

BREEDING TROPICAL SHEARWATERS USE DISTANT FORAGING SITES WHEN SELF-PROVISIONING

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SUMMARY

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To determine whether breeding tropical shearwaters use “at-distance” locations during the long-trip phase of their bimodal foraging cycle, we deployed PTT satellite tracking devices on adult Wedge-tailed Shearwaters *Ardenna pacifica* of the Great Barrier Reef (GBR), Australia, over three breeding seasons. During the long-trip phase (8–14 d), a component of a bimodal pattern of foraging not seen previously in a tropical shearwater, birds travelled to distant sites in the Coral Sea between 300 and 1 100 km from the breeding colony, primarily to the north and east. At-distance foraging sites were in deeper water and closer to seamounts than were near-colony foraging sites used for chick provisioning, a combination of features indicating enhanced prey availability at these at-distance locations. These findings imply that long-term reproductive success at this and likely other GBR colonies is strongly dependent on the continued stability of these at-distance locations, yet at present all are outside the current Great Barrier Reef Marine Park management zone. To adequately conserve GBR seabirds and other marine species using these resources, a conservation strategy integrated with current management practices is needed for the open waters of the Coral Sea.

Keywords: Wedge-tailed Shearwaters, *Ardenna pacifica*, at-distance foraging, PTT satellite tracking, seamounts, tropical seabirds

INTRODUCTION

Procellariiform seabirds that breed in areas of low productivity are unable to simultaneously provide for chicks and maintain their own physical condition using only locally available food resources. Parents of temperate species overcome this limitation by using a bimodal foraging cycle composed of (1) multiple short trips to nearby, often resource-poor local waters to provision the chick, and (2) a single long trip to foraging grounds of higher productivity “at-distance” from the colony to replenish adult body reserves depleted during the short-trip phase (Weimerskirch *et al.* 1993, Weimerskirch 1998, Magalhaes *et al.* 2008).

For this strategy to be viable, the food supply at distant foraging grounds must be reliable and provide sufficient return to offset the energetic costs of both the chick provisioning cycle and additional travel. As a consequence, at-distance foraging locations for temperate species consistently occur in regions of high productivity (Catard *et al.* 2000, Becker & Beissinger 2003, Weimerskirch 2007), where specific bathymetric or oceanographic features drive large forage-fish aggregations and high prey encounter rates (Gende & Sigler 2006). In years when local productivity is sufficient, some species are known to facultatively switch to a unimodal provisioning pattern using only near-colony resources (Granadeiro *et al.* 1998, Waugh *et al.* 2000, Welcker *et al.* 2009). This strategic variation further suggests that bimodal foraging is directly linked to poor levels of local prey availability.

In contrast, a model by Ropert-Coudert *et al.* (2004) highlights the disadvantages of extended travel to more distant foraging grounds

during breeding in Adélie Penguins *Pygoscelis adeliae* of the southern Ross Sea. This species is known to use a bimodal foraging strategy composed of long- and short-duration trips (Clarke 1998, 2001, Angelier 2008). However, foraging individuals consistently undertake both trip types to the same foraging locations (Ballard *et al.* 2010). This suggests birds are able to compensate for a poor local foraging environment by altering the rate at which they return to the colony without the need to travel long distances to access discretely different foraging areas (Ropert-Coudert *et al.* 2004). Similarly, in Little Auks *Alle alle*, Wojczulanis-Jakubas *et al.* (2010) hypothesize that increased surface resting time in nearby foraging grounds, rather than extended travel time to distant locations, is their strategy. These models imply that, when resources are patchy or unreliable, it is more advantageous for adults to replenish body reserves at near-colony foraging grounds while minimizing the energetic costs of short-trip travel by not returning to the colony each night.

Little is known about how tropical Procellariiformes deal with the energetic constraints of breeding, especially as they are unlikely to be able to access highly productive temperate waters to compensate for poor local resource availability (Congdon *et al.* 2005). Wedge-tailed Shearwaters *Ardenna pacifica* that breed in the subtropics, in Hawai'i and on Lord Howe Island, access near-colony foraging sites that enable them to maintain condition, while simultaneously provisioning chicks. These populations use a unimodal foraging strategy (Baduini 2002, Peck & Congdon 2005). By contrast, a breeding colony of these shearwaters in the tropical waters of the Australian Great Barrier Reef (GBR) is known to employ a bimodal foraging cycle during the breeding season, interspersing multiple, short, 1–2 d trips with a long trip averaging 8–10 d. During short

trips, changes in adult body mass suggest that the majority of food obtained is provisioned to the chick and adult reserves are depleted. The demonstrated increase in adult mass over the subsequent long trip implies this trip serves to replenish lost condition (Congdon *et al.* 2005, Peck & Congdon 2005).

While the adults at this GBR colony use a bimodal foraging strategy, it is not known whether trips are conducted in two discrete foraging habitats, with adults travelling to distant foraging grounds on the longer trips, or in one habitat, with adults remaining longer in the relatively oligotrophic near-colony waters of the GBR (Congdon *et al.* 2005). If the former is true, then the viability of Wedge-tailed Shearwater colonies on a regional scale is likely dependent on a small number of at-distance sites with enhanced prey availability. Since the Wedge-tailed Shearwater populations of the southern GBR are amongst the largest in the Pacific (Dyer *et al.* 2005), such key foraging sites that are necessary to immense numbers of birds may have considerable conservation importance.

Our objective in this study was to examine the long-trip foraging behaviour of Wedge-tailed Shearwaters breeding on Heron Island in the southern GBR, to determine whether they travel to distant locations on these trips, or merely spend more time foraging locally. We also aimed to (1) identify the potential number and location of the shearwaters' foraging sites, (2) determine whether such sites are associated with specific bathymetric phenomena known to enhance prey availability to upper trophic level predators, and (3) determine the relationship of such sites to current conservation and management zones.

METHODS

This study was conducted at Heron Island (23°26'S, 151°51'E), in the Capricorn Bunker Group of reefs in the GBR Marine Park, Australia (Fig. 1), in February and March 2006, 2011 and 2012. The timing coincided with the chick-rearing portion of the Wedge-tailed Shearwater breeding season (Table 1), which runs from October to May with chicks hatching in early February. The bimodal foraging cycle occurs throughout the chick-rearing period. To ascertain the timing of adult foraging trip cycles, we monitored the arrival and departure of each adult at 20–30 nests daily. Burrow entrances were partially obstructed with markers that allowed adult visits to be detected, with nests being checked every 10 min. Nests were then obstructed with clear plastic so that adults could be captured on departure from the nest. At this time, individuals were identified and weighed; chick weights were also taken to determine meal masses. Knowing adult visitation schedules and timing enabled us to predict when adults would likely depart on long trips. In some instances, both adults were found to visit the nest on the same night. This was a clear indication that the adult that had been attending the nest the previous week was about to depart on a long trip (Congdon *et al.* 2005), so a logging device was deployed. Otherwise, we deployed the logging device on the short-tripping adult on the eighth day of its short-trip cycle, in anticipation of long-trip departure. Long trips were defined as longer than five days (Congdon *et al.* 2005), during which the bird did not return to the colony to provision the chick.

Solar-powered ARGOS Platform Terminal Transmitters (PTT-100) (Microwave Telemetry, USA) provide precise location information (accuracy ~150–250 m) in “real-time” via ARGOS satellites (<http://www.argos-system.org>). PTTs weighing 9–11.2 g and measuring ~17 mm (height), 36–40 mm (length), 16 mm (depth), were

mounted at the base of an adult's tail feathers with TESA tape for the duration of one long trip per adult (three in 2006; four in 2011 and six in 2012). We deployed devices on adults weighing > 380 g in order to maintain the weight of the transmitter within the accepted 3–5% body weight limit for seabirds (Kenward 2001, Phillips & Croxall 2003). Adult weight range of Heron Island Wedge-tailed Shearwaters during breeding is ~350–500 g (McDuie & Congdon, unpubl. data). No evidence of birds attempting to remove the tape or device, or any damage to tail feathers, was observed. Devices were deployed on adults upon their exit from the nest following chick feeding. Duty cycles for transmitters in 2006 and 2012 were set to 12h on/48h off (default factory setting by manufacturer). The 2011 setting was “continuous,” which means production of location fixes is fairly consistent, depending upon device battery power, and at least once daily (Table 1). Batteries recharge via solar power, resulting in obligatory downtime for recharge that causes occasional interruptions in data. We would recommend use of the continuous

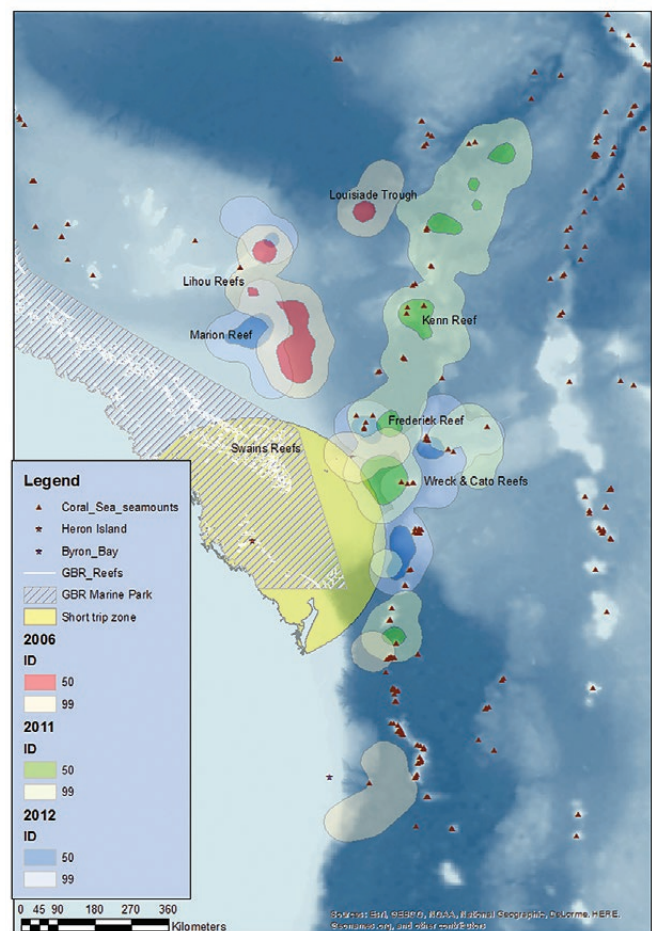


Fig. 1. Regional map of the Coral Sea with 50% and 99% kernels for three years of tracking. PTT electronic satellite transmitter tracks of 13 long-tripping, breeding Wedge-tailed Shearwaters of Heron Island, Great Barrier Reef (GBR), in 2006 (red), 2011 (green) and 2012 (blue). Kernels are mapped with the darker-colored areas representing the 50% (core-use) kernels and lighter areas the 99% (maximum-use) kernels. The non-use (short-trip zone) region is designated by the yellow area extending to a maximum radius of 300 km from the Heron Island colony, which is indicated by a red star. The GBR Marine Park is indicated by the dark grey striped zone. Seamounts are indicated by brown triangles.

setting in tropical environments where there appears to be sufficient sunlight for frequent recharge, thereby considerably increasing the amount and resolution of data obtained. Moreover, this better allows assumptions on types of activity and when birds are more likely to be actively searching or foraging for prey.

Based on average flight speeds of ~30–33 km/h observed in this as well as other studies, we removed any data points that required flight speeds > 50 km/h or > 35 km/h sustained over 48 h (following Catry *et al.* 2011). Unfortunately, due to the temporal irregularity of fixes and obligatory recharge downtimes, it is not possible to distinguish between foraging and transit activity. Therefore, we employed kernel density estimation (KDE) to estimate the home range of the birds using four utilization distribution (UD) contours: 25, 50, 75 and 99%. The 99% and 50% UD contours (kernels) represented the observed overall and core-use foraging areas for long-tripping shearwaters, respectively. When birds are moving at low speeds with many changes in direction during foraging, they are more likely to accrue larger numbers of satellite fixes over a given area than when transiting more rapidly over the same area. Therefore, core-use areas (50% kernels) indicate the most important locations and are more likely to highlight foraging activity (Hamer *et al.* 2007, Catry *et al.* 2009).

Greater than 90% of short trips used for chick provisioning are 1–2 d (Congdon *et al.* 2005), and foraging occurs primarily during daylight hours. Therefore, to determine whether birds on long trips consistently foraged outside the area used during short-trip cycles,

a maximum short-trip foraging distance was defined as the area that could be accessed by an adult on a two-day foraging trip with average flight speeds of ~30 km/h. This delineated an area within a ~300 km radius from the colony. Results from the 50% kernel analysis were then overlaid on this region to determine whether the majority of long trips fell outside this zone.

Kernel analyses were performed in R version 2.15.2 (R Core Team 2013) using the *adehabitat* package (Calenge 2006, Calenge 2014). KDEs were created with a smoothing factor (*h*) of 20 km based on shearwater foraging ecology and transmitter accuracy. Inter-annual differences in duty cycles resulted in widely divergent numbers of fixes obtained from loggers among years (Table 1). For this reason, we produced separate kernel densities for each year on one map to highlight overlap and differentiation of core-use areas between and among years.

To determine whether at-distance foraging locations were more closely associated with specific bathymetric features known to enhance prey availability, data-logger points within each 50% long-trip kernel were designated “bird presence” locations (*n* = 309; Table 1). The characteristics of bathymetry and topography in these areas were compared with those in “bird absence” locations (*n* = 309) produced randomly from within the defined maximum short-trip foraging zone. To undertake this analysis, Etopo1 Ice surface bathymetry data (1 km resolution) were downloaded from the US National Geographic Data Center (<http://www.ngdc.noaa.gov/mgg/global/relief/ETOPO1/image/>).

TABLE 1
Tracking data from Wedge-tailed Shearwaters 2006, 2011 and 2012^a

Logger ID	Bird ID	Deployment dates	Duration of trip, d (d with fixes)	Total number of fixes	Average fixes d-1 (only days with fixes)	~Maximum distance from Heron Is., km
2012						
56055 ^b	20	27 Feb–7 Mar	8 (4)	9	2.25	800
56054	28	28 Feb–11 Mar	13 (8)	15	1.88	540
62359	30	17–30 Mar	14 (7)	19	2.71	535
62361	36	2–12 Mar	11 (6)	20	3.33	675
62359	48	8–16 Mar	9 (6)	18	3.00	385
62361 ^b	50	16–23 Mar	8 (3)	10	3.33	–
2011						
56054	1	12 Feb–4 Mar	21 (9)	157	7.48	720
56054	10	5–14 Mar	9 (9)	107	11.89	385
56055	3	16 Feb–1 Mar	13 (13)	158	12.16	1 150
56055	17	3–10 Mar	7 (7)	54	7.71	340
2006						
62359	5	18 Feb–2 Mar	14 (8)	32	4.00	750
62360	2	13–27 Feb	14 (7)	31	4.43	580
62361	4	9–24 Feb	15 (7)	15	2.14	550

^a Deployment data from PTT-100 satellite transmitters for all Wedge-tailed Shearwater long foraging trips.

^b Logger failures in 2012 resulted in two incomplete tracks. Bird#62361 was unlikely to have reached its maximum distance and was not included in further analyses.

Seamounts, in particular, are a distinctive bathymetric feature known to increase prey availability to upper trophic level predators such as seabirds (Morato *et al.* 2008, Morato *et al.* 2010). Therefore, we also tested whether data-logger points within each 50% long-trip kernel (“bird presence”) were closer to seamounts than locations within the short-trip foraging zone (“bird absence”). This analysis was done with ArcGIS 10.2 for desktop. The seamount location map was produced from the Global database of undersea features (http://www.gebco.net/data_and_products/undersea_feature_names), Deep Reef Explorer high resolution depth model for the Great Barrier Reef and Coral Sea (<http://www.deeprf.org/bathymetry/65-3dgr-bathy.html>) (Heap 2008, Beaman 2010), and the Seamounts Catalog of the Seamount Biogeosciences Network (SBN) (<http://earthref.org/SC/>). We assessed distance to the nearest seamount and difference in the average depth of points in presence and absence locations with Welch’s two-sample *t*-tests in R, which assume unequal variances and apply Welch’s df modification (R Core Team 2013).

RESULTS

In total, we obtained 645 fixes from 13 transmitter deployments during the study, 309 of which were within the 50% kernels ($n = 41$, 2006; $n = 205$, 2011; and $n = 59$, 2012; Table 1, Fig. 1). The average length of a long trip was 12 SD 1.97 d and average lengths by year were: 2006: 14.3 SD 0.76 d, 2011: 12.5 SD 2.17 d, and 2012: 10.5 SD 1.61 d. The average maximum distances travelled from the colony each year were: 2006: 626.67 km, 2011: 648.75 km, and 2012: 587 km.

Eleven of 13 tracks provided position fixes for the full length of a long trip, although not always for each day of tracking. The remaining two loggers, on Birds #62361 and #56055, lost their antenna and only tracked for 2.5 and 4 d of an 8-d trip, respectively. In general, birds reached the maximum extent of their long trips around the halfway point. Therefore, it is unlikely Bird #62361 was tracked to, or near, its maximum distance from the colony, and so this track was excluded from further analyses. Otherwise, all birds on long trips travelled to locations that were > 300 km from the breeding colony, and all but one adult travelled > 450 km. The maximum distance travelled by an adult in a single day of constant flight was 450–500 km, yielding an average sustained speed flight of ~ 30 – 35 km/h during daylight hours.

In 2006, two individuals travelled northward, one stopping within the Swains Reefs National Park and at Marion Reefs (Fig. 1), a maximum distance of ~ 500 km from Heron Island. The second travelled further northward, visiting Lihou Reef Nature Reserve and the Louisiade Trough in the central Coral Sea, a round trip of almost 2000 km. The third individual spent a number of days off the northern coast of New South Wales (NSW), approximately 750 km south of Heron Island. It followed a deep-ocean seamount ridge on its return and spent almost a week foraging off the edge of the continental shelf ~ 400 km east of Heron Island.

In 2011, three adults travelled to locations in the central eastern Coral Sea at distances of 400 km (Wreck Reefs), 700 km (seamounts) and 1100 km (Louisiade Trough) from Heron Island (Fig. 2). All locations were well outside the GBR Marine Park. The fourth adult tracked in 2011 spent approximately a week foraging at a location ~ 200 – 250 km southeast of Heron Island, reaching a maximum distance of approximately 340 km.

In 2012, birds were tracked to the same region north of Heron Island as in 2006 and 2011, as far as the Lihou Reefs (Fig. 1). They also travelled to the east around Cato, Wreck, Kenn and Frederick Reefs (Fig. 1), to other locations visited by birds in 2011. Birds from all years routinely conducted long trips of more than 2000 km. There was some congruence among core-use areas (50% kernels) across years, but in each year birds were also tracked to one or more additional locations not used previously (Fig. 1).

In both 2011 and 2012, multiple tracks followed a deep-ocean seamount ridge extending through the Coral Sea northeast of Heron Island (Fig. 2). During these trips, foraging occurred in the vicinity of Wreck, Kenn and Frederick Reefs (Fig. 1) or the nearby continental shelf edge, as well as adjacent to the Louisiade Trough, 1200 km northeast of Heron Island. Shearwater long-trip foraging locations (50% kernels) were significantly closer to seamounts and in deeper water (bathymetry) than non-foraging locations (99% kernels, Table 2).

DISCUSSION

On long trips, adult Wedge-tailed Shearwaters at Heron Island foraged a long way from the breeding colony. Long-trip foraging areas were consistently outside the zone adults could access on short, chick-provisioning trips of 1–2 d at average flight speeds. Therefore, in general, tropical Wedge-tailed Shearwaters of the southern GBR access foraging locations for self-provisioning

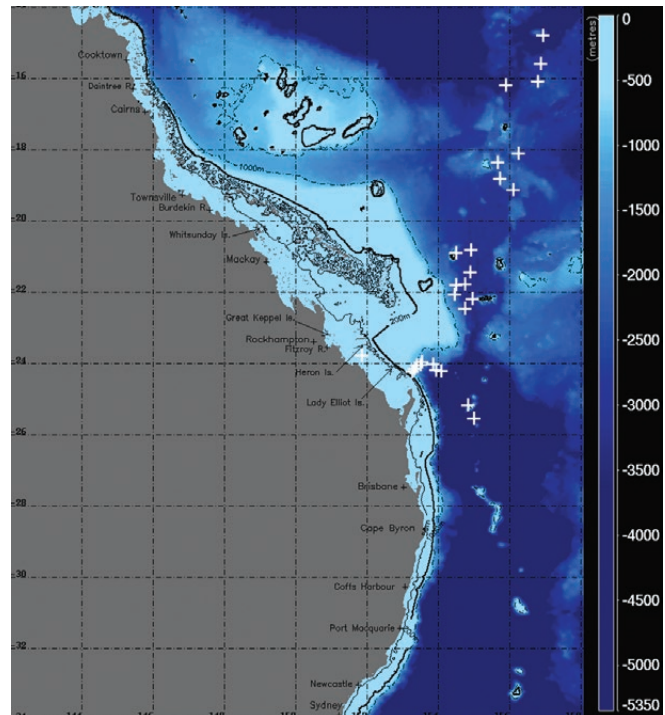


Fig. 2. “At-distance” foraging tracks with regional bathymetry in 2011. Long-trip foraging tracks from Heron Island, GBR ($n = 4$), determined from electronic satellite transmitters deployed on Wedge-tailed Shearwaters during the breeding season are overlaid on bathymetric gradient map of the GBR and Coral Sea region. Crosses show fixes from shearwater tracks highlighting occasions when shearwaters were positioned over seamounts or steep bathymetric gradients/drop-offs.

that are both outside and independent of sites used to obtain food for chicks. This result implies that adults do not self-provision by remaining at sea locally longer to offset the energetic cost of returning to the colony each day (as suggested in the models of Ropert-Coudert *et al.* 2004, and Wojczulanis-Jakubas *et al.* 2010).

Instead, our results suggest that Heron Island shearwaters travel to distant locations to take advantage of sites that provide greater prey availability than near-colony sites, as observed in temperate Procellariiform species (Weimerskirch *et al.* 1994, Weimerskirch & Cherel 1998). In support of this, we find clear links between bathymetric features and long-trip foraging locations. Long-trip foraging sites are characterized by deep water close to rapidly changing bathymetric gradients near seamounts. Such areas are known to be associated with increased biodiversity (Clark *et al.* 2010) and also to facilitate prey aggregation and use by top predators such as seabirds (Haney *et al.* 1995) and tuna (Hui 1985, Blaber 1986, Haney *et al.* 1995).

Tropical seabirds have well-known foraging associations with sub-surface predators that enhance prey availability by driving forage fish toward the surface when they feed (Au & Pitman 1988, Le Corre & Jaquemet 2005, Spear *et al.* 2007). Importantly, our results also imply that prey availability near the colony is unlikely to be able to support both chick and adult requirements simultaneously and that access to at-distance foraging locations is necessary to maintain viable shearwater colonies in this region. These findings are consistent with previous findings that the tropical waters surrounding Heron Island are relatively low in productivity (Peck *et al.* 2004).

There are a number of possible explanations for the variation in at-distance foraging locations used by Wedge-tailed Shearwaters from one year to another. First, location choice may simply differ among individuals, with some adults having preferred locations, a trait that has been observed in both Shy Albatross *Thalassarche cauta* (Hedd *et al.* 2001) and Cory's Shearwater *Calonectris*

diomedea (Paiva *et al.* 2010). Similarly, variations in parental sex, age, experience or even starting physical condition may influence choice of at-distance foraging locations (e.g. Norris 1967, Weimerskirch *et al.* 1997). Conversely, birds may, on any given day, depart on a foraging trip, with the choice of foraging location being influenced by day-to-day, or season-to-season, spatial and temporal variation in environmental parameters such as wind speed and direction (Navarro & González-Solís 2009), ocean productivity (Navarro & González-Solís 2009), sea surface temperature (O'Hara *et al.* 2006), salinity (de León & Mínguez 2003), or patterns of oceanic circulation (Reese & Brodeur 2006). The importance of these various parameters in determining at-distance foraging location choice remains to be tested.

There is a trade-off between potential energy gains and expenditure on long-distance flight for central-place foraging seabirds (Weimerskirch 1998) such as Wedge-tailed Shearwaters. The fact that these pelagic foraging seabirds travel such great distances in order to replenish their body reserves implies that the use of distant foraging grounds must be advantageous and profitable. Accordingly, these sites are likely known locations that provide some guaranteed rate of prey encounters upon which fitness and long-term reproductive success depend.

Importantly, the majority of at-distance foraging locations detected in the present study, and the locations most heavily used, occur outside the current GBR Marine Park management zone. It is not known whether Wedge-tailed Shearwater populations breeding elsewhere in the Coral Sea region, particularly New Caledonia, are also dependent on the same or similar locations. If so, the breeding success of this species both in the GBR and throughout the region may be strongly dependent on the continued stability of food availability at these locations. Moreover, Wedge-tailed Shearwaters are known to forage in mixed-species flocks (Ballance *et al.* 1997, Jaquemet *et al.* 2004, Spear *et al.* 2007), so numerous other seabird species representing different foraging guilds may be similarly dependent upon these same food resource environments.

TABLE 2
Comparisons of bathymetry and distance to the nearest seamount at non-foraging and foraging locations for breeding Wedge-tailed Shearwaters in Great Barrier Reef, 2006, 2011 and 2012

	Mean non-foraging area	Mean foraging area	Difference (95% CI)	<i>t</i>	<i>df</i>	<i>P</i>
2012						
Distance to nearest seamount, degrees	2.48	0.52	1.96 (1.65–2.27)	12.73	80.84	< 2.2 × 10 ⁻¹⁶
Bathymetry depth, m	-499.02	-2 406.96	1 907.94 (1 542.61–2 273.28)	10.35	112.99	< 2.2 × 10 ⁻¹⁶
2011						
Distance to nearest seamount, degrees	2.23	0.43	1.808 (1.657–1.96)	23.53	222.79	< 2.2 × 10 ⁻¹⁶
Bathymetry depth, m	-667.90	-2 959.74	2 291.84 (2 098.37–2 485.31)	23.30	357.52	< 2.2 × 10 ⁻¹⁶
2006						
Distance to nearest seamount, degrees	2.18	1.41	0.769 (0.46–1.08)	4.97	56.54	6.37 × 10 ⁻⁶
Bathymetry depth, m	-485.91	-1 563.46	1 077.55 (675.69–1 479.40)	5.34	73.95	9.72 × 10 ⁻⁷

Wedge-tailed Shearwaters are particularly sensitive to climate-driven changes in the marine environment (Smithers *et al.* 2003, Peck *et al.* 2004, McDuie *et al.* 2013, Weeks *et al.* 2013). They are also sensitive to oceanographic variations known to affect breeding participation and food availability to other less trackable seabird species of the GBR (Smithers *et al.* 2003, Devney *et al.* 2010). This, as well as the fact that Wedge-tailed Shearwaters are widespread and abundant (IUCN 2013), means they represent a suitable “umbrella species” (Lambeck 1997) useful for identifying a wide range of human-induced impacts on upper trophic level marine predators (Roberge & Angelstam 2004) and for developing strategies to effectively manage critical seabird foraging habitats of the GBR and Coral Sea region.

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