Seabirds as environmental indicators: foraging behaviour and ecophysiology of common diving petrels (*Pelecanoides urinatrix*) reflect local scale differences in prey availability.

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Abstract

Seabird foraging behaviour can reflect prey abundance at sea, and is influenced by stress hormone levels, thus providing a potential indicator of at sea conditions. Using common diving petrels (*Pelecanoides urinatrix,* hereafter CDPs), a procellariform that preferentially forages on crustacean zooplankton, we sought to understand how spatially-separate colonies responded behaviourally and physiologically to contrasting prey levels with a view to recruiting this species as an environmental indicator.

In 2016, incubating CDPs from Tiritiri Matangi (-36.59S; 174.88E, low levels of preferred prey) and Burgess (-35.91S; 174.12E, high levels of preferred prey) Islands within the Hauraki Gulf, New Zealand were tracked using GPS devices. We hypothesised that Tiritiri birds would exhibit greater foraging effort and higher stress hormone levels across the breeding season due to lower levels of available prey. Hidden Markov methods were used to model foraging effort; and prey trophic level (stable isotopes: $\delta^{13}C$ and $\delta^{15}N$) and stress hormone levels (CORT) quantified in plasma samples.

During incubation birds were spatially segregated when foraging. Tiritiri birds exerted more effort chasing higher trophic level prey at larger distances from the colony, and had higher body weight and lower CORT than Burgess birds. However, bird CORT levels responded more to reproductive duties (peaking during chick rearing) as opposed to colony location i.e. CORT was not consistently higher in Tiritiri birds. Although a snapshot, our findings illustrate the promise of integrating multiple parameters when recruiting seabirds as ocean indicators, resulting in improved resolution of future monitoring programmes based upon them.

Keywords: Stable isotope, Corticosterone, Hidden Markov Modelling, Foraging Ecology

Introduction

Seabirds are found in nearly all marine environments and are considered sensitive indicators of oceanic productivity (Cairns 1988). This is because seabird foraging behaviour, prey type targeted, and physiology can all respond to differences in oceanic productivity (Harding et al. 2013). As central place foragers, behavioural flexibility is critical for seabirds if they are to maintain energy balance and successfully reproduce (Christensen-Dalsgaard et al. 2018). Albatrosses and petrels, for instance, travel large distances before returning to provision their chick at their breeding site (Rayner et al. 2012). Accordingly, seabird foraging strategies are tuned to accommodate varying distances between breeding sites and areas of resource abundance; in addition to the spatial and temporal variation in marine productivity (Kokubun et al. 2018). Uncovering such behavioural flexibility is often a complex and time-consuming task, but recent algorithms such as Hidden Markov Modelling (HMM) are showing potential in predicting behavioural states (commuting, area restricted searches) related to foraging from global positioning system (GPS) tracking data (Bennison et al. 2018). For example, many Manx shearwaters (*Puffinus puffinus*) breeding on different colonies in the North Atlantic travelled to the Irish front to feed (Dean et al. 2012). Birds breeding further away from the front were found to spend more time commuting than actively seeking prey, and this was hypothesised to be more energetically demanding (Dean et al. 2012). In some seabird species such increases in foraging activity are known to be associated with higher levels of stress hormones (Crossin et al. 2012).

For avian taxa, corticosterone (CORT) is the glucocorticoid hormone released in the avian stress response (Romero and Romero 2002) which may be triggered by a number of intrinsic and extrinsic stressors (Madliger and Love 2016). For seabirds, measuring baseline CORT has been used to compare population stress levels in response to varying resource availability (Sorenson et al. 2017). By coupling blood CORT levels with estimates of bird condition (e.g. weight) and foraging behaviour, any apparent life-history trade-offs made by parents from colonies adjacent to low productivity environments, can be quantified (Storey et al. 2017). Understanding these dynamics is especially important during breeding, as increases in CORT are linked with negative effects on seabird reproductive success (Kitaysky et al. 2007). Furthermore, reduced breeding success can also be related to elevated CORT levels experienced months prior e.g. during the energetically demanding pre-breeding moult stage (Harms et al. 2015). Such carry-over effects demonstrate the value of CORT as a biomarker of reproductive success in birds.

Coupled with GPS tracking and CORT analysis, stable isotope ratios of carbon and nitrogen in avian tissues can help to understand relationships among hormone stress levels, trophic ecology, movements, and reproduction of individuals and populations (Fleming et al. 2018). Measurements of $\delta^{13}C$ values provides information on a broad spatial scale, (e.g. latitudinal distribution at sea), and at finer scales can indicate reliance on foraging from benthic versus pelagic, and inshore versus offshore food webs (Cherel and Hobson 2007). Alternatively, measurements of $\delta^{15}N$ values increase stepwise by ~3 to 5 ‰ with each trophic level (Post 2002) and can provide an excellent comparative measure of the broad type of prey consumed by differing populations (Bearhop et al. 2002). For studies requiring an indication of short term dietary assimilation, blood plasma is particularly useful as plasma proteins

have a short half-life (2-4 days) and thus reflect the isotope values of prey consumed by an animal over a period of approximately a week prior to sampling (Hobson and Clark 1993). Whilst seabirds have been recognised as indicators of oceanic productivity for decades (Parsons et al. 2008); their predictive ability can be hampered by differences in resource acquisition among colonies (e.g. prey switching, adjusting foraging budgets) that can mask actual declines in productivity (Grémillet and Charmantier 2010). Given that much seabird monitoring typically occurs at a single colony location, such plasticity can often go undetected. Therefore, integrative studies incorporating analyses of behaviour, stress hormone production, and stable isotopes among colonies can yield a more informative understanding of seabird responses to fluctuating oceanic productivity (Harding et al. 2013). To investigate this, we undertook an integrative study of common diving petrels (*Pelecanoides urinatrix;* hereafter CDP) to understand how this species coped with differences in environmental conditions between colonies. Recent work by Zhang et al. (2019) tested the ability of an HMM approach to identify at sea foraging behaviour (commuting, area restricted searches) in CDPs during breeding; with birds found to forage locally i.e. within 45 km (maximum linear distance) of the colony. As predators, CDPs are considered specialists of mesoplanktonic prey, particularly euphausiid and copepod marine crustaceans (Reid et al. 1997) where a significant portion of time (i.e. average 76 dives per hr) is spent underwater chasing prey (Dunphy et al. 2015). Moreover, CDPs differ from other procellariiforms, as day long foraging trips are undertaken during breeding, with a nightly return to breeding colonies, which limits trip duration and helps explain their limited foraging range (Rayner et al. 2017). Thus, we hypothesised that geographically separated colonies of CDPs might act as sensitive ocean indicators of discrete patches of ocean on local (10's km) scales. Such information could be particularly relevant for local government

118 agencies whose jurisdictions span 10-100's km of coast. However, at present there is little
119 tracking data for this species to confirm this.

120 Therefore, to test our hypothesis, we used GPS tracking, stable isotope analysis, and stress
121 hormone profiling (CORT) of incubating CDPs breeding on two islands of the Hauraki Gulf,
122 Auckland, New Zealand during September 2016. Tiritiri Matangi Island (hereafter 'Tiritiri')
123 lies approximately 70 kilometres from Burgess Island and is positioned within the inner
124 Hauraki Gulf, in waters where the mesoplankonic community is dominated by non-
125 crustacean zooplankton during the CDP breeding season (Austral spring) (Zeldis and Willis
126 2015). Conversely, Burgess Island lies in the outer Gulf, approximately 25 kilometres from
127 the shelf slope and is surrounded by waters abundant in crustacean (copepods/euphausiids)
128 zooplankton prey during the CDPs breeding season (Zeldis and Willis 2015). Accordingly,
129 we predicted that:

130 1) Nitrogen stable isotope data would show no difference in the trophic level of prey
131 consumed by birds from each colony i.e. both would target crustacean zooplankton.
132 2) However, in order to gain sufficient food, Tiritiri birds would exhibit greater
133 plasticity in foraging ranges and travel times than Burgess birds (where the colony is
134 located closer to optimal foraging habitats);
135 3) Due to this decreased food availability, birds from Tiritiri will thus exhibit higher
136 CORT levels than those from Burgess measured across the breeding season.

137

Methods

Study site and timing

This study was conducted simultaneously at two CDP breeding colonies within the Hauraki Gulf, namely on Burgess Island of the Mokohinau Island group (estimated 10,000 breeding pairs, 35°54′10″S, 175°07′05″E) and Tiritiri Matangi Island (estimated 500 breeding pairs, 36° 36' S, 174° 53' E) (Fig. 1). To gain a high-resolution snapshot into foraging behaviour, birds were tracked simultaneously using GPS over 11 days between the 25th September to 9th October 2016 during the CDP incubation period. Blood samples were also collected from tracked birds for stable isotope analysis to gain insight into any dietary and habitat segregation. To assess changes in baseline corticosterone across the breeding season, bird plasma was obtained during the pre-laying (June), incubating (Sept – during tracking study) and chick rearing (Nov) phases at each location.

Foraging distribution and behaviour of GPS-tracked CDPs

Tracking data for Tiritiri Matangi used in this study have already been published in Zhang et al. (2019) which also describes and the methods of device attachment, and interpolation of missing data. In brief, during incubation breeding CDP pairs jointly occupy their burrow at night, but alternate on a two-day cycle between daily incubation and daily foraging bouts at sea (Rayner et al. 2017). At each breeding colony, CDPs (Tiritiri Matangi, n = 10; Burgess Island, n = 14), previously banded as a result of population studies, were captured in the late afternoon of their daily incubation shift from established wooden nest boxes. Captured birds were fitted with GPS data-loggers (nanoFix-GEO45_30m, Pathtrack Ltd, Otley, UK, hereafter GPDs,) using adhesive tape and super glue to fix the devices to clusters of central

back feathers. GPDs were less than 3% of the total mass of the study birds (i.e. tag weight: 2.5 – 3.0 g; bird weight: 130 g -155 g) and were configured to record locations at five-minute sampling intervals. Tagged birds were then returned to the nest box and allowed to leave naturally for foraging at sea, prior to dawn the following morning. Tracked birds were re-captured in their nest boxes the following evening, GPD's removed and data downloaded. Individuals were only tracked once during the course of the study i.e. total number of tracks = 24, however four GPD's were redeployed on the partners of tracked birds on Burgess Island following their retrieval.

Comparison of bird diets via stable isotope analyses

Ten and 11 blood plasma samples were collected for stable isotope analysis from CDPs recaptured following tracking from Tiritiri and Burgess respectively. Approximately 50 μl of plasma was obtained by spinning down whole blood collected from the metatarsal vein of each tracked bird upon its return to the colony using a 1 ml syringe. Samples were stored in heparinised tubes at 4°C, centrifuged within 2 hours of collection and blood plasma was decanted into 75% ethanol and stored at -20°C. Prior to analysis, ethanol was removed by heating lidless samples in an incubator for 12 hours at 50°C. Stable isotope analyses of dried blood plasma were carried out at National Institute of Water & Atmospheric Research (NIWA) using an AS200 LS autosampler and NA 1500N (Fisons Instruments, Rodano, Italy) elemental analyser combustion furnace connected to a DELTA^{Plus} continuous flow, isotope ratio mass spectrometer (Thermo-Fischer Scientific, Bremen, Germany). Operational details are outlined in (Rayner et al. 2016) with the exception that $\delta^{13}C$ values were calibrated against a CO_2 reference gas, relative to the international standard Carrara Marble NSB-19 (National Institute of Standards and Technology (NIST), Gaithersberg, MD, USA). This, in

turn, was calibrated against the original Pee Dee Belemnite (PDB) limestone standard and was then corrected for ^{17}O. Carbon isotope data were corrected via a two-point normalisation process using NIST 8573 (USGS40 L-glutamic acid; certified $\delta^{13}C$ = -26.39 ± 0.09 ‰) and NIST 8542 (IAEA-CH-6 Sucrose; certified $\delta^{13}C$ = -10.45 ±0.07 ‰). A two-point normalisation process using NIST 8573 (USGS40 L-glutamic acid; certified $\delta^{15}N$ = -4.52 ± 0.12 ‰) and IAEA-N-2 (ammonium sulphate: certified $\delta^{15}N$ = +20.41 ± 0.2 ‰) was applied to $\delta^{15}N$ data. DL-Leucine (DL-2-Amino-4-methylpentanoic acid, $C_6H_{13}NO_2$, Lot 127H1084, Sigma, Australia) was run every ten samples to check analytical precision and enable drift corrections to be made if necessary. Additional international standards NIST 8574 (USGS41 L-glutamic acid; certified $\delta^{13}C$ = +37.63 ±0.10‰ and $\delta^{15}N$ = +47.57 ±0.22 ‰), NIST 8547 (IAEA-N1 ammonium sulphate; certified $\delta^{15}N$ = +0.43 ±0.04 ‰) were run daily to check isotopic accuracy. Repeat analysis of standards produced data accurate to within 0.25 ‰ for both $\delta^{15}N$ and $\delta^{13}C$, and a precision of better than 0.32 ‰ for $\delta^{15}N$ and 0.24 ‰ for $\delta^{13}C$. Finally, carbon isotope data were retrospectively corrected for lipid content using C:N molar ratios following equations in (Fry 2002).

CORT secretion between colonies

CORT secretion among colonies was assessed across the breeding season (i.e. Pre-laying, Incubating, and Chick rearing) with no birds sampled repeatedly. To obtain sufficient plasma for baseline CORT levels, non-GPS tracked birds were randomly collected as they landed at the colony. Before drawing blood, the tarsus of each bird was cleaned with a cotton gauze pad soaked with 100% ethanol and approximately, 250 µl of blood was drawn from the metatarsal vein using a 1 ml syringe within three minutes of first sighting each bird. Blood was rapidly transferred to a heparinised tube (Sarstedt, Nümbrecht, Germany)

and stored on ice before being spun (10 mins at 10,000 rpm) back in the laboratory (< two hours later) to obtain plasma. Plasma samples were then stored frozen at -20°C until analysis.

Plasma CORT levels were measured using enzyme linked immunosorbent (ELISA) methods. A commercially available kit (ENZO Life Sciences Inc., kit ADI-900-097), was used with samples of plasma to determine CORT plasma concentrations (Crino et al. 2017; Xie et al. 2017), as per the kit instructions. Briefly, a 1:40 dilution of sample was created using the steroid displacement reagent (to prevent protein binding) and the assay buffer provided. Samples and standards (20,000, 4,000, 800, 160 and 32 pg ml^{-1}) were then added to wells, and randomly assigned among the assay plates. All samples were assayed in duplicate and the average of duplicates used to calculate final CORT concentrations (ng ml^{-1}) for that sample.

Statistical methods

Determining foraging distributions and behaviour via Hidden Markov Models (HMM)

Methods used to determine foraging behaviour are outlined in Zhang et al. (2019). Briefly, all GPS observations that were over the land (the breeding colony) were removed and any sampling gaps present at the end of a trip due to GPS running out of battery, were also excluded from further data analysis. As HMM analyses require input data to have equal sampling intervals (in our case every 5 min), we estimated missing observations (e.g. satellite fix being missed as bird was underwater chasing prey) within the trip based on a 'continuous-time correlated random walk', using the crawlWrap function in the R package 'crawl', as described in (McClintock 2017). Imputed, temporally-regular location data at every five-minutes (the same as the original GPS configuration) were then processed to

calculate speeds and relative turning angles (RTAs) between all sequential position fixes for use as inputs for the HMM. We used a likelihood-based method to determine the number of distinct behavioural states within foraging trajectories of all birds, following Dean et al. (2013). Based on the biological knowledge of the species and the interpretability of the likelihood-based method results, we chose a two-state HMM i.e.'area restricted search' = slow flight speed <0.5 m s^{-1} and 'commuting' = flight speed >0.5 m s^{-1} (Pohle et al. 2017). We then fitted the speed and relative turning angle of the CDPs' foraging trajectories into a two-state HMM algorithm, with each observation classified into one of two correlated random walks, characterised by unique distributions of speeds and turning angles (Morales et al. 2004). For the two-state model, we applied a gamma distribution for step length, and a wrapped Cauchy distribution with mean zero and concentration parameter $\varrho_z \in (0, 1)$ for turning angle. The HMM was implemented using 'momentuHMM' package (McClintock and Michelot 2018) in R (R Core team 2015).

The spatial distribution of CDP's from each colony when foraging within the Hauraki Gulf was mapped in ArcMap 10.3 (© ESRI Inc). For spatial analyses individual kernel density distributions were created for each tracked individual using the Spatial Analyst extension with a grid size of 100 m and search radius of 1 km. Kernels were then averaged across all individual kernels in a population to create a final density surface for each population and then overlain on satellite derived Chlorophyll-a (Chl-a) data obtained from NASA (https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MY1DMM_CHLORA). Number of fixes obtained by the GPS devices, trip duration, linear distance from colony, and total flight path length were compared between Islands using Students t-tests.

Comparison of stable isotope, bird weight, and CORT secretion between colonies

Bird weight (g) and initial CORT (ng ml^{-1}) data were tested for normality (Shapiro-Wilk), and homogeneity of variance (Brown-Forsythe) and subsequently log transformed to ensure the assumptions of ANOVA were met. To test the effect of *Island*, *Breeding stage* and *Island* × *Breeding stage*, Two-way ANOVA tests were performed on logged CORT data with significant differences among effects identified via pairwise Holm-Sidak tests. Comparisons of stable isotope values between colonies were made using Student t-tests. All values are presented as mean ± S.D. and univariate analyses were performed in Sigmaplot v13.0 (SYSTAT, San Jose, CA, USA) with a threshold of significance set at $\alpha = 0.05$.

Finally, all data is freely available in our fig share repository (xxxx) or available on request.

Results

Foraging distribution of GPS-tracked CDPs

We obtained 14 and ten tracks from Burgess and Tiritiri birds respectively (mean fix rate 67% and 62% respectively), with no significant difference in the number of GPS fixes per track between populations (Burgess 111.14 ± 58.33 fixes per track, Tiritiri 101.70 ± 25.8 fixes per track; Students t-test, $p = 0.63$). Departure times for tracked birds occurred between 4:10 and 5:20 am on Tiritiri Island, and between 4:02 and 4:55 am for birds on Burgess Island (prior to sunrise which was 06:56 am during this study).

There was no overlap in the tracking locations of CDP from both colonies within the Hauraki Gulf (Fig 1). CDPs from Burgess Island were distributed predominantly to the west of the colony with the greatest concentration of locations in a south-west direction towards the Hauraki Gulf. By comparison, CDPs tracked from Tiritiri moved east and north-east over the centre of the inner Hauraki Gulf, with one bird making an extended foraging trip northward.

Trip duration was not significantly different between populations (Burgess 14.79 ± 6.47 hours versus Tiritiri 14.70 ± 3.32 hours; Students t-test $p = 0.95$, Fig 2), but Tiritiri CDPs travelled significantly further from their colony than Burgess birds (33.82 ± 4.68 km versus 19.19 ± 7.30 km; Students t-test $p = 0.00005$) and had significantly longer total path distances (78.76 ± 17.87 km versus 51.95 ± 25.33; Students t-test $p = 0.006$, Fig 2).

These differences were further evidenced in the modelling of flight behaviour via HMM (Figure 3). When compared to birds from Burgess Island, the Tiritiri Island colony birds commuted further and undertook area-restricted search behaviours at a greater distance

from the colony as evidenced in Figure 3. At both sites, a small number of birds (two from Burgess Island and one from Tiritiri Matangi) undertook an extended trip to forage as evidenced by the small peak in behaviour at greater distances from their respective colonies (Figure 3). No significant differences were observed in the mean percentage of trip time spent in an area restricted search state (i.e. Burgess Island 64.3 ± 2.6% of time spent foraging vs 59.62 ± 4.6% for Tiritiri Matangi; Students t-test $p = 0.18$).

Comparison of bird diets via stable isotopes

Mean blood plasma $\delta^{15}N$ and $\delta^{13}C$ values were higher for Tiritiri birds i.e. $\delta^{15}N$ Tiritiri 13.98 ± 0.22 ‰, versus Burgess 11.74 ± 0.48 ‰; t-test, $t = 13.49$ $p < 0.00001$) and $\delta^{13}C$ Tiritiri -18.56 ± 0.28 ‰ versus Burgess -19.33 ± 0.17 ‰; t-test, $t= 6.78$, $p < 0.00001$) (Figure 4).

Comparison of bird weight, and CORT secretion between colonies

Weights (g) of adult CDPs recorded at Burgess Island were 140.2 ± 20.7 (Prelaying), 129.7 ± 14.8 (Incubating) and 152.6 ± 15.2 (Chick rearing); whilst Tiritiri birds weighed 148.4 ± 10.9 (Prelaying), 142.0 ± 13.7 (Incubating) and 145.3 ± 20.8 (Chick rearing, Figure 5A).

Results of two-way ANOVA are given in Table 1 and show that *Island* had no significant effect on bird weight (i.e. overall means: 142.2 ± 16.0, Burgess; 145.1 ± 15.1, Tiritiri). However, weight significantly differed due to *Breeding stage* with birds lighter during 'Incubating' i.e. overall means: 144.3 ± 16.0 (Pre-lay); 135.8 ± 16.0 (Incubating); 149.0 ± 16.3 (Chick rearing). This result likely derives from the low weights of Burgess Island birds during 'Incubation', which were significantly lighter than Tiritiri (Figure 5) which also resulted in a significant *Island* × *Breeding stage* interaction effect (Table 1).

303 Levels of CORT (ng mL^{-1}) recorded in Burgess birds were 14.6 ± 7.7 (Prelaying), 25.6 ± 5.3
304 (Incubating) and 40.2 ± 6.6 (Chick rearing); whereas CORT levels in Tiritiri birds were 25.8 ±
305 8.0 (Prelaying), 12.7 ± 5 (Incubating) and 53.2 ± 6.8 (Chick rearing, Figure 5B). The effect term
306 '*Island'* had no significant effect on bird CORT i.e. overall means: 27.5 ± 31.6, Burgess; 28.1 ±
307 27.5, Tiritiri (Two-way ANOVA). However, like weight, CORT significantly differed due to
308 *Breeding stage* with CORT significantly higher during 'Chick rearing' i.e. overall means: 20.0
309 ± 20.1 (Pre-lay); 19.4 ± 20.2 (Incubating); 46.5 ± 38.2 (Chick rearing). Lastly, across the
310 breeding season CORT levels in CDPs varied depending on colony, with CORT
311 concentrations in Tiritiri birds significantly higher than Burgess Island birds during
312 'Prelaying'; whereas Burgess Island birds recorded higher CORT levels than Tiritiri during
313 'Incubating'. There were no differences in CORT between islands during 'Chick rearing'
314 (Figure 5B).

315 **Discussion**

316 As central place foragers, seabirds are well known indicators of oceanic resources within the
317 surrounding environment (Burke and Montevecchi 2009). In line with our predictions,
318 breeding CDPs surrounded by resource-poor waters exhibited greater foraging effort
319 compared to colonies located near waters with reported greater prey availability (Zeldis and
320 Willis 2015).

321 *GPS tracking data and Hidden Markov Modelling*

322 By modelling GPS track data using HMM methods we gained a detailed insight into at-sea
323 behaviour for CDPs from each colony. Comparison of flight metrics showed that whilst
324 duration of daily foraging trips and time spent undertaking area restricted searches were

equal, adult CDPs breeding on Tiritiri likely expended more energy commuting and up to 1.5 times further than conspecifics at the Burgess Island colony. This contrasts with the 'flexible time budget' approach of adult common murres (*Uria aalge*), where birds breeding at colonies experiencing poor foraging conditions adjust time budgets and dedicate more time to foraging (Harding et al. 2007). Thus, for CDP, which are constrained to daily foraging bouts, trip duration cannot be increased; rather behavioural flexibility in foraging relates to extending trip distance, and potentially increasing energetic investment. To resolve this however, measures of energy expenditure are needed either via doubly labelled water methods, detailed analyses of time budgets, or accelerometery (Elliott et al. 2013; Wilson et al. 2019).

Using geolocator devices, Rayner et al. (2017) highlighted the continental shelf as a focal foraging area for CDPs breeding on Burgess Island. With the greater resolution afforded by GPS units, (i.e. spatial resolution ± 50 m GPS *versus* ± 180 km geolocators), our results showed that Burgess Island birds did not commute to the continental shelf, rather remained within the Hauraki Gulf. Furthermore, a distinct spatial segregation between these two CDP colonies (seperated by 70 km) was confirmed, with birds restricted to foraging within 45 km distance of their colony. Whilst spatial segregation is known between foraging CDPs, and South Georgian diving petrels (*Pelecanoides georgicus*) breeding at two colonies seperated by 9 km within Iles Kerguelen (Bocher et al. 2000), this is the first record of colony-specific segregation in breeding CDPs that we are aware of.

Due to logistics, we could only obtain a snapshot of foraging strategies during a key stage of breeding (incubation) for this species. Nevertheless, it appears that breeding CDPs from each colony forage widely, rather than commuting to a key oceanographic features as seen

348 in some other procellariiformes (Rayner et al. 2012). Of note, is the trend for Burgess Island
349 birds to direct their foraging trips towards the west and south-west. An explanation for this
350 pattern may be that in the austral spring this area has high zooplankton productivity, which
351 results from the penetration of nutrient-rich waters from the shelf slope into these shallower
352 waters. For Tiritiri birds it is apparent they are restricted to foraging within a north to north-
353 east wedge of water due to the proximity of land to the west. This may further exacerbate
354 the already reduced foraging opportunities for birds occupying this colony.

355 As seabird colony size increases, breeding adults are expected to increase their foraging
356 ranges to cope with density-dependent reductions in prey availability (Lamb et al. 2017).
357 However, we saw no evidence of this in our dataset, with Burgess Island birds having
358 shorter foraging distances than Tiritiri Island birds, despite residing in a colony with 20 x
359 more birds. Whilst such a result may bode well for this species as it rebuilds its numbers in
360 the region, it also suggests that differences in foraging behaviour between sites may not be
361 related to density-dependent effects. Rather, differences in prey availability may be a greater
362 driver of foraging distance as was shown in northern gannets (*Morus bassanus*) by Garthe et
363 al. (2011). Such a finding is of interest given that CDPs prey on zooplankton, a prey item
364 that should supposedly be less limiting than the teleost prey sought by Gannets.

365 *Plasma stable isotope analyses*

366 The use of stable isotopes to infer food web relationships of seabirds has a rich history (Inger
367 and Bearhop 2008). Given that marine crustaceans (copepods, euphausiids) are a dominant
368 feature of CDP diets (Reid et al. 1997; Bocher et al. 2000) we expected the plasma stable
369 isotope profiles of tracked birds would be similar between colonies and reflective of lower
370 trophic level zooplankton values. However, CDPs in our study were both spatially, and

371 trophically segregated with significant differences in $\delta^{15}N$ values between populations.
372 Tiritiri CDPs were targetting prey approximately half a trophic level higher than Burgess
373 Island CDP and surprisingly both populations had $\delta^{15}N$ values above those of conspecific
374 sub-Antarctic diving petrels populations whose diets were dominated by crustacean prey
375 ($\delta^{15}N$ 8-11, Bocher et al. 2000).

376 Although we did not characterise the dietary components of birds in our study, it is known
377 that marine crustaceans ($\delta^{15}N$: commonly 3.9 to 8.5 ‰ in the Tasman Sea although 10.3‰
378 has been recorded for some euphasiid species, Henschke et al. 2015) occupy a lower trophic
379 level than fish and cephalpods. For the Hauraki Gulf, $\delta^{15}N$ values range from 7.5 to 14.7 ‰
380 (fish) and 8.1 to 10.2 ‰ (cephalopods) (MacDiarmid et al. 2011; Pinkerton et al. 2012). The
381 differences in $\delta^{15}N$ between our colonies suggests plasticity in targeted prey. This is
382 particularly the case for Tiritiri CDP which had blood plasma values closer to those of
383 specialist piscivorous seabirds (Bearhop et al. 1999; Cherel et al. 2014; Camprasse et al. 2017).
384 One explanation may be that the low density of preferred crustacean prey in inner Hauraki
385 Gulf waters, forces Tiritiri birds to include a greater proportion of higher trophic level prey
386 in their diet. Alternatively, $\delta^{15}N$ baseline values may be elevated in this region, however we
387 do not have synoptic Hauraki Gulf baseline nitrogen isotope field data to verify this at
388 present.

389 *CORT secretion among colonies*

390 Titre of stress hormones recorded in CDP from both colonies were similar to previous values
391 recorded for sub-Antarctic adults of this species (Smith et al. 1994). For seabirds, elevated
392 CORT levels have been linked to greater nutritional stress (Kitaysky et al. 1999; Kitaysky et
393 al. 2007) however secretion of this hormone is also responsive to both extrinsic

394 environmental changes and intrinsic biological drivers e.g. circadian rhythms (Sorenson et
395 al. 2017). In some seabird species e.g. Little auks (*Alle alle*), the relationship between seabird
396 mass and CORT level has been shown to be negative, with lighter birds having higher CORT
397 levels (e.g. Harding et al. 2011). Thus, we predicted that due to decreased food availability
398 (i.e. low crustacean zooplankton biomass), birds from Tiritiri would have higher baseline
399 CORT levels. However, Birds from Tiritiri presented higher levels of CORT than Burgess
400 birds only during the pre-laying period but there were no significant differences in weight
401 between colonies during this period. In contrast, during incubation, although birds from
402 Tiritiri travelled longer distances to forage than birds from Burgess, they had lower CORT
403 levels and higher body mass. Reasons for this are difficult to discern but may reflect the
404 dynamics occurring both within the colony (e.g. competition) and/or local environment
405 (dynamics of prey abundance, type etc) given that the zooplankton community of the
406 Hauraki Gulf is known to vary both spatially and seasonally (Carroll et al. 2019). Thus,
407 whilst our snapshot study is interesting and demonstrates the utility of an integrative
408 approach, longer term datasets collected over multiple months and spanning several years
409 may be required to fully unpick the dynamics between prey abundance and CORT
410 secretion. Finally, we used bird weights as opposed to body condition indices in our study,
411 which may influence relationships between bird mass and CORT levels, thus readers are
412 advised to be mindful of this when comparing our results to other studies within the
413 literature.

414 Nevertheless, by analysing CORT levels across the breeding season, it is apparent that the
415 predictable life-history events during the breeding season may mediate pronounced
416 elevations in CORT levels, rather than the island (and thus foraging habitat), where the bird

colonies were located. In particular, the (presumably) energetically expensive period of chick rearing caused a significant upregulation in baseline CORT for birds from both sites. A meta-analysis by Sorenson et al. (2017) found that reductions in food availability, as opposed to foraging effort, were a greater driver of increased baseline CORT levels in seabirds. During chick rearing, adult CDPs are known to feed chicks a meal of around 26 g (18 % of adult mass) each night (Roby 1989). Thus, it may be that the increased CORT recorded in CDPs during chick rearing reflects parental weight loss that is masked by meals being brought ashore and destined to provision chicks.

Due to the logistics and costs of maintaining teams on remote islands, we were only able to track birds during the incubation phase of breeding. In the absence of precedents, this phase was chosen as work by Adams et al. (2005) on New Zealand grey-faced petrels showed incubation to be the most crucial phase. Thus, it may well be that foraging behaviour and target prey of CDPs change across and among breeding seasons. Moreover, there may be sex specific differences in foraging and CORT secretion, which were not captured in our dataset. Future work is thus planned to address this issue and characterise any influence of these phenomena. Finally, we were unsure whether our degree of handling might be deemed excessive by common diving petrels, leading to abandonment of eggs. Thus, we kept handling to minimum, and did not obtain CORT samples from birds carrying loggers. Now that we are confident such handling regimes are within the species' range of tolerance, we are intending to quantify logger effects on CORT levels in future work.

Conclusions

Given that CDPs are believed to preferentially forage on euphausiids and copepods, we predicted that birds residing on Tiritiri were foraging within a poor food resource

environment (i.e. low numbers of preferred crustacean prey) and would thus exhibit greater foraging effort when breeding. In our brief study, the prediction of longer foraging ranges for Tiritiri CDP was supported, however nitrogen isotopic segregation was evident between colonies, indicating a reliance on prey of different trophic levels for birds between each site. This suggests that Tiritiri CDP were flying further, not to access more crustacean prey, rather to target a potentially more energy rich and/or more abundant prey. If correct, this may explain why CORT secretion levels were reduced during incubation for Tiritiri CDP, i.e. while the greater foraging effort may have incurred extra costs, there was sufficient benefit in doing so. Lastly, our prediction of higher overall CORT levels in Tiritiri CDP across the breeding season was not upheld. CORT levels varied between colonies during pre-laying and incubating stages but peaked equally during the demanding phase of chick rearing, possibly in response to enforced fasting of adults as they provision chicks.

Our results highlight the value of integrative assessments of seabird breeding biology. By drawing on telemetry, behavioural modelling, stable isotopes trophic data, and physiology (CORT) we show that neighbouring colonies differ in responses to localised habitat conditions over 10's of km. Our results reveal that different CDP populations may target prey from different trophic levels and this integrative snapshot suggests that these responses (foraging behaviour, niche exploitation) help the birds maintain homeostasis, and in turn allows us to identify the most relevant stressors on these populations. However, longer term studies are required to incorporate these data with CDP breeding success, survival rates and population stabilities.

Grémillet et al. (2018) found that by feeding on krill and small schooling fish, diving petrels have experienced the greatest decrease in prey consumption over recent decades, and are

significantly threatened by proposed "balanced harvesting schemes" that seek to exploit all trophic levels of oceanic food webs. Our work highlights the fine scale at which such fishing operations may impact seabird species. However, by monitoring a diverse array of biological parameters, from multiple colonies, and over small spatial scales, a more accurate account of human impacts on seabird populations can be reported and ultimately lead to more effective management responses and more accurate environmental monitoring.

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Compliance with ethical standards

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Conflict of interest: All authors declare they have no conflict of interest.

Ethical approval: All work was performed under ethics approval granted by the University of Auckland Animal Ethics Committee (approval No 001392) and via a Wildlife Authority granted by the Department of Conservation (38016-FAU).

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645 Figures

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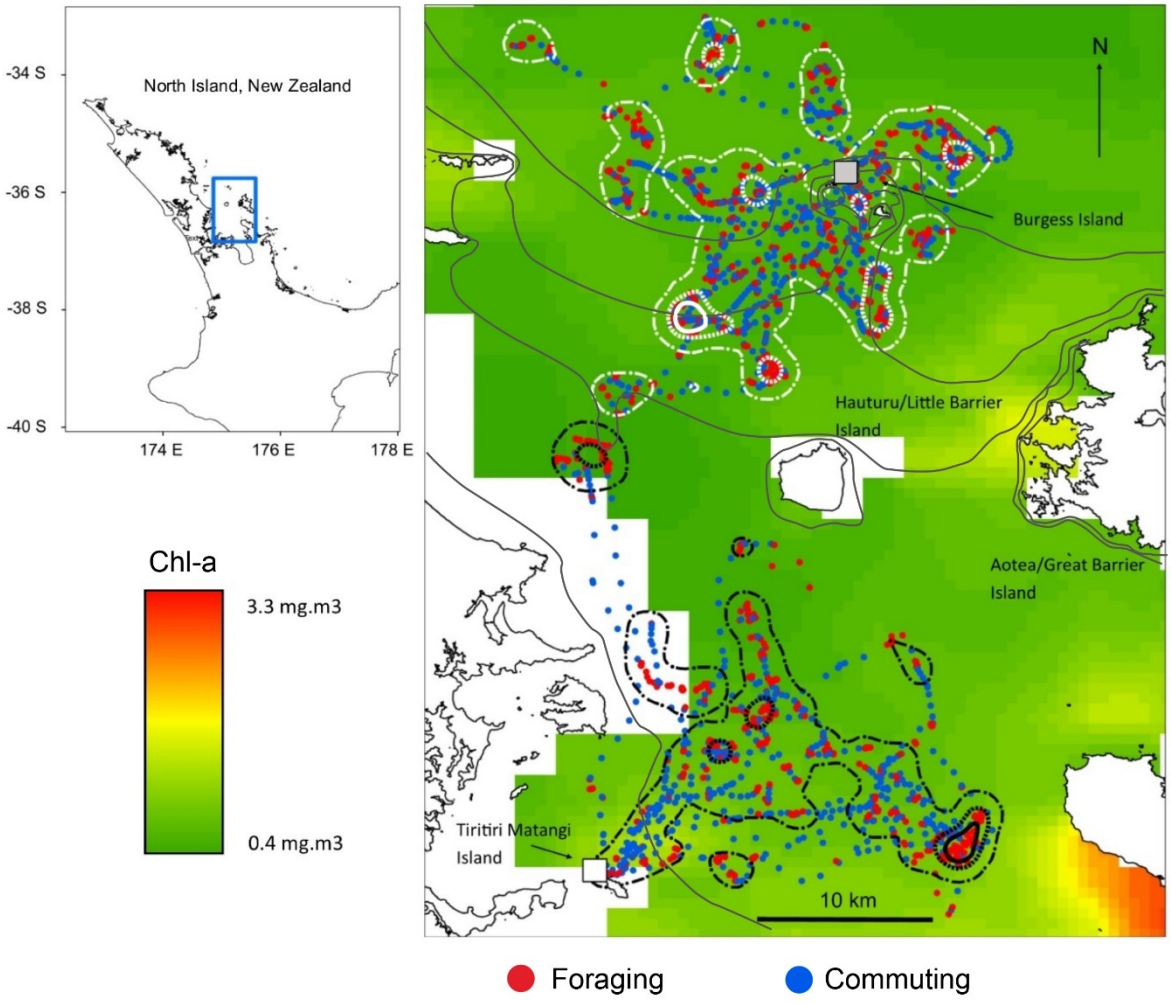

648

649 **Figure 1.** Foraging distributions of incubating common diving petrels (*Pelecanoides urinatrix*) tracked
650 with GPS from breeding colonies on Burgess Island (n = 14, grey square) and Tiritiri Matangi Island (n
651 = 10, white square) in New Zealand's Hauraki Gulf (20 m bathymetric lines shown in dark grey).
652 Individual tracking locations, are overlain on satellite derived estimates of Chl-a (sourced from
653 https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MY1DMM_CHLORA), and are represented by
654 coloured points to define the results of Hidden Markov Models i.e. red dots = area restricted

655 foraging behaviour (low speed and high turning angle) and blue dots = commuting behaviour (high
656 speed, low turning angle). Kernel density distributions, calculated using all data for each population,
657 are shown as 25% (solid lines), 50% (dotted lines), and 75% (dashed lines) kernel contours coloured
658 black for Tiritiri Matangi and white for Burgess Island.

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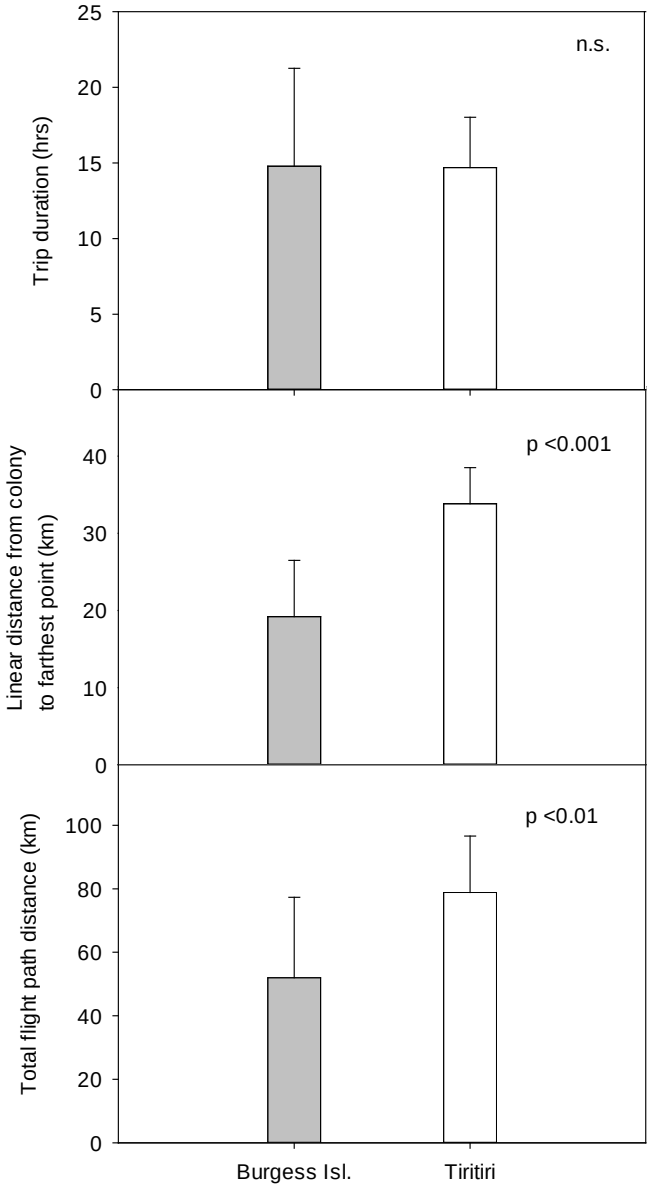

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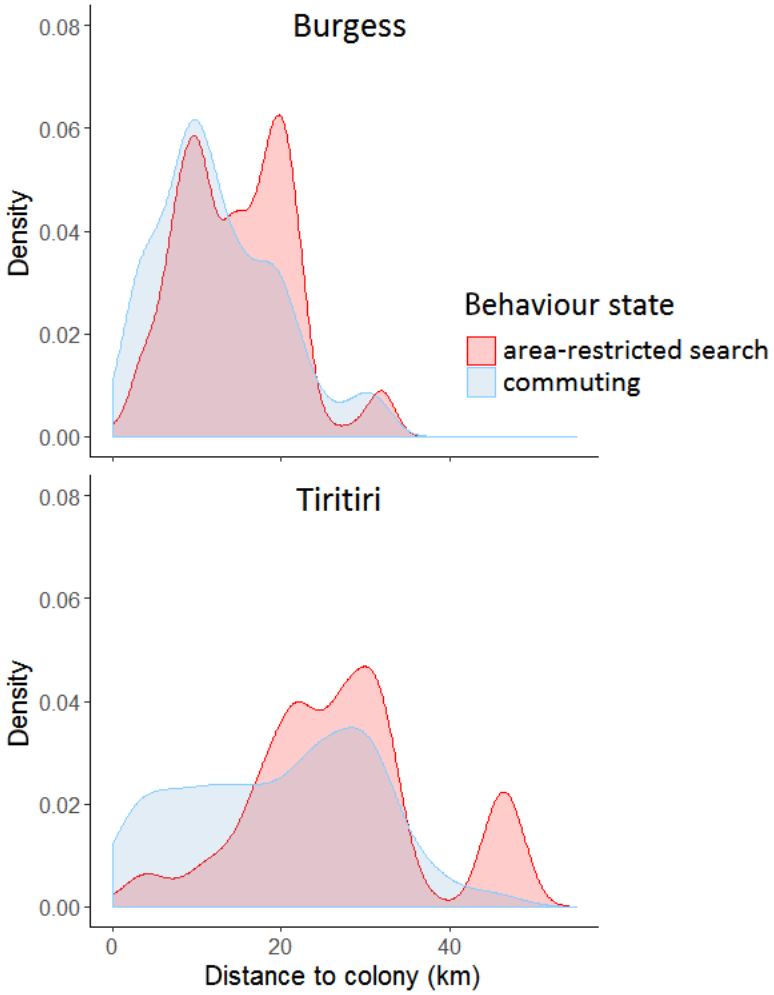
661 **Figure 2.** Comparison of mean (± S.D.) trip duration, linear distance from colony to farthest point,
662 and total flight path distance of foraging common diving petrels (*Pelcanoides urinatrix*) which were
663 GPS tracked during incubation from Burgess Island (n = 14) and Tiritiri Matangi Island (n = 10),
664 Hauraki Gulf, New Zealand.



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667 **Figure 3.** Behavioural state-dependent densities, derived from a Hidden Markov model, and
668 weighted to the proportion of observations assigned to each state for foraging common diving
669 petrels (*Pelcanoides urinatrix*) which were GPS tracked during incubation from Burgess Island (n =
670 14) and Tiritiri Matangi Island (n = 10), Hauraki Gulf, New Zealand.

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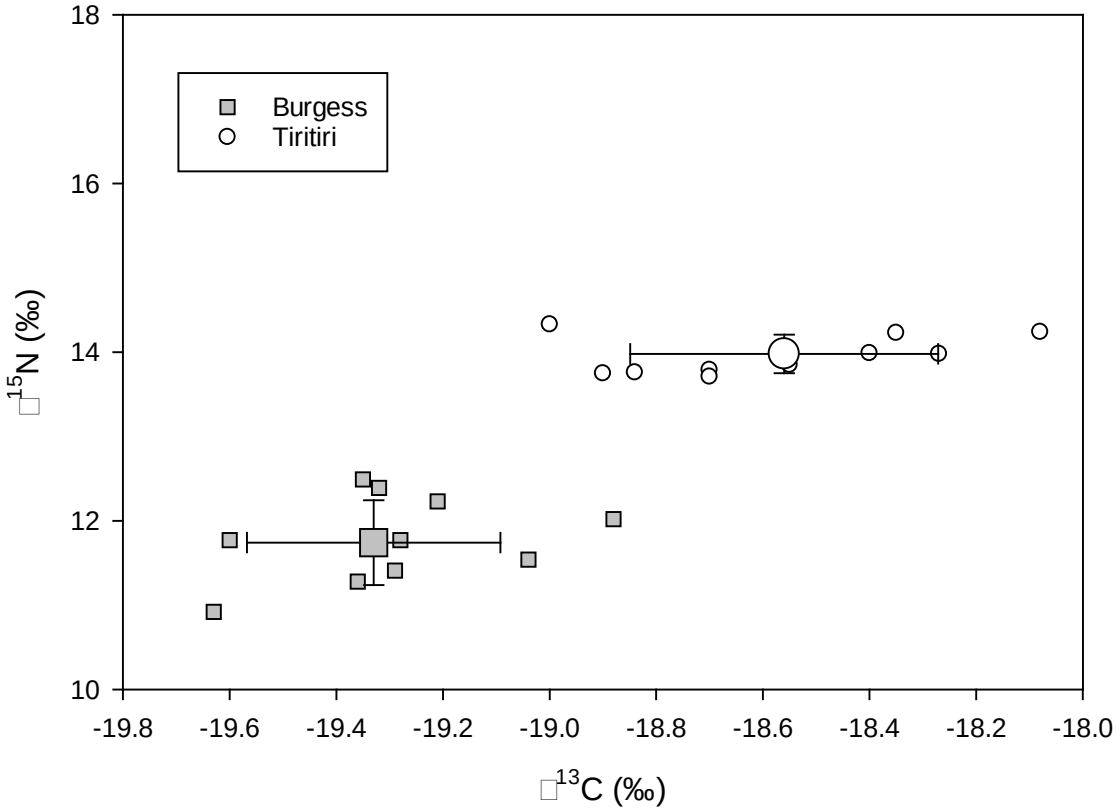

Figure 4. Stable isotope values in the plasma of foraging common diving petrels (*Pelcanoides urinatrix*) which were GPS tracked during incubation from Burgess Island (n = 11) and Tiritiri Matangi Island (n = 10), Hauraki Gulf, New Zealand. Mean and S.D. of each site depicted by larger symbols.

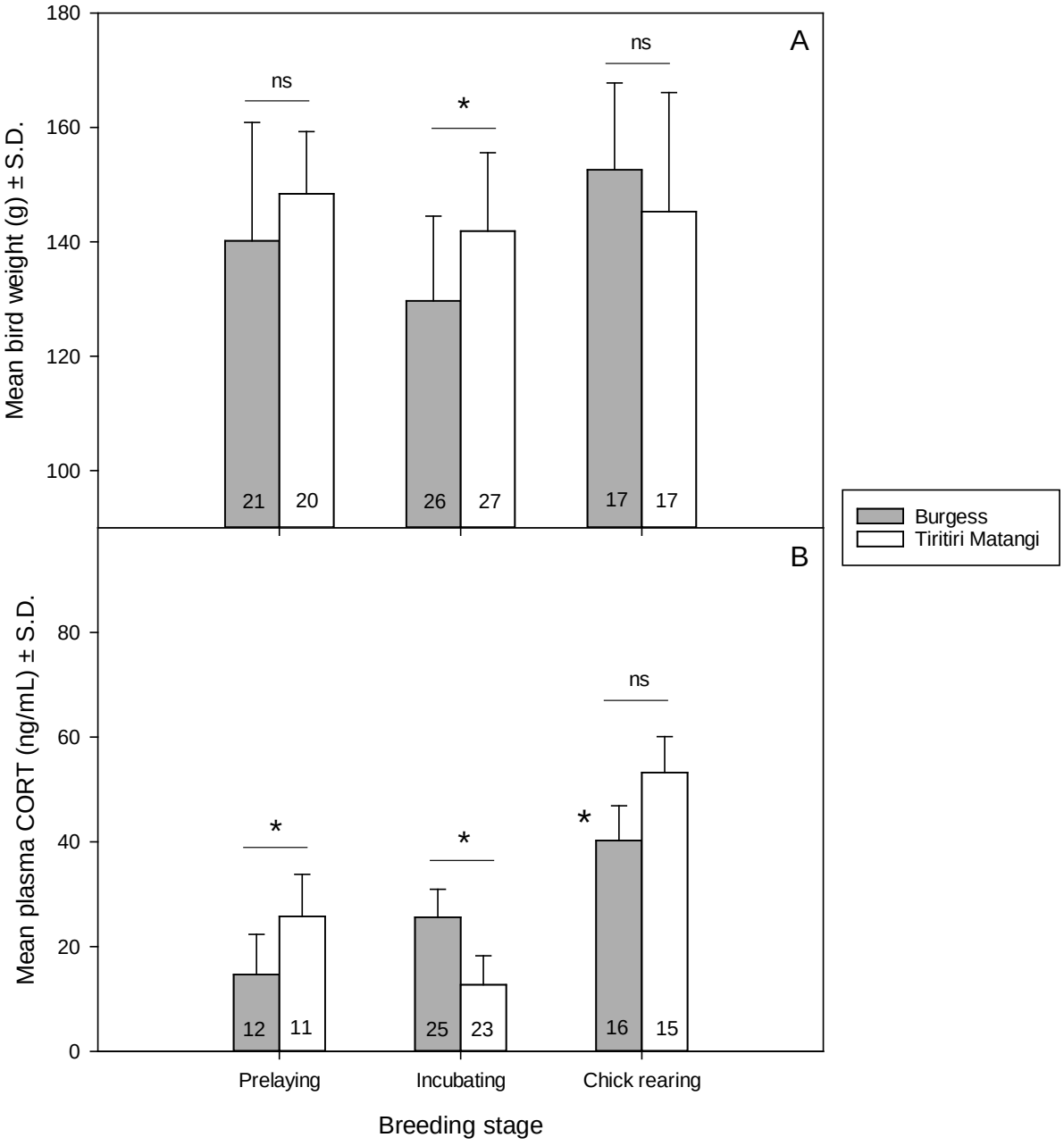

Figure 5: A) Changes in mean weight (g); and B) baseline secretion of corticosterone (CORT) stress hormone across the breeding season in common diving petrel (*Pelecanoides urinatrix*) adults breeding on Burgess and Tiritiri Matangi islands in the Hauraki Gulf, New Zealand, 2016. Numbers of replicates are given on each bar. Pairwise comparisons between islands within a breeding stage are indicated by horizontal bars, * = $p<0.05$, , n.s. = not significant, $\alpha = 0.05$.

688 **Table 1:** Summary Table of Two-way ANOVA results comparing bird weight and secretion of
689 corticosterone (CORT) stress hormone across the breeding season in common diving petrels
690 (*Pelcanoides urinatrix*) adults breeding on Burgess Island and Tiritiri Matangi Island in the Hauraki
691 Gulf, New Zealand, 2016.

692

	Source of variation	DF	SS	MS	F	P
Weight	Island	1	0.035	0.035	2.734	0.101
	Breeding stage	2	0.189	0.095	7.295	**0.001**
	Island × Breeding stage	2	0.117	0.0595	4.509	**0.013**
	Residual	122	1.583	0.013		
	Total	127	1.947	0.015		
CORT	Island	1	0.151	0.151	1.022	0.314
	Breeding stage	2	3.508	1.754	11.849	**0.00003**
	Island × Breeding stage	2	1.613	0.806	5.447	**0.00574**
	Residual	96	14.210	0.148		
	Total	101	19.290	0.191		

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694