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Individual non-breeding site fidelity diverges between sympatric congeneric seabirds

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Abstract

Background Migratory behaviour varies among individuals, years and species, yet single-species studies rarely separate these sources of variation. Tracking the same individuals of two sympatric congeners in parallel over consecutive years separates these sources and tests whether individual consistency diverges between species.

Methods We tracked two sympatrically breeding South Pacific seabirds using geolocators, the White-necked Petrel (*Pterodroma cervicalis*) and Black-winged Petrel (*P. nigripennis*), over three consecutive non-breeding seasons. Because both species depart from the same colony, differences in their migrations cannot be attributed to breeding location or to conditions experienced there, and should instead reflect differences between the species themselves. We compared migration routes, non-breeding distributions and timing between the species, and quantified within-individual repeatability of migration timing and between-year fidelity to non-breeding areas.

Results Both species undertook long, looping trans-equatorial migrations across the Pacific with round trips of up to ~56 000 km to subtropical and transition-zone waters of the western and central North Pacific. In both, birds departed in May and returned roughly six months later, with outbound and return legs differing by ~100° in heading, and no sex differences in migratory behaviour or space use. Within this shared migration, the species differed strikingly

in what individuals repeated. Black-winged Petrels returned to the same non-breeding longitudes year after year (R = 0.93), whereas White-necked Petrels showed only weak fidelity (R = 0.36). Timing showed the reverse: White-necked Petrels returned to the colony on highly consistent dates (R = 0.76), whereas Black-winged Petrels were barely repeatable (R = 0.21). In both species, partners migrated independently in space but on closely matched dates, reuniting only at the colony; in Black-winged Petrels this synchrony arose despite low individual repeatability of return date.

Conclusions Individual fidelity can diverge sharply between closely related, sympatric species with similar population-level migrations, and consistency can be expressed in different dimensions, spatially in one species and temporally in the other. Fidelity cannot be inferred from population distributions or assumed conserved across congeners; characterising migratory strategies requires repeatedly tracking the same individuals.

Keywords: biologging; light-level geolocation; migration; migratory connectivity; petrels; *Pterodroma*

1. BACKGROUND

Where migratory animals spend the non-breeding season, and whether individuals return to the same places each year, determines how breeding populations are linked to non-breeding regions and exposed to threats across the annual cycle. Migratory connectivity (the degree to which breeding and non-breeding populations remain associated) and individual site fidelity (the tendency of individuals to return to the same non-breeding area in successive years, quantified as the repeatability of their non-breeding location) are therefore central to the ecology and conservation of migratory species [1]. Animal-borne tracking now quantifies these relationships across entire ocean basins [2] and shows that site fidelity shapes connectivity: where most individuals are site faithful, breeding populations hold stable associations with particular non-breeding regions; where fidelity is low, those associations become diffuse and variable. Whether site fidelity is conserved across closely related species remains poorly

understood, because comparisons are typically confounded by differences in breeding location, ocean basin, tracking period and methodology.

Site fidelity is not a fixed trait but varies markedly within and among species, reflecting how animals sample and respond to their environments. Many seabirds return to the same non-breeding areas in successive years, but the strength of this consistency depends on age and experience, the prey and habitats exploited, foraging success, and the predictability and productivity of the environment [3, 4]. Fidelity is stronger where profitable conditions recur in the same place each year, such as persistent shelf or frontal systems, and weaker where resources are patchy or shift among years [5, 6]. Consistency is not necessarily expressed equally in space and time: individuals may be highly repeatable in where they travel yet variable in when, or the reverse [7]. Because such strategies appear to be shaped during development and canalised in adulthood rather than fixed from birth [8–11], individuals maturing under similar conditions might be expected to converge on comparable repeatability; whether closely related species in the same environment nonetheless diverge in the strength and expression of individual fidelity is largely unknown, a question that a sympatric species pair is unusually well placed to answer.

Gadfly petrels (*Pterodroma*) are well suited to these questions. Their long, high-aspect-ratio wings make them efficient gliders, and many species undertake long, often trans-equatorial migrations across ocean basins by exploiting predictable wind regimes through dynamic soaring [6, 12–15]. Yet because they spend most of their lives over remote pelagic waters and come to land only to breed, the non-breeding distributions and migratory strategies of most species remain poorly described. Individuals of some species show high between-year fidelity to non-breeding areas [6, 11, 16], but whether closely related species share similar levels of individual repeatability, in space and in time, is unknown, existing comparisons of congeners being at the population level [17, 18].

We therefore used two gadfly petrels breeding in sympatry on Phillip Island, in the Norfolk Island Group of the south-western Pacific Ocean, the White-necked Petrel (*Pterodroma cervicalis*) and the Black-winged Petrel (*P. nigripennis*), as a natural experiment

to test whether individual repeatability in migratory behaviour is conserved in close relatives. The species share a colony but differ in body size and broader ecology: the White-necked Petrel is two to three times heavier than the Black-winged Petrel yet only about 1.5 times greater in wingspan and wing loading [13], differences likely to influence flight performance and wind use. Because both depart from the same island, cross the same ocean basin and follow the same seasonal schedule, the geographic and environmental differences that typically confound interspecific comparisons are largely controlled for, so any difference in non-breeding distribution or migratory repeatability is more likely to reflect intrinsic, species-specific responses to a shared environment than the environment itself [19]. Tracking both members of some breeding pairs also allowed us to ask whether partners coordinate their migrations in space and time or migrate independently, reuniting only at the colony, a question addressed in few seabirds, where partners have generally been found to migrate separately even when they occupy the same regions [20, 21].

Similarity between partners may arise from shared routes, destinations or environmental conditions, and from similar age and phenotype through assortative pairing, rather than from coordination directed at the mate [20]. Coordinated timing nonetheless matters: in long-lived socially monogamous seabirds, well-matched arrival at the colony underpins breeding performance and pair-bond maintenance [22, 23], so how closely partners align their schedules carries direct fitness consequences.

Using archival light-level geolocators, we first characterise the shared migration (routes, destinations, phenology and space use), predicting looped, wind-assisted trans-equatorial migrations to the North Pacific subtropical and transition frontal zones and little sexual segregation. We then test whether non-breeding space use and migratory phenology are individually repeatable and whether repeatability differs between the species. Finally, we ask whether breeding partners migrate independently or coordinate in space and time, predicting independent movements but closely aligned schedules.

2. METHODS

2.1. Tracking devices and deployment

Fieldwork was carried out on Phillip Island (29°07′S, 167°57′E), a small (207 ha), uninhabited subtropical island in the Norfolk Island Group, south-western Pacific Ocean, where 13 seabird species breed, including five gadfly petrels: 19 000 breeding pairs of Black-winged Petrels [24] and, in the only Australian breeding population of the White-necked Petrel, at least 101 pairs (unpublished data).

Adults of both species were fitted with 1 g archival light-level geolocators (Intigeo C65, Migrate Technology Ltd), attached as described by Halpin et al. [25] and representing 0.2% of mean adult body mass in White-necked (464 g, n = 27) and 0.6% in Black-winged Petrels (171 g, n = 48 [26]). Loggers were deployed on breeding adults at the colony in January–April of 2018, 2019 and 2020 and recovered the following breeding seasons. Each geolocator logged ambient light and saltwater immersion (as every change of state, or as the number of wet samples per 4-h period; Additional file 1 (S5)), from which we derived the percentage of time wet within each migratory phase, a proxy for time on the water rather than in flight, which also helped define migratory phenology.

2.2. Position estimation

All analyses were conducted in R v.4.5.1 [27]. Positions were estimated from the light data with the threshold-free, twilight-free method of Bindoff et al. [28], implemented in SGATII [29] as a Bayesian state-space model that infers location from the full light pattern rather than from scored twilights, which suits the noisy light profiles of burrow-nesting seabirds. Locations were estimated twice daily under a light model that tolerates shading and a movement model with a weakly informative Gamma prior on travel speed (mean ≈ 12 km h^{-1}), with identical settings for every track; estimates were confined to the ocean by a land mask and fixed at the colony during attendance, and each location was summarised by its posterior mean and 95% credible interval (full settings in Additional file 1 (S1)). As is general for light-level geolocation, latitude is unreliable near the equinoxes and least precise at low latitudes [25]. Phenology and site fidelity were therefore based primarily on longitude, settled positions were summarised as

medians over the core-residency period to buffer short-lived latitude errors, latitudinal metrics are reported as secondary, and the species contrast in site fidelity was re-estimated after excluding positions within ±14 days of the equinoxes (Additional file 1 (S9)). Journey metrics (tracking duration, total distance travelled and maximum range from the colony) were computed from daily mean positions after a plausibility filter, so total distance is a conservative minimum estimate (Additional file 1 (S1)).

2.3. Migratory phenology

For each track we defined the dates of colony departure and first return from the estimated positions and their great-circle distances from the colony, the raw light data and the 4-hourly immersion data (criteria in Additional file 1 (S1)). For 8 of 53 Black-winged Petrel tracks, departure or return dates could not be measured directly and were imputed from the median of the species-and-season cohort (7 individuals) or, for one track, from the same bird's multi-year deployment record; all 53 White-necked Petrel tracks had directly measured dates.

Arrival at and departure from the non-breeding core area were defined for each bird-season as the first and last day of the longest continuous run of daily mean positions falling inside that bird's own 50% kernel utilisation distribution for the non-breeding window (kernel settings as in section 2.4; full rule in Additional file 1 (S1)). From these dates we derived the durations of outbound transit (colony departure to core arrival), core residency (core arrival to core departure) and return transit (core departure to first return). As a sensitivity check, both dates were re-estimated from a 7-day-smoothed displacement change-point rule applied to each bird's daily distance from the colony (Additional file 1 (S3)).

2.4. Species-level utilisation distributions

Males and females did not differ in their space use (tests in Additional file 1 (S2) and Table S1, with the individual bird as the sampling unit and repeat deployments pooled), so the sexes were combined. Non-breeding space use was summarised by kernel utilisation distributions computed in a Lambert azimuthal equal-area projection centred on the colony, so that areas were comparable across the very large span of the data, using the *kernelUD* function of

adehabitatHR [30] with a fixed smoothing parameter h = 300 km (the mean geolocation error reported for gadfly petrels by Halpin *et al.* [25]) and a common output grid. We extracted the 50% contour (core-use area) and the 95% contour (broader range). So that birds with longer tracks or repeat deployments did not dominate the density surface, species-level utilisation distributions were the equal-weighted mean of per-individual distributions rather than a kernel fitted to pooled fixes, computed for each non-breeding season and, pooling each individual's fixes across years, for all years combined.

2.5. Migratory directions and circular statistics

To describe migratory directions we calculated, for each track, the initial bearing from the colony to the first estimated position more than 500 km away on the outbound journey (the departure direction) and the bearing to the last position more than 500 km away before return (the direction from which the bird returned), using the *geosphere* package [31]. Departures (April–May) and returns (November) fell about two months from the nearest equinox, outside the periods of unreliable equinoctial latitude, so no latitudinal correction was required. Bearings were summarised per species and leg by the mean vector bearing and the mean resultant length r (0 = uniformly scattered, 1 = perfectly concentrated), with uniformity tested by the Rayleigh test, and are shown as rose diagrams centred on the colony. The population mean migration tracks and the prevailing-wind field were derived as described in Additional file 1 (S8).

2.6. Individual non-breeding site fidelity

To test whether individuals returned to the same non-breeding area between years, we summarised each bird-season by its settled non-breeding position: the median latitude and longitude over its core-residency period (core arrival to core departure). For each species we estimated the repeatability (R; the intraclass correlation, the proportion of total variance attributable to differences among individuals; Additional file 1 (S1)) of settled latitude and longitude (longitude on a 0–360° scale to maintain continuity across the Pacific) from an intercept-only Gaussian linear mixed model with individual identity as the random effect, with

95% confidence intervals by parametric bootstrap (1000 replicates) and *p* values by permutation (9999) in *rptR* [32]. Repeatability was estimated across all 53 bird-seasons per species with a settled position (35 Black-winged and 32 White-necked Petrel individuals, of which 18 and 15 respectively were tracked in ≥ 2 seasons). As an interpretable effect size, we also computed the mean great-circle distance between settled positions of the same individual in different years (the within-individual return distance) and between different individuals, with a 95% confidence interval on the within-individual distance from a cluster (individual) bootstrap. As a sensitivity check, we repeated the analysis with settled positions defined over the middle 40% of the non-breeding period instead of the core-residency period (Additional file 1 (S3)).

Repeatability and return distance each summarise a bird-season by a single settled position, which for a bird using more than one core area lies between them, so we also compared the full core areas directly. For each bird-season we built a second utilisation distribution from all positions between core arrival and core departure; positions were selected by date, not location, so this distribution excludes migration but is not constrained by the contour used in section 2.3 to date the core period. Overlap between every pair of bird-seasons from different non-breeding seasons was quantified with Bhattacharyya's affinity, the recommended index of similarity between utilisation distributions [33, 34], calculated on each distribution's 50% contour (which caps the index at 0.5) and divided by 0.5 to restore a 0–1 scale (following Dumas *et al.* [35]), a constant rescaling that leaves every test unchanged. All comparisons were made between years, so that conditions shared within a year could not inflate overlap. Individual site fidelity was then measured as the difference between a bird's overlap with itself in other years (within-individual overlap) and its overlap with other individuals in other years (between-individual overlap): where a population concentrates in a small region any two birds overlap heavily whether or not individuals return to the same place, and subtracting the between-individual value removes that shared component. To test whether a bird overlapped its own previous core area more than it overlapped that of other birds, we randomly reassigned tracks to individuals and recalculated the difference 9999 times, taking the proportion of

reshuffles in which it equalled or exceeded the observed value. To test whether individual site fidelity was stronger in one species than the other, we randomly reallocated birds between the two species and recalculated the difference between species means 9999 times, using each bird's mean within- and between-individual overlap so that birds tracked in three seasons did not contribute disproportionately, and compared the two species' repeatability estimates directly by permuting species labels among individuals (9999 permutations). We also checked that the species contrast did not depend on any single bird by leave-one-out removal of individuals and estimated the repeatability of individual departure and return bearings in the same way (Additional file 1 (S9)).

2.7. Individual repeatability of migratory timing

We estimated the repeatability of four phenological events (colony departure, core arrival, core departure and first return to the colony, as day of year) from Gaussian linear mixed models with individual identity as the random effect and non-breeding season as a fixed effect, so that R (as in section 2.6) reflects consistent among-individual differences after accounting for population-level variation in timing; confidence intervals and p values were obtained as in section 2.6, and the among-individual and residual standard deviations from the same model (in days) are reported as an interpretable effect size (Additional file 1 (S4)). Colony-departure and first-return dates used only directly measured windows. Throughout, we adopted a significance threshold of $\alpha = 0.01$ in place of the conventional 0.05, to provide conservative inference given the number of tests applied across the study and the comparative nature of the species contrasts.

2.8. Pair synchrony and at-sea association

We tracked both members of 11 Black-winged and 14 White-necked Petrel breeding pairs in the same non-breeding seasons and asked whether partners, which must reunite at the colony each season, were more similar than expected by chance in where they went, in when they departed and returned, or in neither. Because conspecifics from one colony share broad migration corridors and destinations, similarity between partners was evaluated against a null

distribution generated by re-pairing each male with a randomly chosen female tracked in the same season (excluding his true partner) and recomputing each metric over 9999 permutations; the sampling unit was the breeding pair, for the season with the most time-matched locations. We tested four aspects of similarity: spatial overlap (Bhattacharyya's affinity of the partners' full utilisation distributions); spatio-temporal co-occurrence, the median great-circle distance between partners on time-matched days and the percentage of days within 600 km of one another (about twice the geolocation error); movement synchrony, the correlation of partners' daily longitudes; and phenological synchrony, the absolute difference in departure and return dates (measured dates only). For each metric, p was the one-sided proportion of re-pairings at least as similar as the real partners, judged against $\alpha = 0.01$. To assess whether migratory timing formed a coherent within-season schedule, we tested whether an individual's colony-departure date predicted its own return date in the same season (Pearson correlation on dates centred within each non-breeding season to remove year effects). To test whether pair synchrony reflected a shared breeding schedule, we indexed each nest's breeding phenology and outcome from repeated chick mass measurements (2018 and 2019 broods) and asked whether it accounted for partner synchrony in migratory timing (Additional file 1 (S6)).

3. RESULTS

Across three consecutive non-breeding seasons we reconstructed 106 complete migrations from 67 individual petrels, spanning 20 340 bird-days and some 70 000 estimated positions at sea. Together these birds covered roughly 4.5 million km, on average close to one circumference of the Earth per migration. Thirty-three individuals were tracked in two or more years (72 migrations), providing repeat samples for tests of individual repeatability.

3.1 Migratory range and journey

Both species undertook extensive trans-equatorial migrations spanning essentially the entire width of the Pacific Ocean (Figure 1). After breeding, birds left the south-western Pacific for the North Pacific, where they spent the boreal summer before returning to the colony. The non-breeding period lasted a median of 198 days in Black-winged Petrels and 180 days in White-necked Petrels, during which birds covered a conservatively estimated 46 000 and 39 700 km and reached about 9500 and 8500 km from the colony (Table 1). Colony departure fell in the austral autumn and first return in the austral spring (Table 1). Birds reached their non-breeding core areas about six weeks after leaving the colony (median core arrival 19 and 21 June) and left them in mid to late October (18 and 29 October), giving similar core residencies in the two species (122 ± 17 vs 117 ± 25 days; Mann–Whitney U = 1249, p = 0.33). The longer non-breeding period of Black-winged Petrels reflected their earlier colony departure (median 7 May vs 27 May) and longer outbound transit (45 ± 14 vs 33 ± 21 days; U = 759, $p < 0.001$); return transits were similar (35 ± 17 vs 32 ± 23 days; U = 1214, p = 0.23). No phenology metric differed between the sexes in either species (all U-test $p > 0.29$). Saltwater-immersion records confirmed that core residency was a settled phase: time on the water rose from about 24% and 27% in transit to 52% and 60% in Black-winged and White-necked Petrels ($p < 0.001$), more so in White-necked Petrels ($p < 0.001$), with no sex difference in either species (Figure 8; Additional file 1 (S5), Table S3).

TABLE 1. Migratory phenology and journey metrics for each species.

Metric	Black-winged Petrel	White-necked Petrel
Tracks (individuals)	53 (35)	53 (32)
Males / females	28 / 25	25 / 28
Colony departure	7 May (1–14 May)	27 May (19 May–1 Jun)
Core arrival	19 Jun (9–28 Jun)	21 Jun (14 Jun–8 Jul)
Core departure	18 Oct (7 Oct–1 Nov)	29 Oct (24 Sep–9 Nov)
Colony return	21 Nov (18–27 Nov)	23 Nov (17–26 Nov)
Tracking duration (days)	202 (186–234)	182 (159–227)
Total distance travelled (km)	46 000 (34 300–56 400)	39 700 (30 400–55 600)

Maximum range from colony (km)	9490 (7530–11 100)	8450 (7230–9640)

The sampling unit is the bird-season (numbers in the first row). Phenology is median (interquartile range) because dates are skewed; journey metrics are mean (range). Colony departure and return use directly measured dates only (n = 45 Black-winged and 53 White-necked Petrel bird-seasons); other rows use all bird-seasons. Total distance is a conservative minimum estimate (section 2.2).

We found no evidence that males and females differed in their space use. Overlap of utilisation distributions between the sexes was as high as overlap within a sex, and neither the randomisation test nor PERMANOVA detected sexual segregation in either species (all p > 0.8; Table S1). The non-breeding centroid, 50% core-area size, maximum range and outbound and return bearing did not differ between sexes (Black-winged Petrel p = 0.27–0.91; White-necked Petrel p = 0.03–0.97, the single nominally significant result (outbound bearing) not surviving Holm–Bonferroni correction, adjusted p = 0.26; Table S1).

3.2 Direction of migration

Migratory directions were strongly oriented in both species on both legs (Rayleigh tests, all p < 0.001; r = 0.84–0.89; Figure 2), and outbound and return directions differed by roughly 100°, indicating looping migrations across the Pacific rather than a direct there-and-back movement. Black-winged Petrels departed south-east to south-south-east (mean bearing ≈ 151°, r = 0.86) and returned from the north-east (≈ 52°, r = 0.87); White-necked Petrels showed the same loop on a slightly more northerly axis (departure ≈ 132°, r = 0.84; return ≈ 30°, r = 0.89). The south-easterly departure carried birds toward the Tasman Sea and the waters around northern New Zealand and the Kermadec Islands before they turned north across the equator, and the more north-easterly return bearings show that they came back along a different, more easterly path. The routes broadly followed the prevailing winds, threading the south-easterly trades on

319 the southern arc and the mid-latitude westerlies on the northern arc rather than crossing them
320 (Figure 3).
321

322 ***3.3 Non-breeding distributions***

323 From about June to October both species occupied the subtropical North Pacific, in the north-
324 western and central basin between the equatorial currents and the North Pacific Current
325 (Figures 1, 4): centred at roughly 27°N (interquartile range ≈ 23–30°N) and around 170°E in
326 Black-winged Petrels, and roughly 20°N (interquartile range ≈ 12–32°N) and around 160°E in
327 White-necked Petrels, the broader latitudinal spread of the latter reflecting their use of several
328 separate core areas (Figures 5, 6). The 95% range of both species was very large,
329 encompassing the southern staging waters traversed during departure and return (the
330 Tasman Sea, the seas around New Zealand and the Coral Sea) as well as the North Pacific,
331 reaching north to the subarctic boundary south of Kamchatka, Russia (Figure 4). At the
332 population level, the two species were nonetheless strikingly alike, sharing the same looping
333 route, the same ocean basin and broadly overlapping core areas.
334

335 ***3.4 Individual repeatability of non-breeding site and migratory timing***

336 Despite sharing similar population-level migration patterns, the species differed markedly in
337 individual non-breeding site fidelity (Table 2; Figures 5 and 6). Black-winged Petrels were
338 highly repeatable in settled longitude (R = 0.93, p < 0.001) and returned to within a mean of
339 654 km of their previous year's settled location, well inside the mean distance separating
340 different individuals (1746 km); White-necked Petrels were not (R = 0.36, confidence interval
341 reaching zero), and their within-individual distance (1821 km) approached the between-
342 individual mean (2377 km). Whole core areas gave the same contrast: Black-winged Petrels
343 overlapped their own previous core area more than twice as much as they overlapped other
344 birds (difference in Bhattacharyya's affinity 0.25, p = 0.002), whereas in White-necked Petrels
345 the difference was small and short of our significance threshold (0.09, p = 0.03). Between

346 species, this difference was greater in Black-winged Petrels (per-individual means 0.25 vs
347 0.06; p = 0.017) and their within-individual return distance far shorter (654 vs 2129 km, one
348 mean per bird; p < 0.001), although the direct comparison of repeatabilities was not significant
349 (p = 0.074). The contrast was robust to leave-one-out removal of individuals, to excluding
350 positions near the equinoxes and to redefining the settled window, and Black-winged Petrels
351 showed no repeatable departure or return headings despite their apparent fidelity to
352 destination (Additional file 1 (S3, S9)).
353 Individual consistency in timing showed the opposite pattern to consistency in space. White-
354 necked Petrels were strongly repeatable in the timing of first return to the colony (season-
355 adjusted R = 0.76, 95% CI 0.52–0.90, p < 0.001; within-individual SD 3.3 days), whereas in
356 Black-winged Petrels return dates were not repeatable between years (R = 0.21, 95% CI 0–
357 0.67, p = 0.23) and departure dates not at all (R = 0, p = 1); no other phase was repeatable in
358 either species (Table S2). Within a season, however, timing was coherent in both species: an
359 individual's departure date predicted its own return date (Black-winged Petrel Pearson r =
360 0.44, p = 0.002; White-necked Petrel r = 0.51, p < 0.001).
361
362 **TABLE 2.** Individual non-breeding site fidelity.

Quantity	Black-winged Petrel	White-necked Petrel
Individuals tracked >1 year	18	15
Repeatability of longitude, R (95% CI)	0.93 (0.85–0.97)	0.36 (0–0.67)
p (permutation)	< 0.001	0.05
Repeatability of latitude, R (95% CI)	0.56 (0.16–0.81)	0.25 (0–0.60)
p (permutation)	0.05	0.113
Within-individual distance, repeat pairs (km, 95% CI)	654 (462–887)	1821 (1231–2536)
Between-individual distance (km)	1746	2377
Own-vs-others core overlap (BA)	0.47 vs. 0.22	0.26 vs. 0.17
Difference (*p*)	+0.25 (0.002)	+0.09 (0.03)

363 Methods, confidence intervals and permutation tests as in section 2.6. R, repeatability of
364 settled latitude and longitude. Core overlap is Bhattacharyya's affinity between 50% core
365 areas in different years (0–1): "own", a bird's overlap with itself; "others", with different

individuals; their difference, not the absolute overlap, measures site fidelity. Within-individual distances pool all season-pairs; the species comparison in the text averages within individuals first.

3.5 Pair synchronicity and at-sea association

Both members of a breeding pair were tracked during the same season for 11 Black-winged Petrel and 14 White-necked Petrel pairs. Partners showed no greater spatial similarity than expected by chance: they were no more similar than randomly paired birds in utilisation-distribution overlap, time-matched distance, time spent within 600 km of one another, or day-to-day movement synchrony (Table 3, Figure 7). In contrast, partners were more synchronised in timing than randomly paired birds, departing 6.3 and 6.8 days apart in Black-winged and White-necked Petrels, respectively, against 14.7 and 14.1 days for random pairs (p = 0.004 and 0.006), and returning 3.4 and 4.9 days apart against 7.8 and 6.8 days (p = 0.001 in Black-winged Petrels; p = 0.04 in White-necked Petrels, short of the predefined threshold; Table 3).

This temporal synchrony was not a by-product of birds keeping to fixed individual schedules. A Black-winged Petrel's timing could not be predicted from its own timing in previous years (section 3.4) but could be predicted from its partner's timing in the same year. In the White-necked Petrel, the two levels coincided: individuals were repeatable in return date and partners returned closer together than random pairs, though short of the α = 0.01 threshold. In the Black-winged Petrel, return synchrony was not explained by a shared breeding schedule: it persisted after accounting for the timing and outcome of the pair's chick-rearing that season, the partners' excess synchrony over randomly paired birds shrinking by only about a third (n = 5 pairs; $p < 0.001$; Additional file 1 (S6)). In the White-necked Petrel, departure synchrony was largely accounted for by the shared breeding schedule (Table S4).

TABLE 3. Tests of pair fidelity in non-breeding movements.

Metric	Black-winged Petrel			White-necked Petrel		
	partners	random	*p*	partners	random	*p*
Pairs tested (n)	11	—	—	14	—	—
Utilisation distribution overlap (Affinity)	0.56	0.55	0.29	0.67	0.68	0.65
Time-matched dist. (km)	2301	2248	0.58	1828	1562	0.96
Days within 600 km (%)	9.9	8.8	0.32	16.5	18.1	0.70
E–W synchrony (*r*)	0.60	0.53	0.12	0.79	0.81	0.74
Departure difference (days)	6.3	14.7	**0.004**	6.8	14.1	**0.006**
Return difference (days)	3.4	7.8	**0.001**	4.9	6.8	0.04

One pair-season per nest. “Partners” is the mean over real partners; “Random” the mean over the within-season re-pairing null, in which each male is paired with a randomly chosen non-partner female of the same season (section 2.8). *p* is the proportion of 9999 re-pairings at least as similar as the real partners, with nest as the sampling unit. Higher overlap, % days within 600 km and east–west correlation, and lower distances and date differences, indicate greater similarity. Four of these metrics are also shown in Figure 7.

4. DISCUSSION

4.1 Divergent individual site fidelity

Our central finding is that two sympatrically breeding gadfly petrels migrate to the same broad area via similar looping routes but differ fundamentally in individual fidelity to their non-breeding areas. Black-winged Petrels returned to individual-specific areas year after year, whereas White-necked Petrels did not but were instead consistent in when they returned, so that individual consistency in these species is organised along different axes: space in the Black-winged Petrel, time in the White-necked Petrel. The contrast we found was strongest for longitude, the more reliable axis of light-level geolocation, making it unlikely to be a measurement artefact. The population-level pattern itself, a figure-of-eight loop to the North Pacific transition zone, closely matches that of Black-winged Petrels breeding in New Zealand [36] and the wind-assisted loop migrations typical of pelagic seabirds [14, 37].

This divergence invites the broader question of what drives individual site fidelity, and why it should differ so strongly between close relatives. Because both species were sampled as breeding adults at the same colony in the same seasons, and share the same non-breeding basin, the contrast is unlikely to reflect differences in the conditions the tracked birds

414 experienced, although we cannot exclude differences in the age or experience structure of the
415 two samples, and we do not know where immature birds of either species go or how their
416 migration strategies are acquired. The two species also differed in which aspect of migration
417 was repeatable, space in the Black-winged Petrel and time in the White-necked Petrel,
418 suggesting that where a bird settles and when it migrates may be governed by partly
419 independent processes [7].

420 One plausible explanation for divergent patterns of non-breeding site fidelity is that the
421 two species exploit habitats differing in their spatial predictability: site fidelity should be
422 advantageous only where profitable non-breeding habitat recurs in the same place from year
423 to year. If so, Black-winged Petrels may exploit more temporally persistent, spatially fixed
424 resources, whereas White-necked Petrels may track resources that are more variable or more
425 broadly distributed. We have no direct evidence for this hypothesis. The two species partition
426 foraging habitat during breeding [26], but whether the resources each targets differ in their
427 year-to-year predictability is unknown, and the non-breeding patterns consistent with the idea,
428 the several separate core areas used by individual White-necked Petrels and their broader
429 latitudinal spread, are the observations to be explained rather than independent support.
430 Testing this hypothesis will require quantifying how much the location of favourable
431 oceanographic conditions and prey within each species' non-breeding range varies between
432 years.

433 High between-year fidelity has been reported in some gadfly petrels [6, 11, 16], but our
434 comparison shows that it is not a genus-wide rule. More broadly, it suggests that population-
435 level similarity does not imply individual-level similarity: near-identical population distributions
436 can arise from fundamentally different patterns of individual behaviour. In the closely related
437 Juan Fernández Petrel *Pterodroma externa*, individuals disperse across several separate non-
438 breeding residency areas yet remain consistent in this strategy between years [38], showing
439 that non-breeding fidelity can be expressed as consistency of strategy rather than fidelity to a
440 single place.

4.2 Pair synchronicity and coordination

We found no sexual segregation in non-breeding distribution in either species, consistent with their breeding-season ecology [26] and with other tropical gadfly petrels [6, 39–41]. The behavioural structure in these populations therefore lies at two levels, the individual, examined above, and the pair. The two are most sharply separated in the Black-winged Petrel, whose partners returned on average about 3.4 days apart, compared with 7.8 days for randomly paired birds from the same season (p = 0.001), even though individuals were not repeatable in their own return dates between years (R = 0.21). The consistency in return timing in this species therefore resided at the level of the pair rather than the individual.

That result narrows the field of mechanisms that could produce return synchrony between partners. An endogenous annual programme is an individual property and would make individuals repeatable in their return dates, which they were not. A shared environmental or photoperiodic cue would synchronise the colony as a whole rather than partners specifically, which the within-season re-pairing null controls for, and behavioural coordination at sea is excluded by the absence of any spatial association between partners. A further possibility was that partners shared a schedule inherited from their joint breeding attempt, since both the timing and outcome of breeding belong to the pair and are known to shift subsequent migration [42, 43]. Indexing each pair's breeding phenology and outcome from chick growth, we found that Black-winged Petrel return synchrony persisted after controlling for it, the gap between partners and the null falling by only about a third, whereas White-necked Petrels had no significant return synchrony to control for, and their departure synchrony was largely accounted for by the shared breeding schedule (Additional file 1 (S6), Table S4). The pair-level determinant of return timing therefore remains unresolved, but it is neither a fixed individual schedule, nor a colony-wide cue, nor at-sea coordination, nor simply a shared breeding timetable.

Comparable arrival synchrony in partners that winter apart and migrate independently has been reported in Black-tailed Godwits *Limosa limosa* (partners arriving within 3.1 days of

one another [44]), Chatham Petrels *Pterodroma axillaris* (females arriving 1–4 days after their mates [39]) and Atlantic Puffins *Fratercula arctica* (pairs migrating separately yet returning synchronously by an unidentified mechanism [45]). Such synchrony is unlikely to be incidental: Common Tern *Sterna hirundo* pairs that reunited had arrived a median of two days apart, whereas those that divorced had arrived 7.5 days apart [46]; pair-bond duration increases fitness independently of age in long-lived seabirds [23]; and pairs that coordinate their pre-laying colony attendance may breed more successfully [22]. Black-winged Petrel partners returned 3.4 days apart, and randomly paired birds of the same season 7.8 days apart, so the synchrony we detected spans precisely the interval that separates retained from divorced pairs in other seabirds. By combining estimates of individual repeatability in migratory timing with a randomised test of pair synchrony, we show that migratory timing can be organised at the level of the breeding pair rather than the individual.

5. CONCLUSIONS

Sympatric gadfly petrels that breed and cross the same ocean by the same looping route nonetheless organise their individual lives differently. Black-winged Petrels return to the same patch of the North Pacific year after year yet keep no individual schedule; White-necked Petrels keep a schedule but not a place. In both species, partners migrate independently in space but on closely matched dates, and in the Black-winged Petrel they do so even though neither bird is repeatable in its own timing, so migratory timing can be coordinated within the pair without being consistent within the individual. Individual fidelity therefore cannot be read from a population's distribution, nor assumed to be shared by close relatives; it must be measured by following the same individuals across years. The conservation consequence follows directly. A fixed protected area covers a similar share of each species' core range in any one year, but for the Black-winged Petrel it shelters the same individuals every year, whereas for the White-necked Petrel it protects a changing sample of the population.

List of abbreviations

BA, Bhattacharyya's affinity; **CI**, confidence interval; **ERA5**, fifth-generation ECMWF atmospheric reanalysis; **GLORYS12**, Global Ocean Physics Reanalysis (1/12°); **PERMANOVA**, permutational multivariate analysis of variance; **R**, repeatability (intraclass correlation); **SD**, standard deviation; **UD**, utilisation distribution.

Declarations

Ethics approval and consent to participate

Fieldwork was approved by the Monash University Animal Ethics Committee (permit BSCI/2017/42) and was carried out under Parks Australia wildlife research approvals and New South Wales scientific licences. No human participants, human data or human tissue were involved.

Consent for publication

Not applicable.

Availability of data and materials

The datasets analysed during the current study are held in the BirdLife International Seabird Tracking Database (dataset IDs 2304 and 2305, https://www.seabirdtracking.org). They are not publicly downloadable because the repository releases tracking data under a data-access request procedure, but they are available from the repository on reasonable request and with the permission of the data owners, and from the corresponding author.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

LRH conceived the study, acquired funding and scientific permits, collected field data, analysed the data and led the writing of the manuscript. RM contributed to conceptualisation, methods, data analysis and interpretation. EJM and CL contributed to field data collection. RHC contributed to conceptualisation, field methods and interpretation. NC contributed to field methods and field data collection. TAC contributed to conceptualisation, data analysis, methods and interpretation. All authors read and approved the final manuscript.

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Additional files

Additional file 1. Format: .docx. Title: Supplementary methods, sensitivity analyses and supporting tables. Description: S1, detailed methods and metric definitions; S2, sexual-segregation tests (Table S1); S3, core-use phenology sensitivity check; S4, individual repeatability of migratory timing (Table S2); S5, activity from saltwater immersion (Table S3); S6, breeding schedule, outcome and pair-level timing (Table S4); S7, oceanographic currents and fronts; S8, mean migration track and prevailing winds; S9, sensitivity analyses and repeatability of migratory bearing.

FIGURE LEGENDS

Figure 1. Population utilisation distributions during the non-breeding period, by season and species. Sexes pooled; rows, seasons 2018, 2019 and 2020; columns, Black-winged Petrel (left) and White-necked Petrel (right). Shading shows the utilisation distribution in 5% increments (darker = more concentrated use); dashed line, the 50% core; black dot, the colony (Phillip Island).

Figure 2. Colony departure and return directions for each species. Departure (outward-pointing) and return (inward-pointing) directions, as rose diagrams centred on the colony. Bar length is proportional to the number of individuals; arrows show the mean bearing, with length proportional to the resultant length *r* (0 = uniformly scattered headings, 1 = identical).

Figure 3. Population mean migration tracks and prevailing winds. Bold lines, the spherical mean of the time-normalised individual tracks, with arrowheads showing direction of travel; faint lines, the contributing individual tracks, for Black-winged (left) and White-necked (right) Petrels. Grey arrows show the prevailing 10 m winds (ERA5 vector mean over the migration months, pooled across years), pointing in the direction the wind blows, with length proportional to wind speed.

Figure 4. Non-breeding utilisation distributions in relation to Pacific surface currents and fronts. Core (50%, dashed) and range (95%, solid) contours of both species (all years; individuals equally weighted), with the axes of major Pacific surface currents and fronts (grey lines, arrowheads showing flow direction; GLORYS12 reanalysis; Additional file 1 (S7)). KURO, Kuroshio Current; KURO Ex., Kuroshio Extension; NPC, North Pacific Current; NEC/NECC, North Equatorial Current/Counter-Current; SEC/SECC, South Equatorial

Current/Counter-Current; EAC, East Australian Current; TF, Tasman Front; STF, Subtropical Front. Black dot, the colony.

Figure 5. Between-year core areas of individual Black-winged Petrels. Between-year 50% core areas (core-residency positions only) of the 18 Black-winged Petrels tracked in more than one non-breeding season, one panel per bird, coloured by season; filled circles, each season's settled position (median over core residency), joined in season order; black dot, the colony. Panels are ordered from most to least site faithful; titles give each bird's mean between-year return distance and mean overlap of its own core areas (Bhattacharyya's affinity, 0–1; between-individual baseline 0.22, Table 2).

Figure 6. Between-year core areas of individual White-necked Petrels. Individuals tracked in more than one non-breeding season (n = 15). Conventions, map extent and panel ordering follow Figure 5; the between-individual baseline overlap for this species is 0.17 (Table 2).

Figure 7. Pair synchrony in non-breeding movements. Breeding partners (coloured by species; 11 Black-winged and 14 White-necked pairs) versus all same-season, opposite-sex non-partner combinations within each species (grey; 224 and 228, so each bird recurs across many points). Top row, difference in departure and return date (lower = more synchronous); bottom row, time-matched daily distance and full utilisation-distribution overlap. Boxes, median and interquartile range; points, one pair each. Permutation $p < 0.01$ in red (Table 3).

Figure 8. Percentage of time immersed in saltwater, by migratory phase and by sex. Immersion is a proxy for time on the water rather than in flight. (a) By migratory phase for Black-winged (blue) and White-necked (orange) Petrels; (b) during core residency, by sex within each species. Boxes, median and interquartile range; points, one bird-season each.

Figure 1

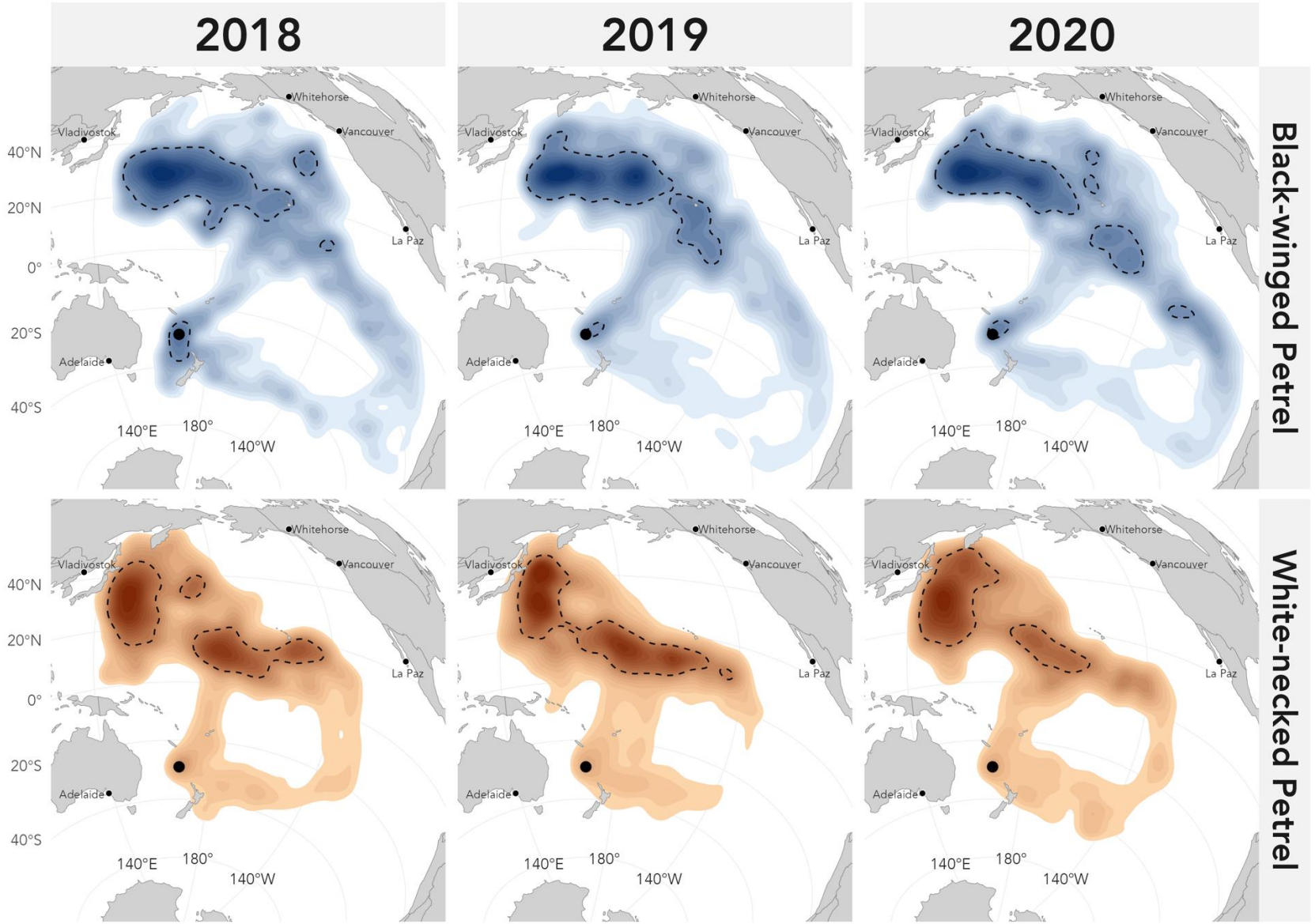

2018
2019
2020
Black-winged Petrel
White-necked Petrel
Whitehorse
Vancouver
Vladivostok
La Paz
Adelaide
40°N
20°N
0°
20°S
40°S
140°E
180°
140°W

Figure 2

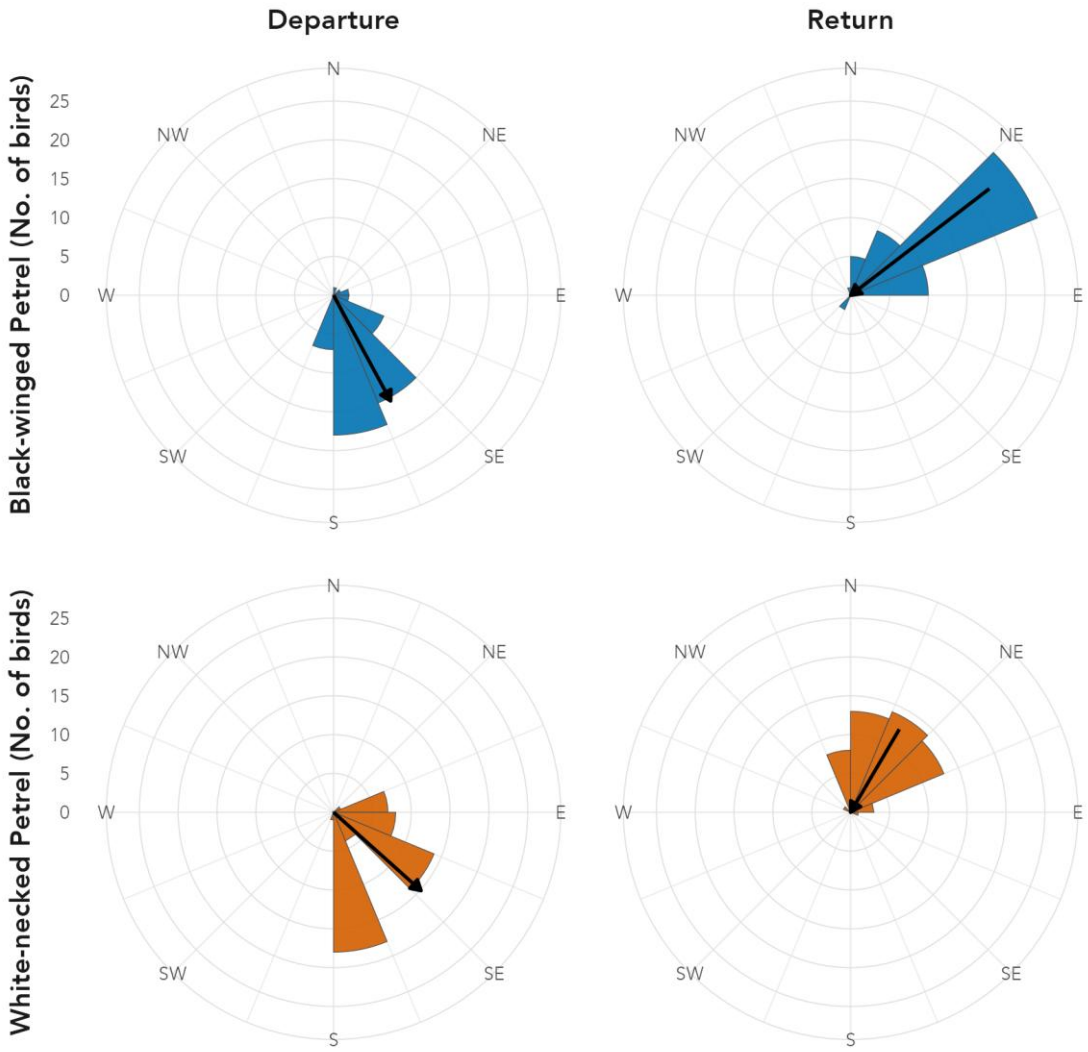

Departure
Return
Black-winged Petrel (No. of birds)
White-necked Petrel (No. of birds)
0
5
10
15
20
25
N
NE
E
SE
S
SW
W
NW

Figure 3

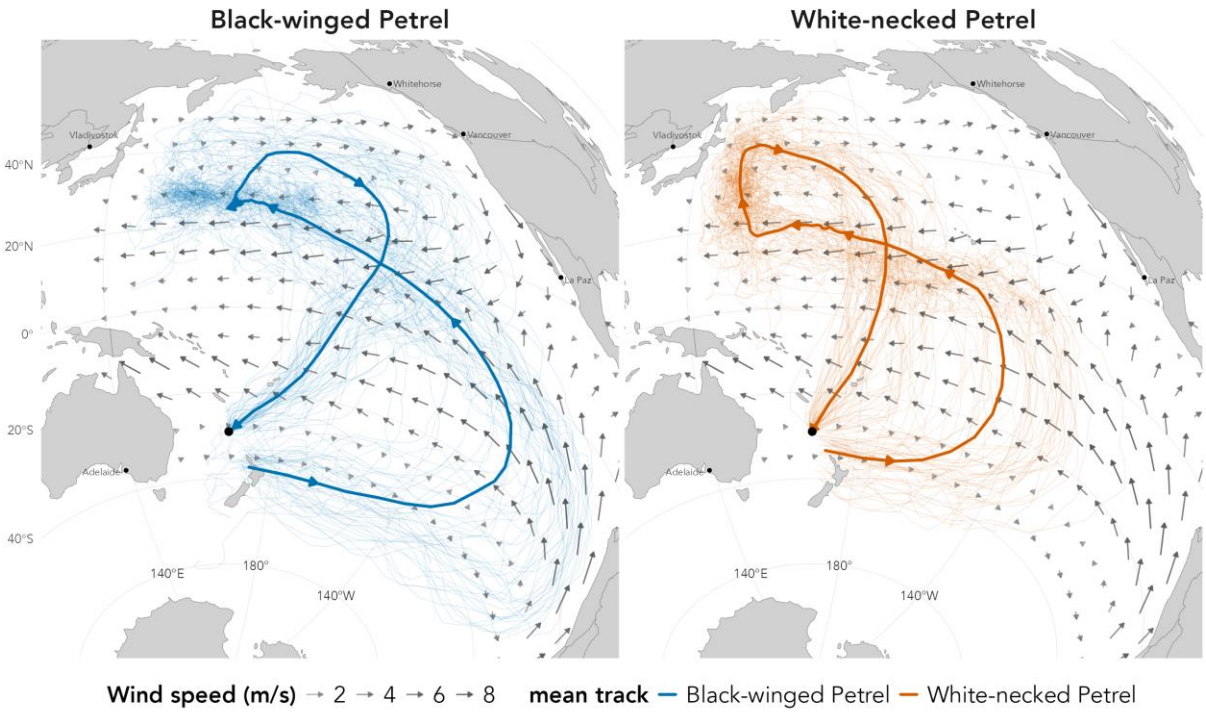

Black-winged Petrel
White-necked Petrel
Whitehorse
Vancouver
Vladivostok
La Paz
Adelaide
40°N
20°N
0°
20°S
40°S
140°E
180°
140°W
Wind speed (m/s) → 2 → 4 → 6 → 8
mean track — Black-winged Petrel — White-necked Petrel

Figure 4

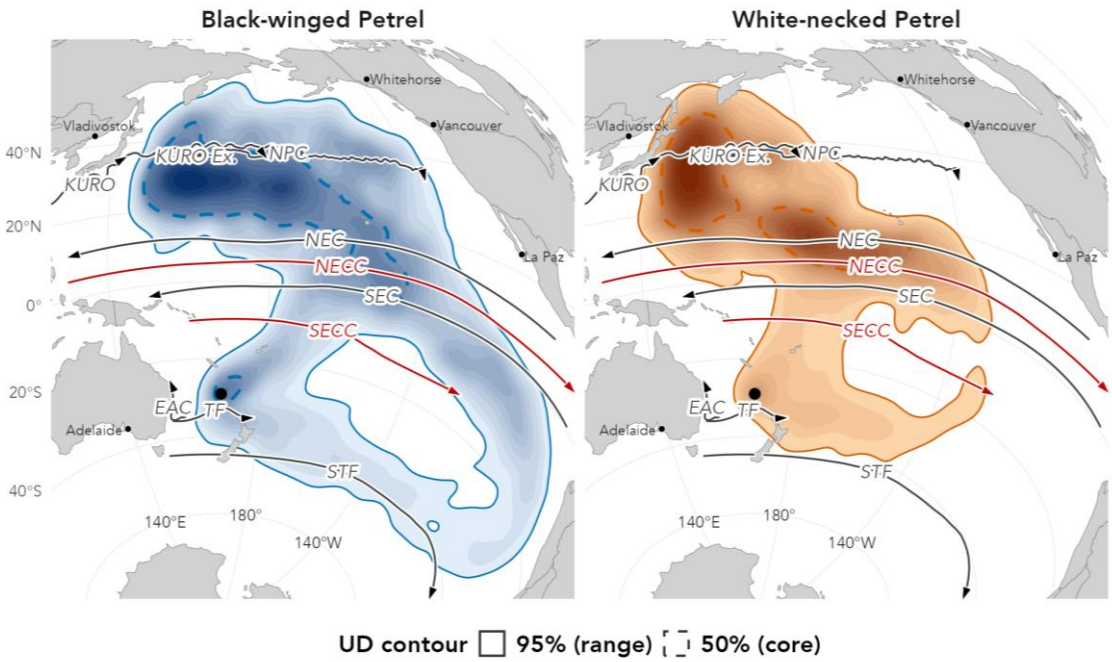

Black-winged Petrel
White-necked Petrel
Whitehorse
Vancouver
Vladivostok
La Paz
Adelaide
40°N
20°N
0°
20°S
40°S
140°E
180°
140°W
KURO
KURO Ex.
NPC
NEC
NECC
SEC
SECC
EAC
TF
STF
UD contour
95% (range)
50% (core)

Figure 5

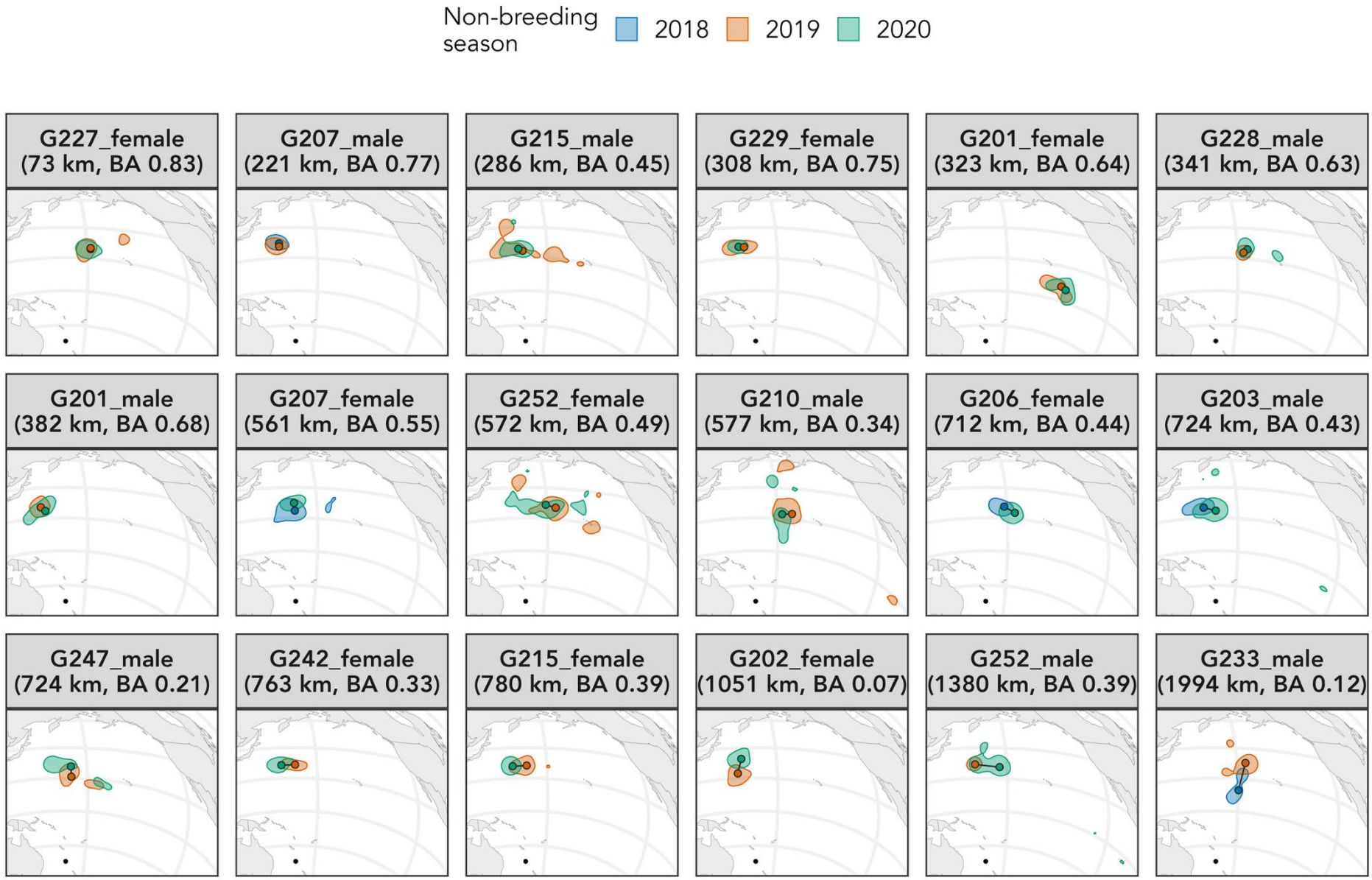

Non-breeding season
2018
2019
2020
G227_female (73 km, BA 0.83)
G207_male (221 km, BA 0.77)
G215_male (286 km, BA 0.45)
G229_female (308 km, BA 0.75)
G201_female (323 km, BA 0.64)
G228_male (341 km, BA 0.63)
G201_male (382 km, BA 0.68)
G207_female (561 km, BA 0.55)
G252_female (572 km, BA 0.49)
G210_male (577 km, BA 0.34)
G206_female (712 km, BA 0.44)
G203_male (724 km, BA 0.43)
G247_male (724 km, BA 0.21)
G242_female (763 km, BA 0.33)
G215_female (780 km, BA 0.39)
G202_female (1051 km, BA 0.07)
G252_male (1380 km, BA 0.39)
G233_male (1994 km, BA 0.12)

Figure 6

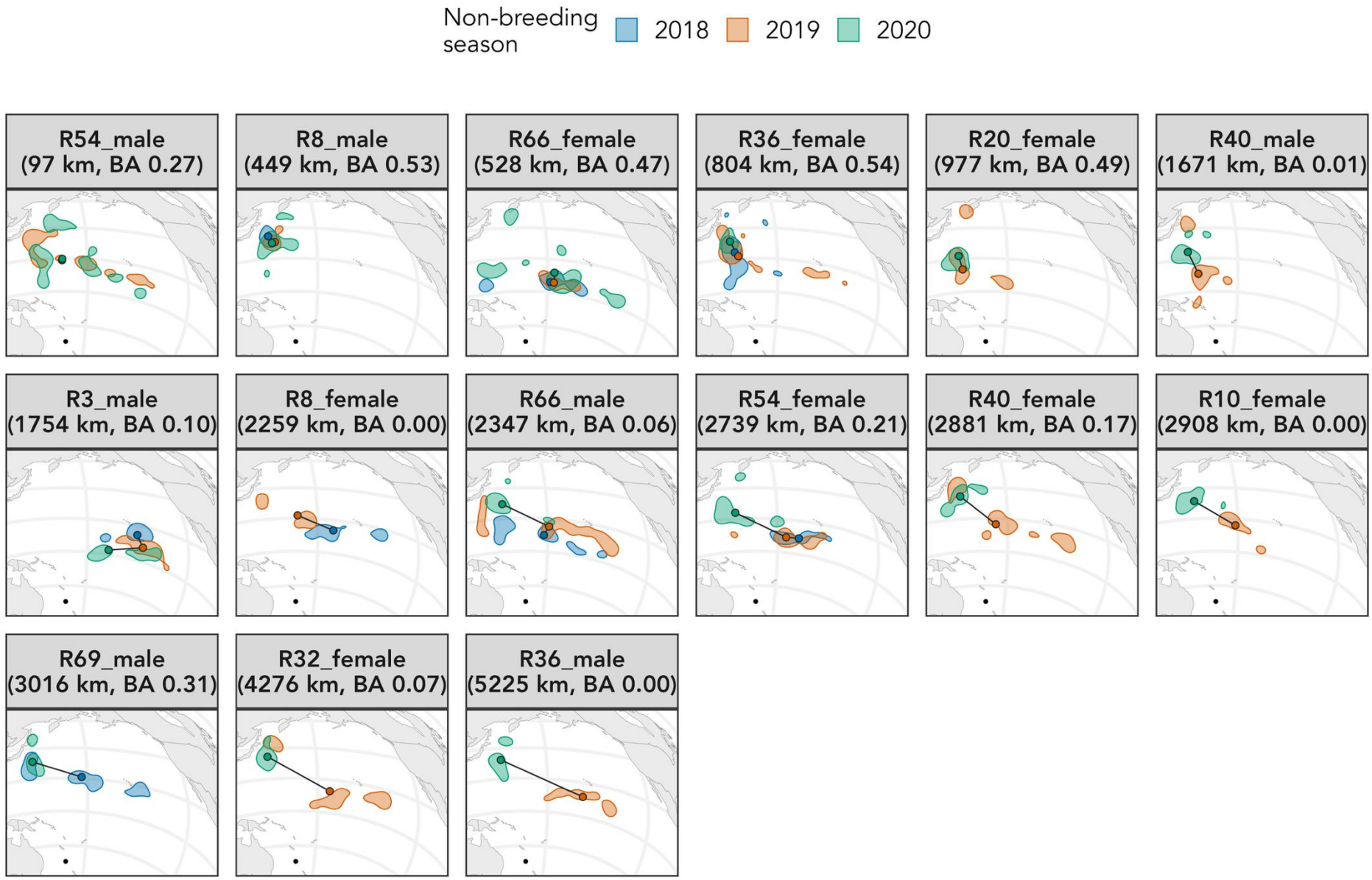

Non-breeding season
2018
2019
2020
R54_male (97 km, BA 0.27)
R8_male (449 km, BA 0.53)
R66_female (528 km, BA 0.47)
R36_female (804 km, BA 0.54)
R20_female (977 km, BA 0.49)
R40_male (1671 km, BA 0.01)
R3_male (1754 km, BA 0.10)
R8_female (2259 km, BA 0.00)
R66_male (2347 km, BA 0.06)
R54_female (2739 km, BA 0.21)
R40_female (2881 km, BA 0.17)
R10_female (2908 km, BA 0.00)
R69_male (3016 km, BA 0.31)
R32_female (4276 km, BA 0.07)
R36_male (5225 km, BA 0.00)

Figure 7

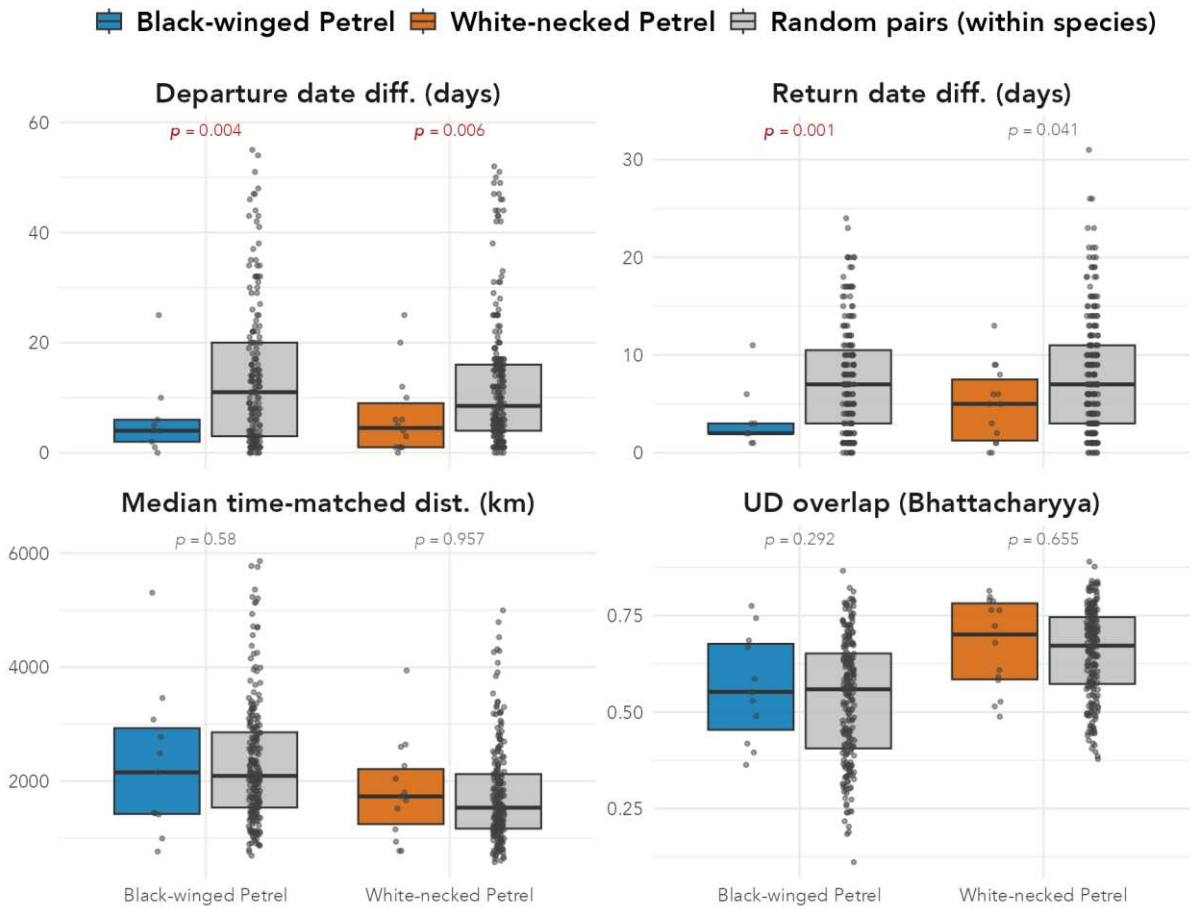
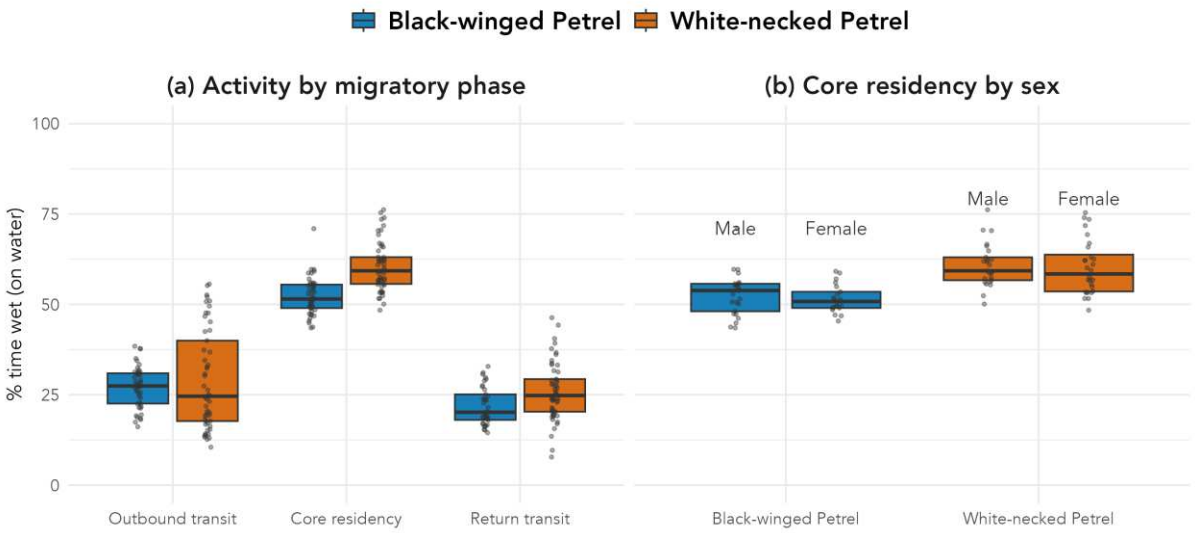

Black-winged Petrel
White-necked Petrel
Random pairs (within species)
Departure date diff. (days)
p = 0.004
p = 0.006
Return date diff. (days)
p = 0.001
p = 0.041
Median time-matched dist. (km)
p = 0.58
p = 0.957
UD overlap (Bhattacharyya)
p = 0.292
p = 0.655
Black-winged Petrel
White-necked Petrel

Figure 8


Black-winged Petrel
White-necked Petrel
(a) Activity by migratory phase
(b) Core residency by sex
% time wet (on water)
100
75
50
25
0
Outbound transit
Core residency
Return transit
Male
Female
Male
Female
Black-winged Petrel
White-necked Petrel

REFERENCES

1. Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT. Links between worlds: unraveling migratory connectivity. *Trends Ecol Evol*. 2002;17:76–83. doi:10.1016/S0169-5347(01)02380-1.

2. Hindell MA, Reisinger RR, Ropert-Coudert Y, et al. Tracking of marine predators to protect Southern Ocean ecosystems. *Nature*. 2020;580:87–92. doi:10.1038/s41586-020-2126-y.

3. Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Bennett VJ. Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology*. 2005;86:2386–96. doi:10.1890/04-1885.

4. Ceia FR, Ramos JA. Individual specialization in the foraging and feeding strategies of seabirds: a review. *Mar Biol*. 2015;162:1923–38. doi:10.1007/s00227-015-2735-4.

5. Weimerskirch H. Are seabirds foraging for unpredictable resources? *Deep Sea Res Part II Top Stud Oceanogr*. 2007;54:211–23. doi:10.1016/j.dsr2.2006.11.013.

6. Pinet P, Jaquemet S, Pinaud D, Weimerskirch H, Phillips RA, Le Corre M. Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's petrel *Pterodroma baraui*. *Mar Ecol Prog Ser*. 2011;423:291–302. doi:10.3354/meps08971.

7. Vardanis Y, Nilsson J-Å, Klaassen RHG, Strandberg R, Alerstam T. Consistency in long-distance bird migration: contrasting patterns in time and space for two raptors. *Anim Behav*. 2016;113:177–87. doi:10.1016/j.anbehav.2015.12.014.

8. Sergio F, Tanferna A, De Stephanis R, et al. Individual improvements and selective mortality shape lifelong migratory performance. *Nature*. 2014;515:410–3. doi:10.1038/nature13696.

9. Wakefield ED, Cleasby IR, Bearhop S, et al. Long-term individual foraging site fidelity—why some gannets don't change their spots. *Ecology*. 2015;96:3058–74. doi:10.1890/14-1300.1.

10. Votier SC, Fayet AL, Bearhop S, et al. Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proc Biol Sci*. 2017;284:20171068. doi:10.1098/rspb.2017.1068.

11. Franklin KA, Norris K, Gill JA, et al. Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. *Mov Ecol*. 2022;10:13. doi:10.1186/s40462-022-00311-y.

12. Warham J. Wing loadings, wing shapes, and flight capabilities of Procellariiformes. *N Z J Zool*. 1977;4:73–83. doi:10.1080/03014223.1977.9517938.

13. Spear LB, Ainley DG. Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis*. 1997;139:221–33. doi:10.1111/j.1474-919X.1997.tb04620.x.

14. González-Solís J, Croxall JP, Oro D, Ruiz X. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Front Ecol Environ*. 2007;5:297–301. doi:10.1890/1540-9295(2007)5[297:TMAMIT]2.0.CO;2.

15. Ventura F, Granadeiro JP, Padget O, Catry P. Gadfly petrels use knowledge of the windscape, not memorized foraging patches, to optimize foraging trips on ocean-wide scales. *Proc Biol Sci*. 2020;287:20191775. doi:10.1098/rspb.2019.1775.

16. Ramírez I, Paiva VH, Fagundes I, et al. Conservation implications of consistent foraging and trophic ecology in a rare petrel species. *Anim Conserv*. 2016;19:139–52. doi:10.1111/acv.12227.

17. Ramos R, Ramírez I, Paiva VH, et al. Global spatial ecology of three closely-related gadfly petrels. *Sci Rep*. 2016;6:23447. doi:10.1038/srep23447.

744 18. Rayner MJ, Carlile N, Priddel D, et al. Niche partitioning by three *Pterodroma* petrel
745 species during non-breeding in the equatorial Pacific Ocean. *Mar Ecol Prog Ser*.
746 2016;549:217–29. doi:10.3354/meps11707.
747 19. Navarro J, Votier SC, Aguzzi J, Chiesa JJ, Forero MG, Phillips RA. Ecological
748 segregation in space, time and trophic niche of sympatric planktivorous petrels. *PLoS*
749 *One*. 2013;8:e62897. doi:10.1371/journal.pone.0062897.
750 20. Müller MS, Massa B, Phillips RA, Dell'Omo G. Seabirds mated for life migrate separately
751 to the same places: behavioural coordination or shared proximate causes? *Anim Behav*.
752 2015;102:267–76. doi:10.1016/j.anbehav.2015.02.005.
753 21. Kubo A, Takahashi A, Thiebot J-B, Watanuki Y. Rhinoceros Auklet pair-mates migrate
754 independently but synchronize their foraging activity during the pre-laying period. *Ibis*.
755 2018;160:832–45. doi:10.1111/ibi.12583.
756 22. Guilford T, Wynn R, McMinn M, et al. Geolocators reveal migration and pre-breeding
757 behaviour of the critically endangered Balearic shearwater *Puffinus mauretanicus*. *PLoS*
758 *One*. 2012;7:e33753. doi:10.1371/journal.pone.0033753.
759 23. Sánchez-Macouzet O, Rodríguez C, Drummond H. Better stay together: pair bond
760 duration increases individual fitness independent of age-related variation. *Proc Biol Sci*.
761 2014;281:20132843. doi:10.1098/rspb.2013.2843.
762 24. O'Dwyer T, Carlile N, O'Neill L, Halpin LR. Changing fortunes of the Black-winged petrel
763 *Pterodroma nigripennis* following the Lord Howe Island Rodent Eradication Project —
764 interactions with other recovering species. *Bird Conserv Int*. 2022;33:e18.
765 doi:10.1017/S0959270922000132.
766 25. Halpin LR, Ross JD, Ramos R, et al. Double-tagging scores of seabirds reveals that
767 light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar
768 profiles. *Methods Ecol Evol*. 2021;12:2243–55. doi:10.1111/2041-210X.13698.

769 26. Halpin LR, Mott R, Clay TA, Humphries GRW, Chatwin TA, Carlile N, et al. Predicting the
770 foraging habitats of sympatrically breeding gadfly petrels in the South Pacific Ocean.
771 *Front Mar Sci*. 2022;9:853104. doi:10.3389/fmars.2022.853104.
772 27. R Core Team. R: a language and environment for statistical computing. Version 4.5.1.
773 Vienna: R Foundation for Statistical Computing; 2025.
774 28. Bindoff AD, Wotherspoon SJ, Guinet C, Hindell MA. Twilight-free geolocation from noisy
775 light data. *Methods Ecol Evol*. 2018;9:1190–8. doi:10.1111/2041-210X.12953.
776 29. Wotherspoon S, Sumner M, Bindoff A, Raymond B, Lisovski S. SGATII: solar/satellite
777 geolocation for animal tracking II. R package version 0.0.0.9000. 2025.
778 https://github.com/SWotherspoon/SGATII. Accessed 24 Sep 2026.
779 30. Calenge C. The package “adehabitat” for the R software: a tool for the analysis of space
780 and habitat use by animals. *Ecol Modell*. 2006;197:516–9.
781 doi:10.1016/j.ecolmodel.2006.03.017.
782 31. Hijmans RJ. geosphere: spherical trigonometry. R package version 1.5. 2024.
783 https://CRAN.R-project.org/package=geosphere. Accessed 24 Sep 2026.
784 32. Stoffel MA, Nakagawa S, Schielzeth H. rptR: repeatability estimation and variance
785 decomposition by generalized linear mixed-effects models. *Methods Ecol Evol*.
786 2017;8:1639–44. doi:10.1111/2041-210X.12797.
787 33. Fieberg J, Kochanny CO. Quantifying home-range overlap: the importance of the
788 utilization distribution. *J Wildl Manage*. 2005;69:1346–59. doi:10.2193/0022-
789 541X(2005)69[1346:QHOTIO]2.0.CO;2.
790 34. Carneiro APB, Bonnet-Lebrun A-S, Manica A, Staniland IJ, Phillips RA. Methods for
791 detecting and quantifying individual specialisation in movement and foraging strategies
792 of marine predators. *Mar Ecol Prog Ser*. 2017;578:151–66. doi:10.3354/meps12215.
793 35. Dumas K, Gilg O, Courbin N, Corregidor-Castro A, Evanno G, et al. Influence of sea-ice-
794 related features and anthropogenic subsidies on the foraging behaviour of a high-Arctic

seabird, the ivory gull (*Pagophila eburnea*). *Mar Biol*. 2022;169:151. doi:10.1007/s00227-022-04137-5.

36. Rayner MJ, Gaskin CP, Taylor GA. Seasonal movements, foraging activity, and breeding biology of black-winged petrel (*Pterodroma nigripennis*) from three New Zealand colonies. *Notornis*. 2023;70:111–23. doi:10.63172/057819uxtnjz.

37. Shaffer SA, Tremblay Y, Weimerskirch H, et al. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proc Natl Acad Sci U S A*. 2006;103:12799–802. doi:10.1073/pnas.0603715103.

38. Brooke M de L, Clay TA. Dispersive migration of breeding Juan Fernández Petrels *Pterodroma externa* across the eastern Pacific Ocean and overlap with tropical tuna fisheries. *Emu Austral Ornithol*. 2026;126:133–46. doi:10.1080/01584197.2026.2630916.

39. Rayner MJ, Taylor GA, Gummer HD, Phillips RA, Sagar PM, Shaffer SA, et al. The breeding cycle, year-round distribution and activity patterns of the endangered Chatham Petrel (*Pterodroma axillaris*). *Emu Austral Ornithol*. 2012;112:107–16. doi:10.1071/MU11066.

40. Clay TA, Phillips RA, Manica A, Jackson HA, Brooke M de L. Escaping the oligotrophic gyre? The year-round movements, foraging behaviour and habitat preferences of Murphy's petrels. *Mar Ecol Prog Ser*. 2017;579:139–55. doi:10.3354/meps12244.

41. Clay TA, Brooke M de L. Trans-equatorial migration links oceanic frontal habitats across the Pacific Ocean: year-round movements and foraging activity of a small gadfly petrel. *Mar Biol*. 2024;171:60. doi:10.1007/s00227-023-04373-3.

42. Catry P, Dias MP, Phillips RA, Granadeiro JP. Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology*. 2013;94:1230–5. doi:10.1890/12-2177.1.

43. Bogdanova MI, Daunt F, Newell M, Phillips RA, Harris MP, Wanless S. Seasonal interactions in the black-legged kittiwake, *Rissa tridactyla*: links between breeding

performance and winter distribution. *Proc Biol Sci*. 2011;278:2412–8. doi:10.1098/rspb.2010.2601.

44. Gunnarsson TG, Gill JA, Sigurbjörnsson T, Sutherland WJ. Pair bonds: arrival synchrony in migratory birds. *Nature*. 2004;431:646. doi:10.1038/431646a.

45. Fayet AL, Shoji A, Freeman R, Perrins CM, Guilford T. Within-pair similarity in migration route and female winter foraging effort predict pair breeding performance in a monogamous seabird. *Mar Ecol Prog Ser*. 2017;569:243–52. doi:10.3354/meps12083.

46. González-Solís J, Becker PH, Wendeln H. Divorce and asynchronous arrival in common terns, *Sterna hirundo*. *Anim Behav*. 1999;58:1123–9. doi:10.1006/anbe.1999.1235.

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