frequently partitioned across oceanic fronts (Navarro et al. 2013, Navarro et al. 2015, Quillfeldt et al.

344 2015). The ETPO lacks the strong latitudinal gradients in temperature typical of higher latitude  
345 regions in the Southern Ocean. Instead, the SDMs for our study taxa indicate that spatial segregation  
346 was paralleled by subtle taxon-specific differences in habitat niche, across a range of environmental  
347 predictors.

348 Functional relationships with depth of the thermocline (reflecting a subsurface gradient in temperature  
349 below the warm surface mixed layer), SST and depth indicates a division into two strategies of habitat  
350 use by the three taxa; *leucoptera* and *pycrofti* foraged in deep and warm waters where the depth of  
351 the thermocline was the strongest predictor of presence yet where both species had opposing  
352 functional relationships with thermocline depth: *leucoptera* preferring a deeper thermocline and  
353 *pycrofti* a shallower one. There is evidence that in the ETPO, the thermocline depth is a strong  
354 predictor of the abundance and distribution of other seabirds (Ballance et al. 1997, Spear et al. 2001,  
355 Ballance et al. 2006). In the NECC, vertically-migrating prey aggregate at the top of the thermocline  
356 and are frequently driven to the surface by feeding tuna and dolphins and thus exploited by a range of  
357 diurnally-feeding seabirds (Ballance et al. 2006). *Leucoptera* and *pycrofti* in these habitats are  
358 solitary foragers and not considered parts of this tuna-dolphin-seabird feeding assemblage (Spear et  
359 al. 2007), yet their presence was nevertheless predicted strongly by thermocline depth, indicating that  
360 similar ecological processes influence their distribution. Conversely, the presence of *caledonica* in  
361 the SEC was associated with cooler SSTs and shallower waters, particularly over the east Pacific rise,  
362 where thermocline depth was a weak predictor. Bathymetric features associated with the east Pacific  
363 rise in this region likely provide foraging opportunities as a result of upwelling that are targeted by  
364 various *Pterodroma* species (Rayner et al. 2012).

365 In the ETPO low iron availability reduces primary production resulting in a low chl<sub>a</sub> environment  
366 (Pennington et al. 2006). The responses of the tracked birds to chl<sub>a</sub> gradients were weak and  
367 indicated the use of waters with generally uniform and low chl<sub>a</sub> values, particularly by *leucoptera* and  
368 *pycrofti* which maintained core habitats in oligotrophic waters of the NECC. This result is  
369 inconsistent with the results of studies demonstrating spatial relationships between chl<sub>a</sub>, prey and  
370 predators in the ETPO (Ballance et al. 2006) and at higher latitudes where chl<sub>a</sub> is more abundant

371 (Weimerskirch 2007, Peron et al. 2010). The analysis of immersion data from the three study taxa  
372 showed a striking pattern of reduced time resting on the surface, more numerous and longer flight  
373 bouts and higher variance in activity parameters during darkness than daylight. These results suggest  
374 that although our study taxa may forage opportunistically during daylight, their primary foraging  
375 strategy in the ETPO is to exploit nocturnally available prey, which is consistent with previous  
376 research on tropical (Spear et al. 2007, Pinet et al. 2011, Ramirez et al. 2013) and temperate  
377 procellariiform seabirds (Imber 1973, Imber 1996, Rayner et al. 2012). In a nine-year study (1983-  
378 1991), Spear et al (2007) demonstrated that the diet of small procellariform species in the ETPO,  
379 including *leucoptera*, was dominated (>90%) by vertically-migrating mesopelagic fishes that were not  
380 associated with diurnally feeding surface predators. Although our comparison of nitrogen stable  
381 isotope ratios in feathers grown during the nonbreeding period suggest little dietary segregation  
382 between *leucoptera* and *pycrofti*, which occupy waters north of the equatorial front and NECC, the  
383 mean  $\delta^{15}\text{N}$  values in these two taxa were higher than in *caledonica*, which occupy habitats in the  
384 SEC. Values of 13 to 18‰ for  $\delta^{15}\text{N}$  in *leucoptera* and *pycrofti* feathers indicates that the tracked birds  
385 were foraging at a similar trophic level to tropical piscivores (Young et al. 2010), confirming a diet  
386 likely dominated by mesopelagic fishes (myctophids, bregmacerotids, dipterygiids, and  
387 melamphids)(Spear *et al.* 2007). In contrast, the lower  $\delta^{15}\text{N}$  of *caledonica* (11.0 to 14.0‰) suggests  
388 the additional consumption of prey from lower trophic levels, such as cephalopods or marine  
389 crustaceans ( $\delta^{15}\text{N}$  of 8.1 to 10.2‰, and 3.6 to 6.5‰, )(Quillfeldt et al. 2005). This interpretation  
390 assumes there are no differences in regional baselines for  $\delta^{15}\text{N}$ , which is supported by the similarity in  
391  $\delta^{13}\text{C}$  values for all three study taxa, which is consistent with foraging in deep tropical waters within a  
392 narrow latitudinal range (Hobson et al. 1994, Young et al. 2010).

393 In conclusion, our study of three closely-related *Pterodroma* petrels in the ETPO is consistent with  
394 theoretical and empirical data on niche overlap, which predicts divergence in habitat use, diet or  
395 behaviour among competitors that are sympatric in low resource environments. The slight  
396 behavioural differences appear unlikely to reduce inter-specific competition given the high  
397 morphological similarities between the three taxa. Rather, competition appears to be avoided by



398 habitat segregation. The SDMs provide evidence that the spatial separation between these three taxa is  
399 driven by differences in realized habitat niches. However unlike temperate systems, where seabird  
400 distributions can be predicted by strong surface temperature, wind or productivity gradients, two of  
401 three of our species were present in oligotrophic waters north of the equator, and the overall  
402 distribution of our study taxa was mediated by subtle horizontal and vertical temperature gradients, as  
403 well as depth. Thermocline depth in particular was a strong predictor of presence, and its role appears  
404 linked to the unique foraging niche of the study taxa. All three taxa were highly active during  
405 darkness, and thermocline depth likely plays a critical role by governing the proximity to the surface  
406 of the key prey source, which are vertically-migrating mesopelagic fishes. The nocturnal foraging  
407 niche of the *Pterodroma* petrels parallels the diurnal tuna-dolphin-seabird assemblages that make use  
408 of shallow thermoclines in the same region (Spear et al. 2007). Our study highlights the unique  
409 insights that can be gained from comparative studies of foraging ecology between pelagic seabirds in  
410 tropical systems and temperate or polar waters, and reinforces the importance of the ETPO as a  
411 critical habitat for numerous small Procellariiformes that breed in temperate regions. Management  
412 programs seeking to protect key marine habitats for the many highly threatened temperate and tropical  
413 *Pterodromas* would benefit from further tracking to map foraging areas during the breeding and non-  
414 breeding seasons, and to identify oceanographic drivers and their impacts on distributions.

415

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424 legend”, Mr Vince Vaanders (23/03/1970 - 18/08/2013).

425 Table 1. Environmental variables used in construction of boosted regression tree models.

<b>Variable (units)</b>	<b>Product code</b>	<b>Temporal resolution</b>	<b>Spatial resolution (degrees)</b>	<b>Data source</b>
Sea Surface Temperature (°C)(SST)	TMHchla8day	8-day	0.05	MODIS AQUA <a href="http://www.oceancolor.org">www.oceancolor.org</a>
Chlorophyll- <i>a</i> Concentration (mg/m <sup>3</sup> )(Chl)	TMHsstd8day	8-day	0.05	MODIS AQUA <a href="http://www.oceancolor.org">www.oceancolor.org</a>
Sea surface height deviation anomaly (m)(SSHd)	TTAsshd1day	1-day	0.25	DUAACS AVISO <a href="http://www.aviso.oceanobs.com">www.aviso.oceanobs.com</a>
Wind speed (m/s)(Wind)	TQAumod3day	3-day	0.25	METOP ASCAT <a href="http://www.eumetsat.int">www.eumetsat.int</a>
Ekman upwelling (m/day)	TQAwekm3day	3-day	0.25	METOP ASCAT <a href="http://www.eumetsat.int">www.eumetsat.int</a>
Top of thermocline depth (m)		Monthly climatology	2	IFREMER <a href="http://www.ifremer.fr/cerweb/deboyer/mld">http://www.ifremer.fr/cerweb/deboyer/mld</a>
Depth (m)		Static	0.0083	GEBCO <a href="http://www.gebco.net">www.gebco.net</a>
Seabed slope angle (°)(Slope)		Static (derived)	0.0083	GEBCO <a href="http://www.gebco.net">www.gebco.net</a>
Distance to nearest land (km)		Static (derived)	0.0083	GEBCO <a href="http://www.gebco.net">www.gebco.net</a>

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429 Table 2. Timing of arrival and departure in core nonbreeding habitats for *leucoptera*, *caledonica*, and *pycrofti* in the eastern tropical Pacific Ocean in 2010. P values indicate  
 430 significance of contingency analysis to assess differences between species in arrival and departure dates, and time spent in core areas. Data are shown as means  $\pm$  standard  
 431 deviation in days, with range in parentheses.

	<i>P. l. leucoptera</i>	<i>P.l. caledonica</i>	<i>P. pycrofti</i>	P
Arrival nonbreeding habitat	24 Apr $\pm$ 9.8 days (7 Apr – 12 May) n = 14	18 May $\pm$ 13.0 days (4 May – 13 Jun) n = 7	21 Apr $\pm$ 12.35 days (5 Apr – 14May) n = 8	0.20
Departure nonbreeding habitat	14 Sep $\pm$ 18.7 days (15 Aug – 16 Oct) n = 9	4 Oct $\pm$ 23.5 days (31 Aug - 28 Oct) n = 7	5 Sep $\pm$ 4.24 days (2 Sept – 13 Sept) n = 5	0.51
Time in nonbreeding core	141.3 $\pm$ 17.6 days (113-161) n = 9	135.9 $\pm$ 31.1 days (78-174) n = 7	137.0 $\pm$ 16.6 days (110-152) n = 5	0.13

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443 Table 3. Boosted regression tree (BRT) model parameters and validation results for *leucoptera*, *caledonica* and *pycrofti*. Thermocline = thermocline depth; SST=sea surface  
 444 temperature; Slope = seabed slope angle; Chl = chlorophyll a concentration; SSTad = sea surface temperature absolute deviation around median; SSHD = sea surface height  
 445 deviation; Wind = wind speed. AUC varies from 0 to 1, with 1 indicating perfect model fit, 0.5 indicating random assignment. Cross validated deviance represents the mean  
 446 residual deviance per fold across the whole BRT model (lower values denotes better fit, but values cannot be compared between models). Validation deviance indicates the  
 447 mean residual deviance between the withheld presence and absence values (1 or 0) and model predicted values for those points (higher values denote better model fit). rS  
 448 indicates Spearman's rank correlation derived from k-fold cross validation of withheld presence points from each model.

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Species	Number of individuals tracked (total presence points)	Parameters (% contribution)	# of interactions	learning rate	# trees	Cross validated deviance (internal)	Cross validated AUC (internal)	Validation deviance (external)	Validation AUC (external)	rS (P-value) (external)
<i>Leucoptera</i>	22 (1963)	Thermocline (43.0) SST (22.0) Depth (14.3) log(Slope) (9.1) log(Chl) (8.6) SSHD (3.1)	2	0.0025	1350	0.151	0.765	0.938	0.841	0.9904 (<0.0001)
<i>Caledonica</i>	7 (1102)	SST (36.0) Depth (26.8) log(Chl) (15.7) Thermocline (9.4) SSTad (6.6) SSHD ( 5.5)	2	0.0025	1800	0.207	0.822	0.671	0.888	0.9880 (<0.0001)
<i>Pycroft</i>	8 (1659)	Depth (33.3) Thermocline (26.7) log(Chl) (14.8) SST (10.4) SSHD (9.6) Wind (5.2)	2	0.0025	4550	0.294	0.829	0.952	0.833	0.9893 (<0.0001)

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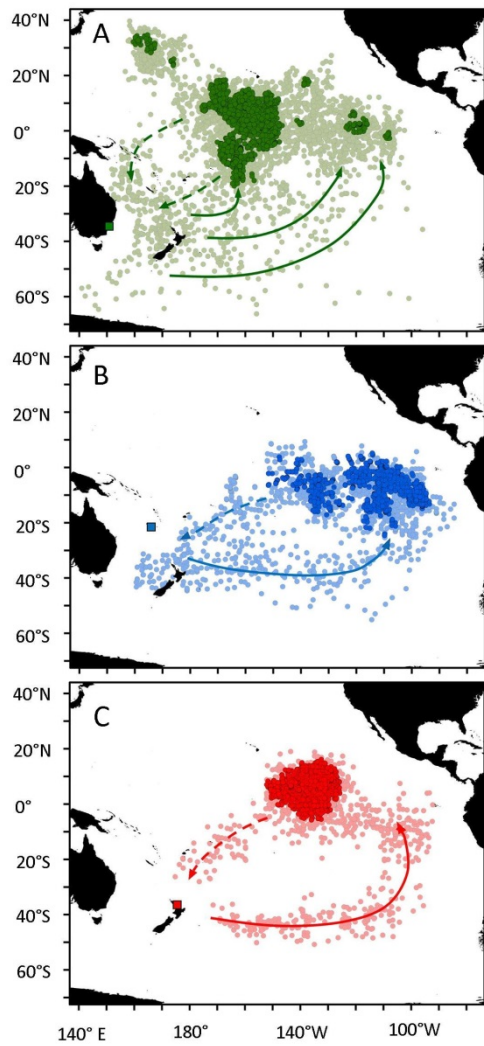
452 Table 4. Activity patterns of *leucoptera*, *caledonica* and *pycrofti* tracked with geolocator-immersion loggers in  
 453 the tropical Pacific during the nonbreeding period. Flight bouts constitute periods where loggers were dry for ten  
 454 minutes or longer. Values are the mean  $\pm$  SD.

	Proportion of time spent on water (%)		Number of flight bouts		Duration of flight bouts (min)	
	Daylight	Darkness	Daylight	Darkness	Daylight	Darkness
	<i>leucoptera</i>	75.6 $\pm$ 6.5	28.9 $\pm$ 17.4	2.0 $\pm$ 0.7	5.6 $\pm$ 1.4	25.1 $\pm$ 5.0
<i>caledonica</i>	75.8 $\pm$ 4.6	7.9 $\pm$ 4.6	1.7 $\pm$ 0.5	7.2 $\pm$ 0.5	21.7 $\pm$ 5.0	67.0 $\pm$ 14.0
<i>pycrofti</i>	83.1 $\pm$ 11.1	51.0 $\pm$ 18.3	2.4 $\pm$ 1.5	4.5 $\pm$ 1.3	25.8 $\pm$ 8.9	45.6 $\pm$ 7.9

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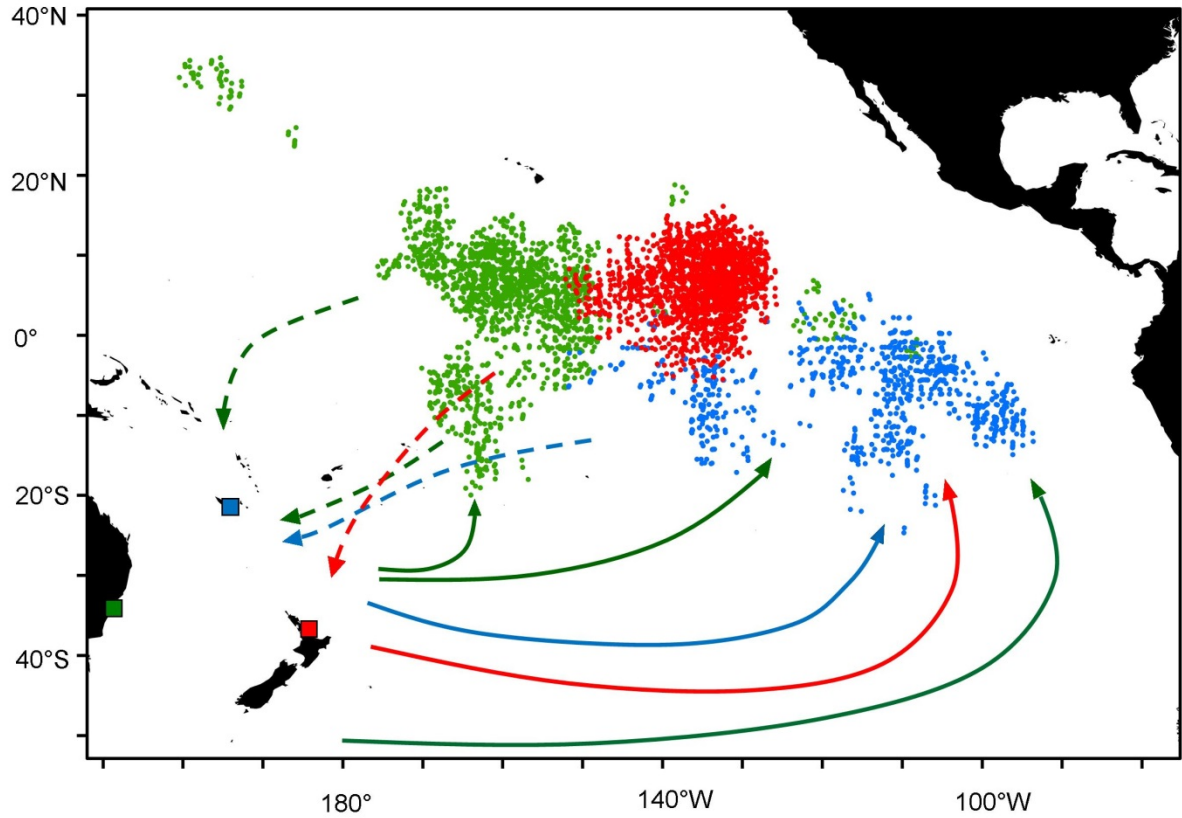


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467 Figure 1 option 1. Locations and general post-breeding (solid lines) and pre-breeding (dashed lines) migration  
 468 routes of (a) *leucoptera*, (b) *caledonica* and (c) *pycrofti* tracked with geolocators between March and November  
 469 2010. Locations shown in bold colour are those that were within monthly 50% kernels during the nonbreeding  
 470 season (Apr-Oct) and used as presence data in the species distribution models.

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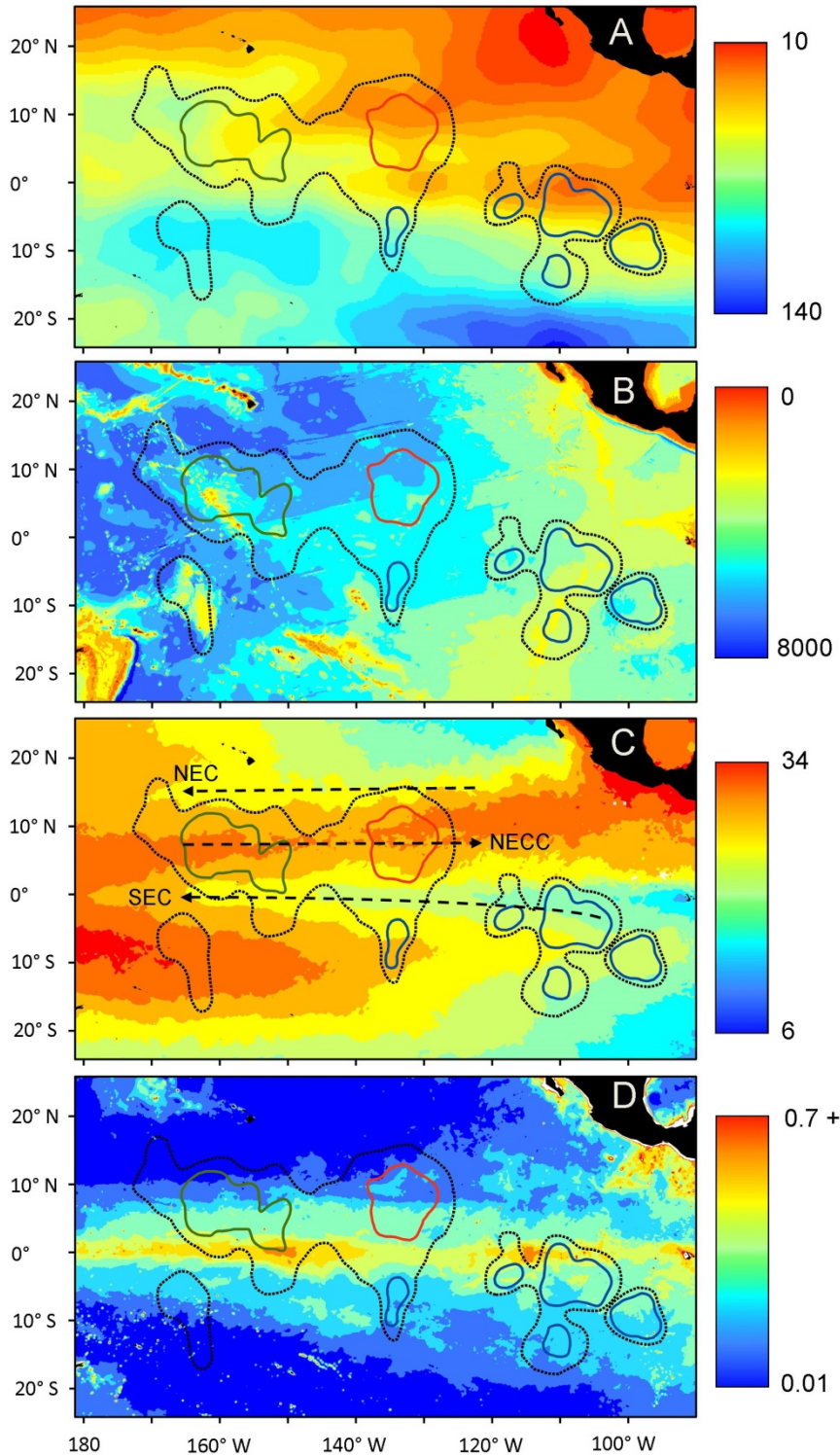
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473 Figure 1 option 2. Locations and general post-breeding (solid lines) and pre-breeding (dashed lines) migration  
 474 routes of *leucoptera*, (green) *caledonica* (blue) and *pycrofti* (red) tracked with geolocators between March and  
 475 November 2010. Locations are those that were within monthly 50% kernels during the nonbreeding season  
 476 (Apr-Oct) and used as presence data in the species distribution models. Respective species colonies shown as  
 477 squares coloured as above.

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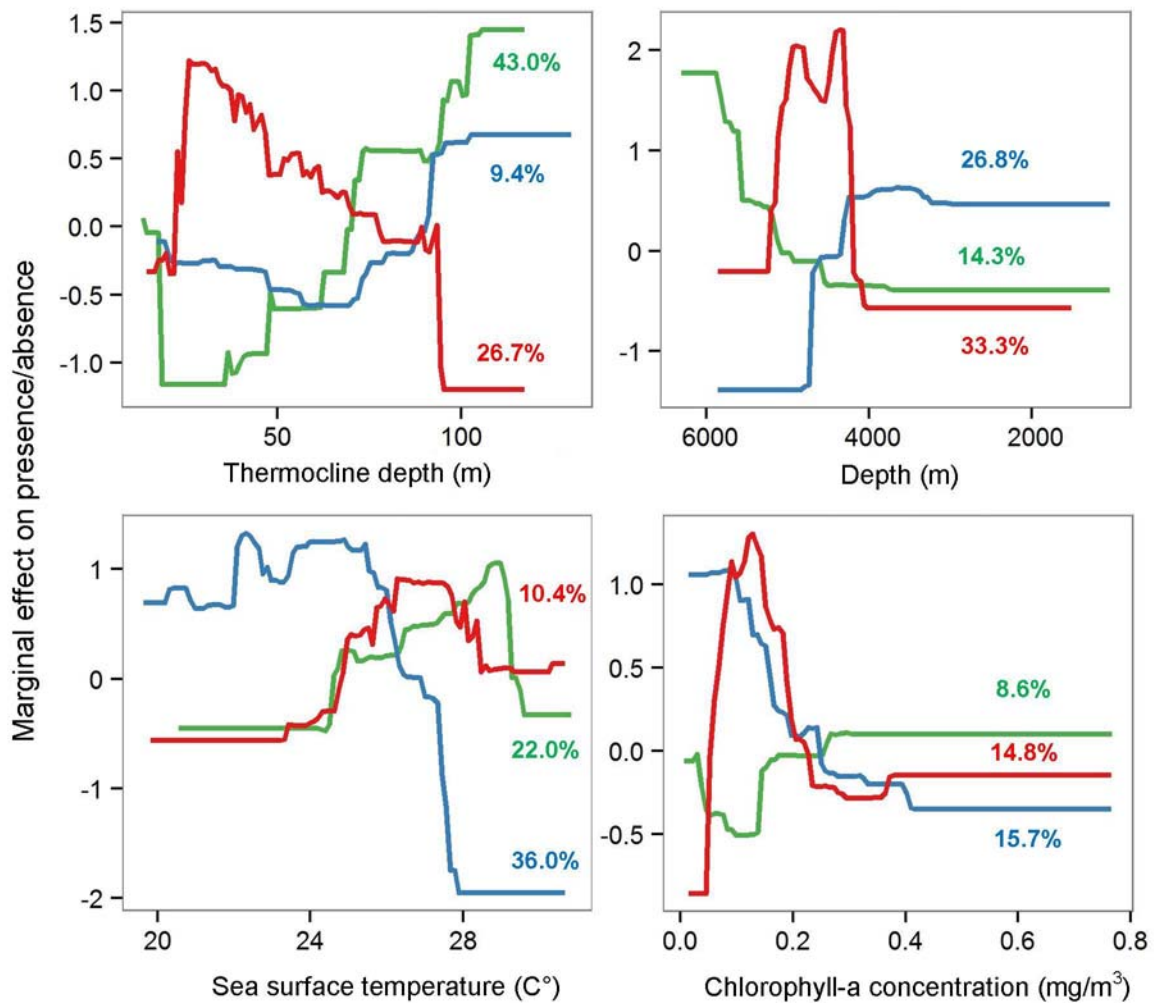
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482 Figure 2. Nonbreeding distribution of *leucoptera*, *caledonica* and *pycrofti* between April and October 2010  
 483 overlaid on averaged oceanographic climatologies for the month of July. The 90% (black dashed lines) kernel  
 484 contours of all species locations and the 50% (coloured solid lines) for each species from April to October:  
 485 *leucoptera* (green lines), *caledonica* (blue lines) and *pycrofti* (red lines). The environmental layers are ordered  
 486 by collective contribution to all three species models: A) Thermocline depth (m), B) Depth (m), C) Sea surface  
 487 temperature (C°) and D) Chlorophyll-a concentration (mg/m<sup>3</sup>). Dashed lines represent approximate locations of  
 488 the North Equatorial Current (NEC), North Equatorial Counter Current (NECC) and South Equatorial Current  
 489 (SEC) adapted from (Pennington et al. 2006).



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491 Figure 3. Comparison of fitted functions derived from presence-availability boosted regression tree models of  
 492 *leucoptera* (green lines), *caledonica* (blue lines) and *pycrofti* (red lines) in relation to the four most influential  
 493 predictor variables across all taxa. Y axes represent the relative effect of each predictor variable (x axes) on  
 494 petrel habitat use while fixing all other variables to their mean value. Positive Y-axis values represent a positive  
 495 contribution by the predictor variable to species presence, and negative values indicate a negative contribution.  
 496 The percent contribution of each predictor variable to each species model is given by labels in plot, coloured as  
 497 per species.

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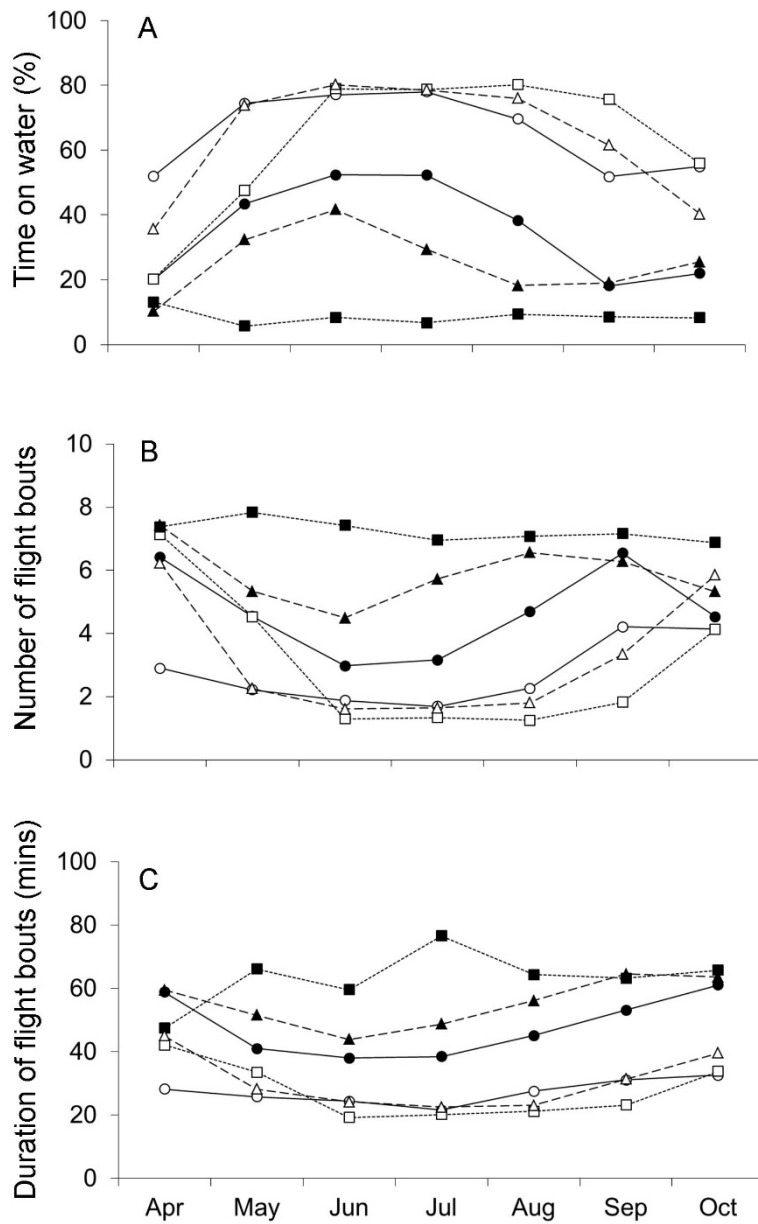
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508 Figure 4. Mean monthly activity metrics during daylight (clear symbols) and darkness (filled symbols) for  
509 *leucoptera* (triangles), *caledonica* (squares), and *pycrofti* (circles) tracked with geolocator-immersion loggers  
510 during the nonbreeding season including A) Percent of time on water, B) Number of flight bouts and C)  
511 Duration of flight bouts.

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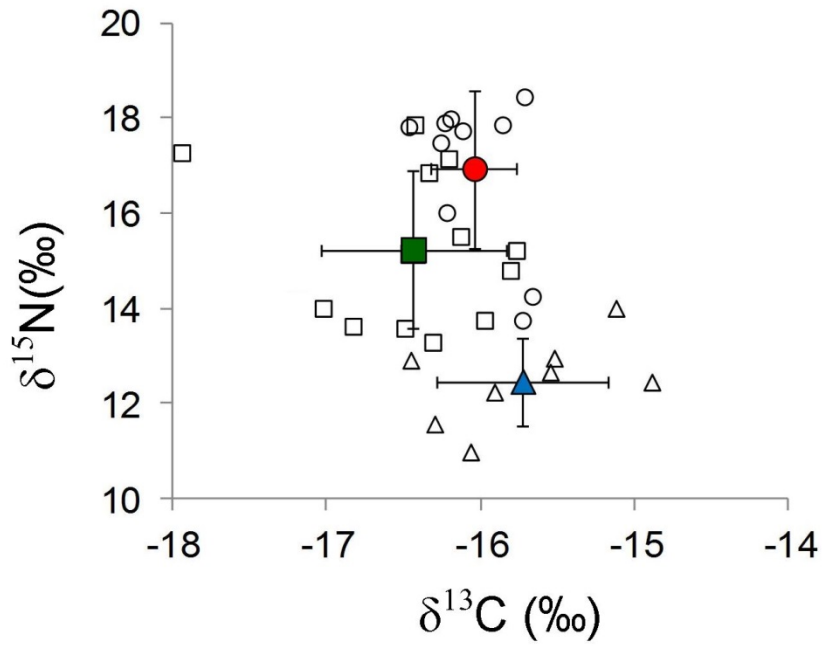
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Figure 5. Feather stable isotope ratios of *leucoptera* (green square, n = 12), *caledonica* (blue triangle, n = 7), and *pycrofti* (red circle, n = 10) tracked with geolocator-immersion loggers during the non-breeding season. Coloured symbols and errors are the mean  $\pm$  s.d., and unfilled symbols correspond to individual values.

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