SEX DIFFERENCES IN INDIVIDUAL FORAGING SITE FIDELITY OF CAMPBELL ALBATROSS

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ABSTRACT

Inter-individual variation in behavioural traits has important implications for evolutionary and ecological processes. Site fidelity, where individuals consistently use the same foraging site, is common among marine predators. Sex differences in foraging are also well studied in marine vertebrates, but the extent to which consistent inter-individual differences in foraging vary between the sexes is poorly known. Here we quantify the effects of sex on individual foraging site fidelity (IFSF), both within and between years, in chick brooding Campbell albatross (*Thalassarche impavida*). Using bird-borne Global Positioning System loggers, we calculated route fidelity (nearest neighbour distance), repeatability of site fidelity (terminal latitude and longitude), and foraging effort (total distance travelled and trip duration) during two to ten repeat trips. Overall, Campbell albatrosses showed a high degree of site fidelity. Birds travelled to similar sites not only within the same year, but also between two consecutive years, suggesting that the within-year consistency is not simply in response to short-term patches of food. Moreover, within the same year there were differences in terms of IFSF between the sexes. Females that foraged closer to the colony in neritic and shelf waters were more likely to follow similar routes on repeated foraging trips and were more consistent in their foraging effort than males. Males that foraged further offshore in pelagic waters had more repeatable foraging longitudes than females. Our study provides further evidence of the importance of IFSF among marine vertebrates. However, it also reveals that the strength of such specialisations may vary with sex.

Key-words: route fidelity, foraging effort, GPS tracking, repeatability, sex effects

INTRODUCTION

Inter-individual trait variation has important implications for conservation, ecology and evolution (Bolnick et al. 2003, Araújo et al. 2011). For example, consistent individual variation in foraging behaviour, or foraging specialisation, can impact upon predator-prey interactions, parasitism risk, population and community dynamics, and lead to disruptive selection and evolutionary divergence (Darimont et al. 2007, Johnson et al. 2009, Duffy et al. 2010).

Individual foraging specialisation is common among a wide range of marine taxa including birds, fish, and mammals (reviews: Bolnick et al. 2003, Araújo et al. 2011, Ceia & Ramos 2015). In marine species, individuals specialise in terms of their diet (Newsome et al. 2009, Tinker et al. 2012), searching behaviour (Woo et al. 2008, Torres & Read 2009, Baylis et al. 2012, Patrick et al. 2014), isotopic niche (Bearhop et al. 2006, Jaeger et al. 2009, Votier et al. 2010) and, in particular, foraging location (Woo et al. 2008, Torres & Read 2009, Baylis et al. 2012, Wakefield et al. 2015). Individual foraging site fidelity (IFSF), where an individual consistently uses only a small part of the population-level foraging range (Wakefield et al. 2015), is a particular form of individual specialisation that may arise as a consequence of predictable oceanographic conditions that generate foraging areas consistent in time and space (Weimerskirch 2007). However, variation in environmental conditions and different constraints such as those imposed by reproductive duties may influence the degree of site fidelity (Weimerskirch 2007, Patrick & Weimerskirch 2017). Here we test for sex differences in IFSF in a marine predator engaged in central-place foraging, the Campbell albatross (*Thalassarche impavida*).

Sex differences in foraging behaviour are well studied in marine vertebrates, including many seabirds (e.g. brown boobies *Sula leucogaster*, Miller et al. 2017; black-browed albatrosses *Thalassarche melanophris*, Huin 2002; northern gannets *Morus bassanus*, Stauss et al. 2012, Cleasby et al. 2015; Hawaiian petrels *Pterodroma sandwichensis*, Wiley et al. 2012; Cory's shearwaters *Calonectris borealis,* Paiva et al. 2017; northern giant petrels *Macronectes halli*, González-Solís et al. 2000). The mechanisms thought to influence sexual segregation include divergent parental roles or nutritional requirements, niche partitioning, competition, and social dominance (Weimerskirch et al. 2009). However, the extent to which IFSF varies between the sexes is not well known. One of the few study systems that have tested for sex differences in foraging individuality, in chick brooding black-browed albatrosses, found that females were more generalist than males (Patrick & Weimerskirch 2014), although males showed stronger habitat fidelity than females (Patrick & Weimerskirch 2017).

Here we studied IFSF in a large pelagic predator, the Campbell albatross, when restricted to foraging from a central place during the breeding season. The Campbell albatross is endemic to Campbell Island, New Zealand (52°32′24″S 169°8′42″E) and travels widely at sea to forage in waters off southern Australia, the Tasman Sea, and the southern Pacific Ocean (Waugh, Sagar, et al. 1999, Sztukowski 2016, Sztukowski et al. 2017). During chick brooding, Campbell albatross demonstrated sex differences in their distance travelled while foraging and also in habitat use (Sztukowski 2016). Such variation may influence IFSF between the sexes. Understanding the extent of IFSF may also be important in terms of conservation. The Campbell albatross population declined from 31,300 pairs in the 1940s to 21,648 pairs in 2012 (Waugh, Weimerskirch, et al. 1999, Sagar 2014); this, in addition to its restricted breeding range, habitat degradation, and the threat of fisheries bycatch led to Campbell albatross being listed as vulnerable (BirdLife International 2012). Reversing these population trends and improving the future prospects of this species requires a more detailed understanding of their spatial ecology, including the degree of IFSF.

We used precision GPS loggers to reconstruct foraging behaviour during the chick brooding period, with the aim of studying IFSF in Campbell albatrosses. We first quantified the extent to which Campbell albatrosses demonstrate IFSF during repeated foraging trips within the same breeding season, specifically in terms of foraging location (distal point of trips), route fidelity (using nearest neighbour distance), and foraging effort (distances travelled and duration). As well as tracking repeat trips by the same individual within the same year, we also tracked some birds across two years to test for long-term IFSF. This will enable us to determine whether site fidelity occurs in response to short-term availability of prey patches, or is instead a longer-term foraging strategy. Finally, we compared the degree of IFSF between the sexes.

METHODS

Instrumentation and tracking

Chick brooding Campbell albatrosses were temporarily captured and tagged during the breeding seasons of November and December 2011/2012 and 2012/2013 (hereafter referred to as 2011 and 2012, respectively). Chicks hatched from late November through to mid-December (peak hatch during 2011 and 2012: 6-7 December, n=81 nests). Modified GPS loggers (GT-600 i-gotU, Mobile Action Technology, Taiwan) were attached to the central back feathers of adult albatrosses using Tesa© tape. Modification involved removing the external plastic housing of each logger then applying heat shrink tubing (FiniShrink, UK) to waterproof each unit. The mass of each GPS unit was ~33 g (~1.1% of body mass) and programmed to record its location every ten minutes (referred to as a ‘point’ hereafter). We studied at-sea foraging behaviour during early to mid-chick rearing; birds were re-captured on the nest to remove the tag and retrieve the data following two or more complete foraging trips determined from nest attendance surveys, generally at the end of the chick brooding stage.

Analysis of tracking data

Foraging trips were reconstructed using the GPS data, from which we calculated three indices for complete foraging trips: (i) foraging route fidelity, (ii) foraging site fidelity, and (iii) foraging effort (details below). All analyses were restricted to individuals with two or more foraging trips; in most instances, our data represent all foraging trips taken by an individual during the chick brooding stage. The degree of IFSF was calculated from 2 to 10 trips.

Foraging route fidelity

We calculated individual route fidelity using Nearest Neighbour Distance (NND, in km). This technique quantifies the spatial similarity between a focal trip and a comparison trip by calculating the distance from each location along a track to its nearest neighbour on the comparison track (Biro et al. 2007). The NND calculated between two trips decreases with the spatial similarity between the focal and comparison tracks. NND was calculated for all possible pairs of trips (within individual trips, i.e. a measure of individual route fidelity, and among-individual trips, i.e. a measure of inter-individual variability). Locations < 2km from the colony were removed to exclude non-foraging rafting behaviour near the colony.

We used linear mixed-effects models (LMM) to assess whether albatrosses showed route fidelity, by comparing within-individual NND to among-individual NND, first across all years (for the ten birds tracked in both years) and then within each year. To test for long-term IFSF, we first tested whether individuals followed more similar routes within the same year than in different years. Next, we tested for potential sex differences in route fidelity, by comparing within-individual NND between males and females. All models included pair as a random effects and the difference in trip length between each pair of trips as a covariate. In models testing data from multiple years, year was also included as a fixed effect. We compared each model with the null (intercept only) model based upon likelihood-ratio tests (LRT). NND was square root or log transformed to obtain normality.

Foraging site fidelity

To measure foraging site fidelity, we first estimated the terminal latitude and terminal longitude (both in decimal degrees; DD) of each foraging trip. Terminal latitude and longitude were defined as the location at the furthest point from the colony as calculated as a straight-line distance. Based on sea-surface temperature (SST) and landing data, Campbell albatrosses do not foraging actively while commuting to foraging zones (Weimerskirch & Guionnet 2002). We assumed the primary foraging zone was located at the furthest point from the colony, but also qualify route fidelity (see above). We then compared the similarity of these values between repeat distal locations based on repeatability (R, i.e. the proportion of variance in a character that occurs among rather than within individuals or intra-class coefficient; Lessells & Boag 1987) for each sex and year. We used a LMM with restricted maximum likelihood (REML) and included individual as a random factor to account for multiple observations of the same bird. One thousand bootstrapping runs were performed to estimate confidence intervals and standard errors (Nakagawa & Schielzeth 2010). For the subset of individuals tracked in both years, we pooled the data from both years and included sex as a factor in LMM results in an adjusted repeatability (R_{adj}). All LMM analyses were undertaken using the “rptR” package in R (version 3.4.2; R Development Core Team 2017). Metrics for foraging behaviour were considered statistically repeatable if p-values were < 0.05 and the degree of specialisation increased as repeatability index values tended towards one.

Foraging effort

Foraging effort was calculated using two metrics: total distance travelled (km) and trip duration (hours), both calculated as the sum of the values from each point-to-point location and then transformed using Box–Cox transformations to obtain normality. We compared individual consistency of foraging effort between each sex and year by calculating repeatability (*R*). For the subset of individuals tracked in both years, we calculated an adjusted repeatability.

RESULTS

Foraging trip summary

We obtained information on at-sea foraging behaviour from 63 birds (n = 237 foraging trips): 12 females in 2011 (n = 42 foraging trips), 26 females in 2012 (n = 80 foraging trips), 11 males in 2011 (n = 36 foraging trips), and 24 males in 2012 (n = 79 foraging trips; Fig.1, 2, and Supplemental material). For ten individuals (6 females and 4 males), we obtained data in both 2011 and 2012 (Fig. 3). Total trip distances from the colony were, on average, significantly longer for males (mean ± standard error: 1580.63 ± 97.93 km) than females (1165.72± 70.74 km; t = -3.43, df = 209.76, $p < 0.001$) and trip durations were also greater for males (56.53 ± 3.03 hours) than females (47.59 ± 2.39 hours; t = -2.32, df = 219.41, $p = 0.02$).

Foraging route fidelity

NNDs demonstrate that Campbell albatrosses showed individually consistent foraging routes, with repeat trips being more similar within than between individuals (Fig 4) – this result being consistent whether drawing comparisons across all years or within the same year (within 2011 LRT: χ^2_1 = 17.515, $p < 0.001$; within 2012 LRT: χ^2_1 = 25.002, $p < 0.001$; across all years LRT: χ^2_1 = 26.124, $p < 0.001$). Moreover, route fidelity varied with sex - females had significantly higher route fidelity compared with males (data pooled for all years; LRT: χ^2_1 = 4.5277, $p = 0.033$; Fig. 5). Trip length and year were both retained in the models, so these differences are not simply a function of the shorter foraging trips of females.

Foraging site fidelity

During 2-10 repeat trips, both males and females showed similar repeatability values (Table 1). Repeatability of terminal latitude and longitude was significant for both sexes and within years, with the exception of females in 2011. Foraging site fidelity was generally higher in 2012 than 2011, with the highest repeatability estimates for male terminal longitude in 2012 (Table 1). For the ten individual with data from both years (n = 59 foraging trips), repeatability of terminal longitude was significant ($R_{adj} = 0.376 \pm 0.155$, $p = 0.007$). Latitude was not significantly repeatable across years ($R_{adj} = 0.166 \pm 0.125$, $p = 0.158$).

Foraging effort

Analysis of within-individual variation in total distance travelled and trip duration of foraging trips reveals that females tended to have higher within-individual variation than among-individual variation (Table 1). Females were significantly repeatable in total distance travelled and trip duration within both years, whereas males were significantly repeatable in total distance travelled in 2012 (Table 1).

Total distance travelled was consistent across both years ($R_{adj} = 0.260 \pm 0.137$, p = 0.023), but duration of foraging trips was not significantly repeatable across years (R_{adj} = 0.149 ± 0.116, $p = 0.109$).

DISCUSSION

During chick brooding, Campbell albatrosses tended to show consistent foraging routes, foraging sites, and foraging effort, suggesting a degree of IFSF. Moreover, for ten birds tracked in two breeding seasons, there was evidence of inter-annual route and site fidelity, indicating that the observed within-year patterns were not simply a response to short-term profitable foraging opportunities (Table 1, Fig 1 - 4). Previous studies of albatrosses have also shown variation with respect to IFSF; for instance, individual shy albatrosses (*Thalassarche cauta*) consistently searched the same broad patch of ocean within a breeding stage, although individuals did not show fidelity to these patches across years (Hedd et al. 2001). Wandering albatrosses (*Diomedea exulans*) also showed short-term consistency in habitat use and trophic level; in the long-term, however, individuals were consistent in habitat use but not trophic niche (Ceia et al. 2012). Black-browed albatrosses showed similar patterns in terms of IFSF as shown in the present study, with strong within-year individuality that persisted, to an extent, across years (Patrick & Weimerskirch 2017). Moreover, Patrick & Weimerskirch (2017) showed that increased site fidelity was linked with higher reproductive success.

One of our key findings is that there were differences in the degree of IFSF between the sexes (Fig. 2, Supplemental material, Table 1). Males travelled further, had longer trip durations, and more consistent terminal longitude than females. Females were, however, more consistent in terms of their foraging route and effort (Fig 2, Supplemental material, Table 1). Previous research into how sex affects specialisation found diverse results. In the closely related black-browed albatross breeding on Kerguelen, males showed more consistent foraging locations than females (Patrick & Weimerskirch 2014). The reasons for the difference from our study are unclear, but may be related to density dependence, since the degree of individual specialisation has been shown theoretically and experimentally to be linked with increased intraspecific competition (Svanbäck & Bolnick 2005, 2007, Bolnick et al. 2010). In our study, females Campbell albatross remained closer to the colony on the Campbell Plateau, where competition is higher, and had a higher degree of route fidelity compared with the more pelagic males. There may also be other factors at play. For instance, studies of three species of inshore foraging pursuit diving shag and cormorant found that females tend to be more consistent in foraging behaviour than males, which was explained by a combination of morphological differences influencing resource accessibility, niche partitioning, and prey choice (Kato et al. 2000, Cook et al. 2005, Ratcliffe et al. 2013). Size may be important in our study species since male Campbell albatross are on average 7.2% heavier than females (Sztukowski 2016), which could affect foraging energetics and behaviour. For example, wing length, wing area, mass, and associated wing loading were consistent with the foraging distribution of male and female wandering albatrosses, which is sexually dimorphic species; the morphological differences may be adaptive to exploiting wind conditions associated with their associated habitats (Shaffer et al. 2001). Niche partitioning may also be present. Female Campbell albatrosses tend to forage on the Campbell Plateau were individuals fed predominantly on fish, whereas birds foraging in more oceanic waters and around the polar front, where males tended to forage, feed mostly on squid (NIWA 1999). However, while size may influence sex-specific foraging specialisation and niche partitioning, specialisation may be linked to competition through size dimorphism, reproductive role, or competitive exclusion (Phillips et al. 2004, Catry et al. 2006, Phillips et al. 2011). Thus, while the factors driving sexual variation in specialisation may be similar to those factors associated with sexual segregation, which include competitive exclusion, or niche specialization associated with breeding role or morphology (Peters et al. 1983, Petit et al. 1990, Marra 2000, Shaffer et al. 2001, Phillips et al. 2004, 2011, Catry et al. 2006, Weimerskirch et al. 2009), more research is required to elucidate the mechanisms.

Highly repeatable terminal latitudes and longitudes indicate that Campbell albatrosses commute to consistent foraging locations suggesting that individuals use previous knowledge to inform foraging decisions (Votier et al. 2017). The birds tracked over two years also tended to show similar foraging site fidelity, routes and total distance travelled. Such longer-term consistency suggests that the within-year consistency is not simply in response to short-term patches of food (e.g. a win-stay, lose-shift tactic; Wakefield et al. 2015). Longer-term site fidelity, like those found in our study, may provide energetic advantages over an individual's lifetime despite environmental variability (Bradshaw et al. 2004). Thus, foraging site fidelity, in conjunction with fine-scale location adjustments within areas associated with predictable resources, may confer consistent energy intake (Bradshaw et al. 2004, Patrick et al. 2014).

To conclude, our study shows that there was generally a high degree of IFSF among chick brooding Campbell albatrosses, and individual consistency in foraging sites persisted across two consecutive years. However females, which remained closer to the colony to forage in neritic/shelf habitats, had a higher degree of route fidelity and more repeatable foraging effort compared with males which tend to use pelagic waters. While the causes of these differences remain unclear, our research highlights the possibility that threats posed by fisheries bycatch are not uniformly distributed across individuals or sexes within the population, due to differences in their overlap with fisheries and reliance on fisheries waste (Ryan 1999, Nel et al. 2002, Votier et al. 2010, Bugoni et al. 2011, Torres et al. 2011, Barbraud et al. 2013, Torres et al. 2013). Further work should explore how these changes in site fidelity vary across the breeding season, as well as quantifying the potential impact of such risks.

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Table 1: Repeatability (*R* ± Standard Error, p-values in parentheses) of female (12 individuals in 2011, n= 42 foraging trips; 26 individuals in 2012, n= 80 foraging trips) and male (11 individuals in 2011, n=36 foraging trips; 24 individuals in 2012, n= 79 foraging trips) Campbell albatross foraging site fidelity and foraging effort. Significant repeatability estimates are highlighted in bold.

Foraging effort	Female	Male
Total distance (km)		
2011	**0.344±0.172 (*p*=0.039)**	0.074±0.129 (*p*=0.362)
2012	**0.340±0.126 (*p*=0.003)**	**0.215±0.121 (*p*=0.039)**
Trip duration (hrs)		
2011	**0.434±0.167 (*p*=0.016)**	0.099±0.134 (*p*=0.327)
2012	**0.322±0.127 (*p*=0.003**)	0.059±0.086 (*p*=0.336)
Foraging site fidelity	Female	Male
Terminal latitude (DD)		
2011	0.295±0.172 (*p*=0.115)	**0.366±0.179 (*p*=0.024)**
2012	**0.554±0.110 (*p*<0.001)**	**0.394±0.122 (*p*<0.001)**
Terminal longitude (DD)		
2011	0.356±0.173 (*p*=0.095)	**0.399±0.173 (*p*=0.013)**
2012	**0.538±0.114 (*p*<0.001)**	**0.603±0.107 (*p*<0.001)**

Figure 1. Foraging trips taken by female (in red) and males (in yellow) Campbell albatrosses in 2011 (panel 1) and 2012 (panel 2). The location of Campbell Island is indicated by the white triangle.

Figure 2. Foraging trips taken by individual Campbell albatrosses. First column illustrates the highest route fidelity (lowest NND) within each sex and year. Second column shows foraging trips from the median individual from each sex-year category when individuals were ranked from lowest average NND to highest average NND. Individual foraging trips in the third columns demonstrate low levels of route fidelity (highest NND). Distal locations for each foraging trip are indicated in green and the location of Campbell Island is highlighted by the white triangle. All foraging trips are available in the supplemental materials which are grouped by sex and year.

Figure 3. Foraging trips taken by individual Campbell albatrosses tracked in both 2011 (in red) and 2012 (in yellow). Distal locations for each foraging trip are indicated in green and the location of Campbell Island is highlighted by the white triangle. Panels are grouped by sex.

Figure 4. Nearest-neighbour distance (NND ± s.d. in km) shows that individual route fidelity across all years is greater within individuals than among individuals.

Figure 5. Nearest-neighbour distance (NND ± s.d. in km) shows that females tend to have higher route fidelity than males.

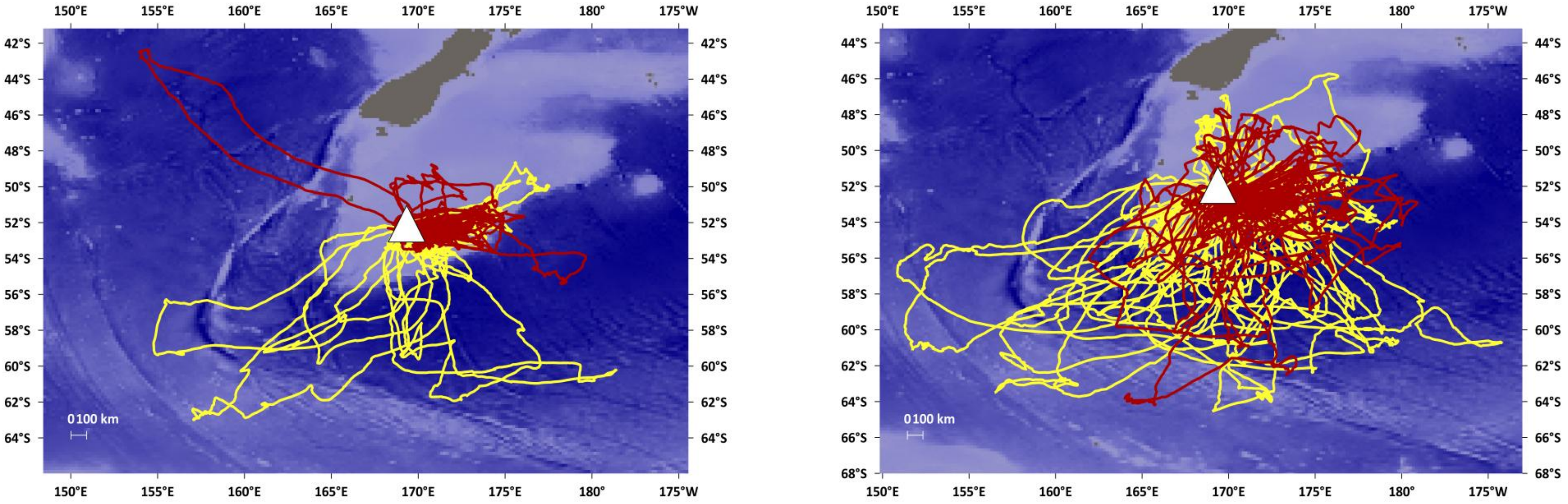
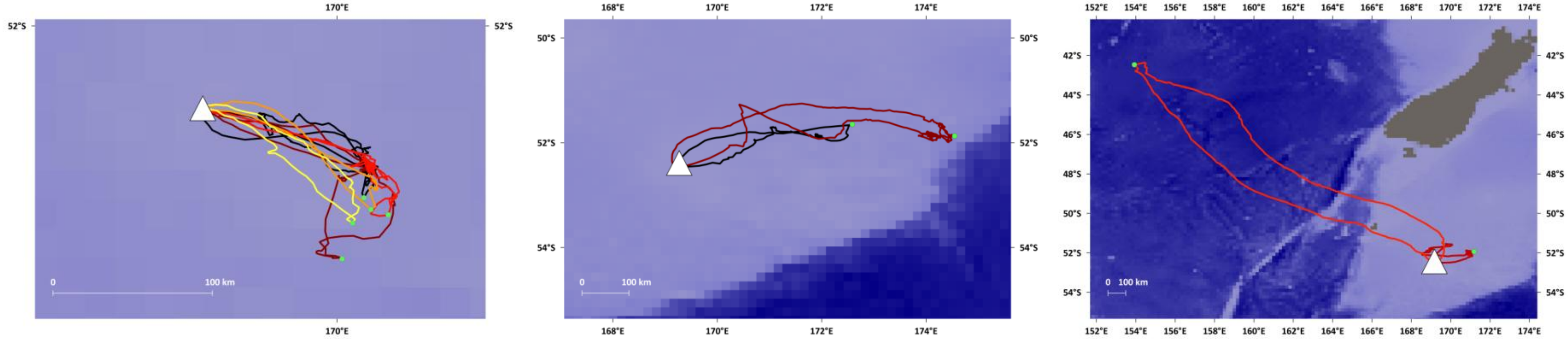

150°E
155°E
160°E
165°E
170°E
175°E
180°
175°W
42°S
44°S
46°S
48°S
50°S
52°S
54°S
56°S
58°S
60°S
62°S
64°S
66°S
68°S
0 100 km

Figure 1

Female 2011



Male 2011

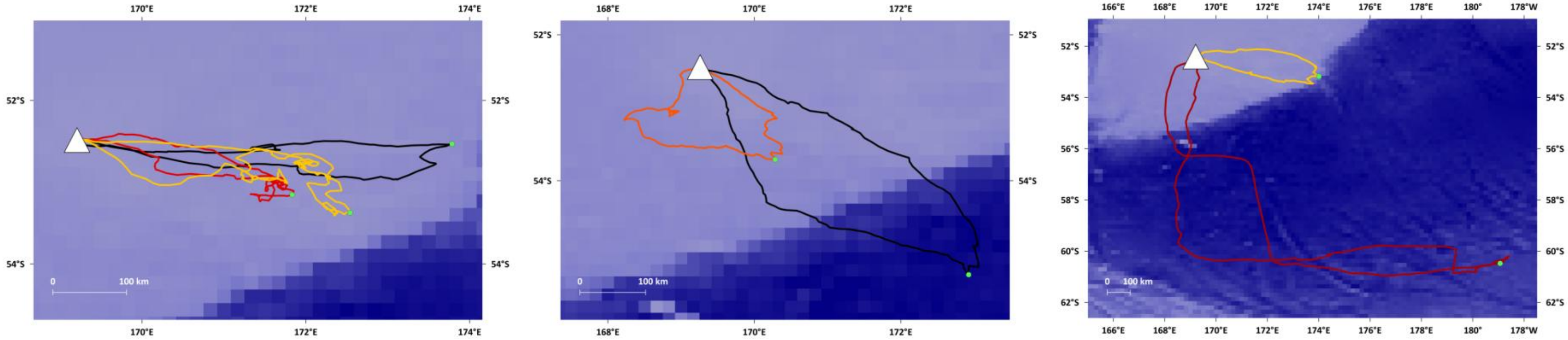
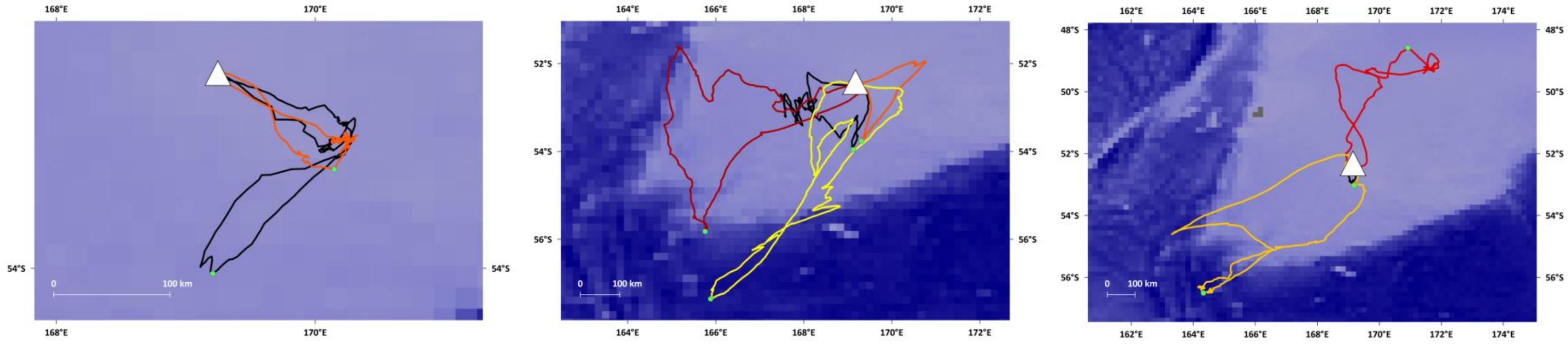


Figure 2

Female 2012



Male 2012

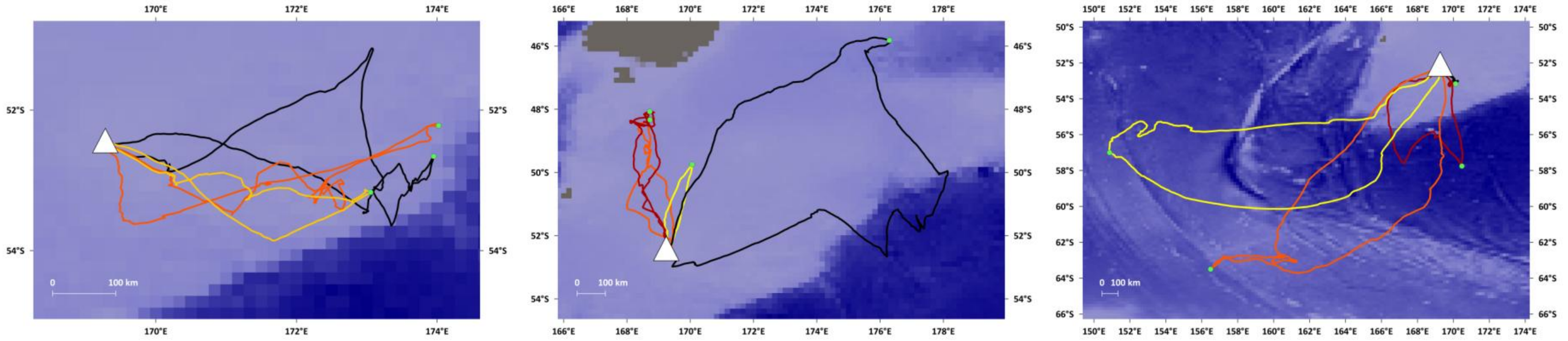


Figure 2 continued

Female

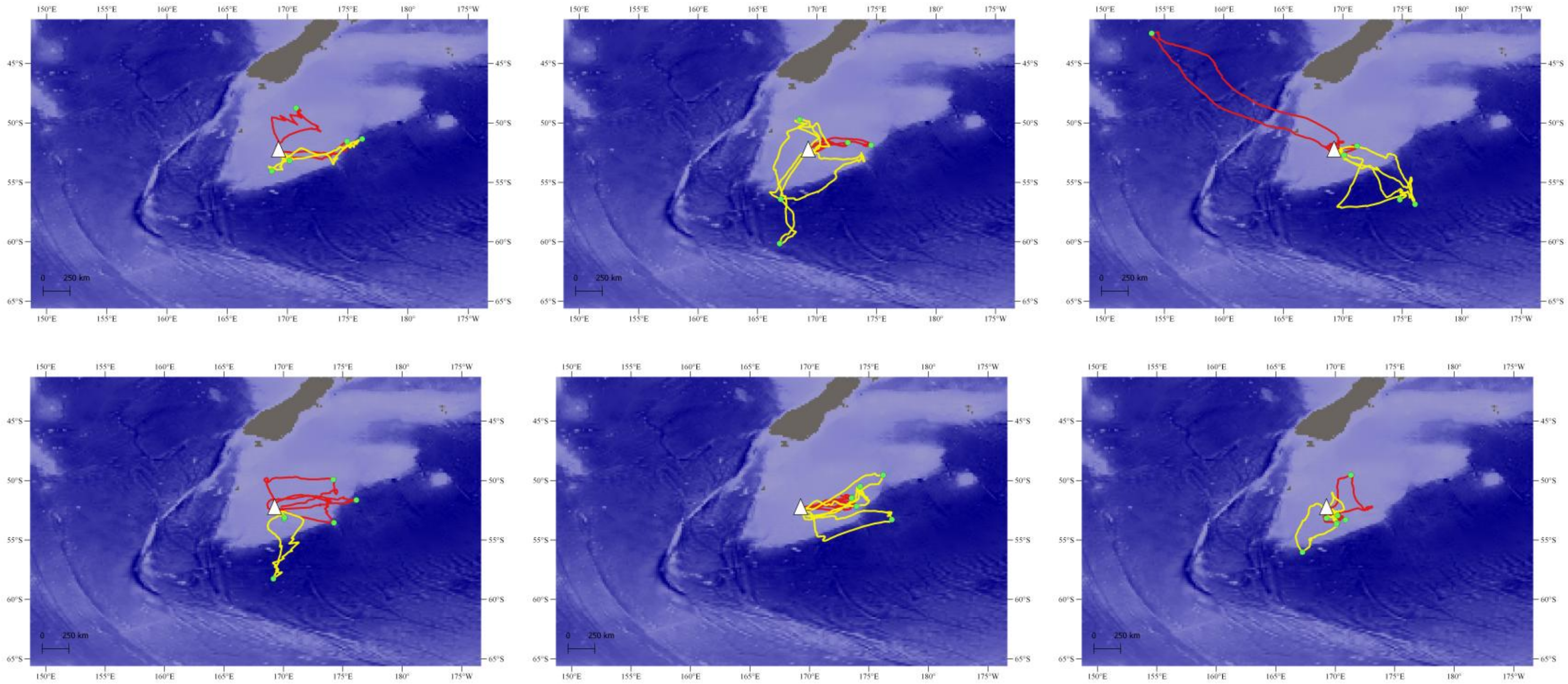


Figure 3

Male

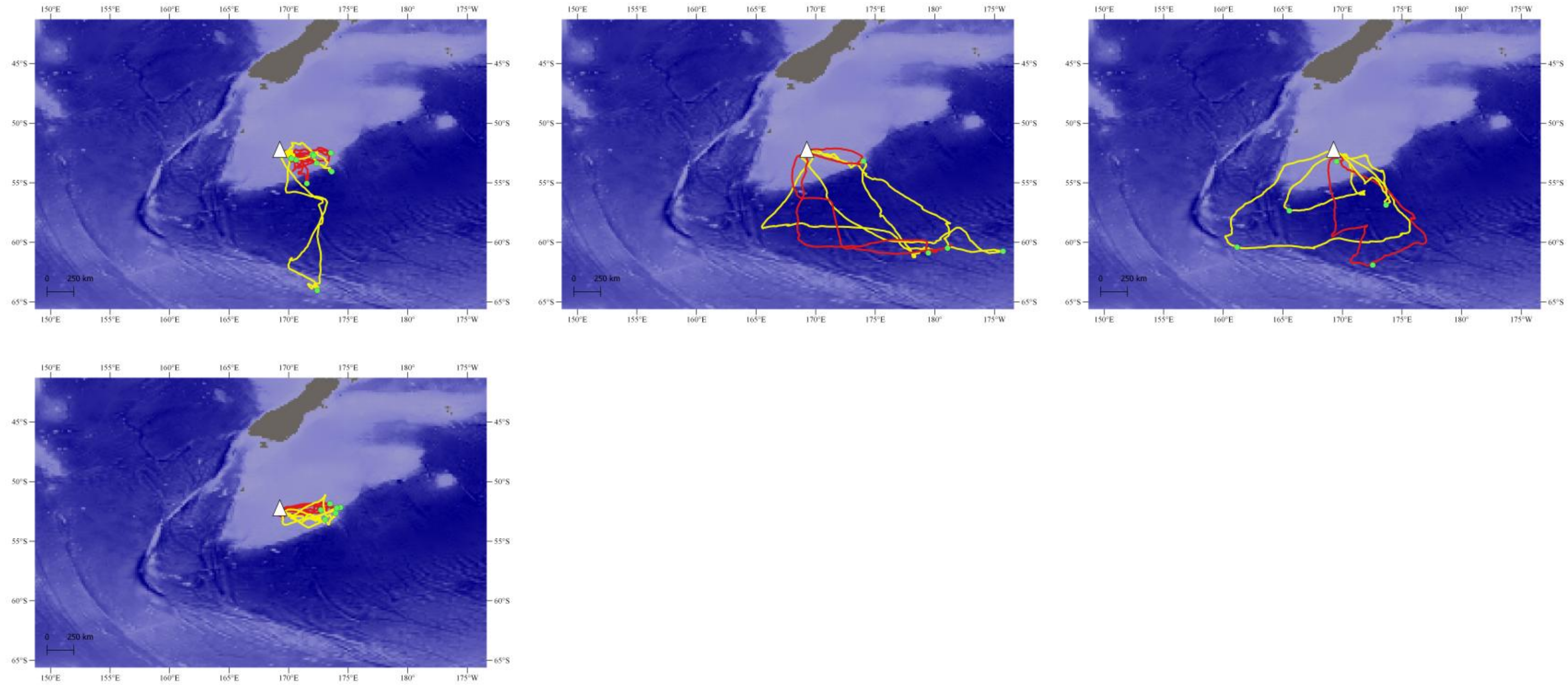


Figure 3 continued

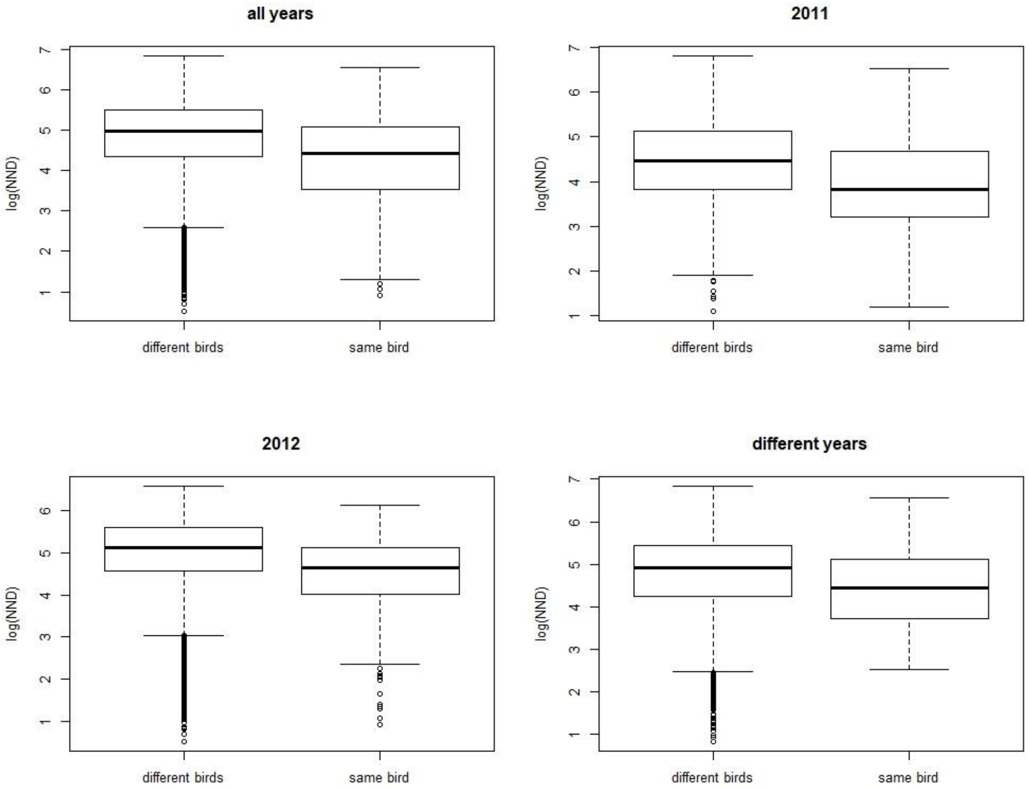


Figure 4

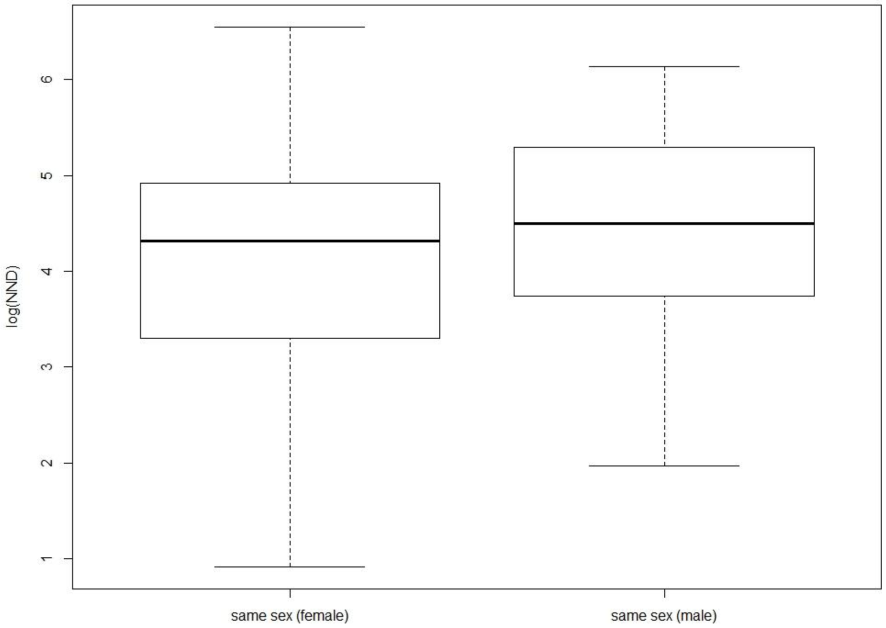


Figure 5