

Pronounced inter-colony variation in the foraging ecology of Australasian gannets: influence of habitat differences

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ABSTRACT: The predictability of prey due to oceanographic features can result in large aggregations of apex predators. Central place foragers, such as seabirds, are limited in their foraging duration and range during the breeding period, which can restrict their ability to reach such locations. Segregation by colony and sex can further restrict foraging range and may have direct implications for the foraging ecology of a species. In parts of its range, the Australasian gannet *Morus serrator* breeds in colonies of relatively close proximity and has recently been found to display sexual dimorphism. Two neighbouring breeding colonies in Bass Strait that experience divergent environmental conditions were investigated to determine whether these conditions or the sex of the individual are important variables influencing foraging behaviour in this species. GPS tracking and accelerometry were paired with stable isotope analysis to compare differences in foraging effort, habitat use and diet. Birds from Point Danger, a large colony located near a seasonally strong upwelling, travelled considerably further (77%) than birds from Pope's Eye, a small colony in a nutrient-poor embayment. However, within colonies no sexual differences in foraging effort were found. While the colonies did not overlap in foraging areas, a degree of sexual segregation was apparent within both colonies (Point Danger 46.3% overlap and Pope's Eye 73.7% overlap in home range). Furthermore, stable isotope analysis indicated birds from each colony fed at different trophic niches. This study reveals differences in habitat use and, consequently, dietary niches between and within neighbouring colonies.

KEY WORDS: Foraging ecology · GPS tracking · Accelerometry · Stable isotopes · Sexual-segregation · *Morus serrator*

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INTRODUCTION

While the marine environment is both temporally and spatially variable, ocean currents, eddies, bathymetry and other physical and biological processes can concentrate primary productivity into specific regions (Haury et al. 1978). This results in locations of predictable prey for marine apex predators by influencing the cascade of secondary and tertiary consumers (Reid & Hindell 2000, Weimerskirch 2007). The presence of such oceanographic features has been found to correlate with large aggregations of marine mammals and seabirds (Tynan 1998, Becker & Beissinger 2003).

Seabirds cover large areas when foraging and are capable of exploiting small- and large-scale prey patches (Fauchald et al. 2000). However, during the breeding season seabirds become central place foragers, restricted in the duration of foraging trips by the fasting ability of their partner (during incubation) or their offspring (during chick rearing) (Orians & Pearson 1979). Hence, a knowledge of profitable and predictable food patches would reduce time searching for prey during this restrictive period. However, inter- and intra-specific factors can influence the foraging range of individuals, therefore affecting their access to the most profitable areas.

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Mutually exclusive foraging areas between nearby colonies have been observed in many seabird species and is thought to be driven by density-dependent competition (Ainley et al. 2004, Wakefield et al. 2011, 2013, Chiaradia et al. 2012). As such, colonies may experience different environmental conditions and, consequently, comparison between and within populations may provide insights into the different adaptive capabilities within a species (Tremblay & Cherel 2003). Spatial segregation is also known to occur between the sexes in seabirds. Sexual segregation most commonly occurs in species with size dimorphism (Ruckstuhl & Clutton-Brock 2005), thought to be driven by sexual selection or nutritional requirements (Shine 1989). Thus, within and between colonies of seabirds, access to profitable food patches may be disproportionate due to colony-specific and sexual segregation. Few studies have compared the foraging range and behaviour of seabirds between colonies located in variable environments (Garthe et al. 2007). Hence, there is a lack of understanding how species may respond to environmental fluctuations.

Gannets (*Morus* spp.) are large, pelagic seabirds found in temperate regions (Nelson 1978). Numerous studies have investigated their foraging ecology, and while these studies have demonstrated colony-specific home ranges (Lewis et al. 2001, Wakefield et al. 2013), foraging behaviour appears generally consistent with individuals performing similar dives across colonies (Grémillet et al. 2004). However, comparisons between colonies have been largely limited to regions of similar oceanographic conditions (Hamer et al. 2001, Grémillet et al. 2004, Pettex et al. 2012). The exception to this is Garthe et al. (2007), who found that 2 colonies of northern gannets *M. bassanus*, located in differing oceanographic regions, varied in prey consumption, foraging distance, duration and dive type.

The Australasian gannet *M. serrator* breeds on coastal islands in Australia and New Zealand (Nelson 1978). To date, studies on the foraging behaviour of the species have been conducted at colonies with similar foraging habitats, and have found little variation in foraging behaviour (Machovsky-Capuska et al. 2014). In south-eastern Australia, some colonies occur within 40 to 60 km of the continental shelf edge in a region influenced by the seasonally predictable, nutrient-rich Bonney Upwelling during the Austral summer (Fig. 1) (Cai & Lennon 1993). The upwelling, which is strongest between January and March, is known to influence a diverse range of marine species, from bryozoans to whales, due to the resulting

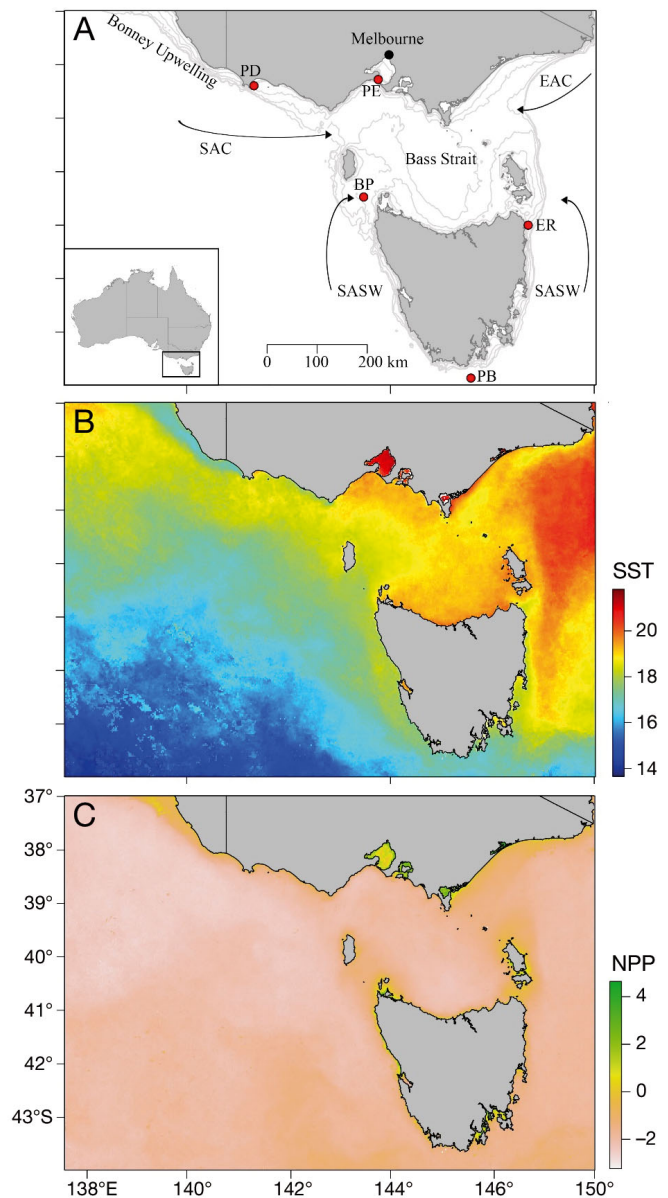


Fig. 1. (A) Location of Australasian gannet *Morus serrator* colonies in south-eastern Australia: PD: Point Danger and Lawrence Rocks; PE: Pope's Eye and Port Philip Bay colonies; BP: Black Pyramid; ER: Eddystone Rock; PB: Pedra Branca. Arrows indicate the direction of currents (SAC: South Australian Current; EAC: East Australian Current; SASW: Subantarctic Surface Water) that may enter Bass Strait. Bathymetry (20 m intervals) to the edge of the continental shelf (200 m contour) is shown in light grey. (B) Averaged sea surface temperature (SST, °C) and (C) net primary productivity (NPP, mg c⁻² d⁻¹) in south-eastern Australia, highlighting the strength of the Bonney Upwelling during the Austral summer (January–March) preceding the gannet breeding season in the present study (monthly SST and NPP data were estimated on a 1 km² grid using data from the Aqua-MODIS sensor. Remote-sensing environmental data were obtained from the National Oceanic and Atmospheric Administration, <http://coastwatch.pfel.noaa.gov/coastwatch/CWBrowserWW360.jsp?get>)

high productivity (Butler et al. 2002). In addition, the cascade effects of this productivity, and its variability, can be seen in the foraging behaviour and breeding success of marine predators in the following summer (Mickelson et al. 1991, Gibbens & Arnould 2009, Hoskins & Arnould 2014, Knox et al. 2014, Berlincourt & Arnould 2015a,b).

Less than 300 km away, gannet colonies have been established on artificial structures inside Port Phillip Bay (Fig. 1A) (Pyk et al. 2013), leading to a unique situation where birds may forage in the shallow embayment (average depth 14 m; Berelson et al. 1998) or in the northern waters of Bass Strait, the shallow (average depth 50 to 70 m; Sandery & Kämpf 2007) continental shelf region between mainland Australia and Tasmania. Bass Strait is a region with a limited nutrient regime (Gibbs et al. 1986) and poorly mixed waters influenced by multiple currents in the summer months (Fig. 1) (Sandery & Kämpf 2005). The influence of these divergent oceanographic regimes on the diet, foraging range, habitat use and behaviour of Australasian gannets is currently unknown.

In addition, since Australasian gannets are (until recently) considered nominally monomorphic (Nelson 1978, Ismar et al. 2014), previous studies on their foraging ecology have not assessed males and females separately (Green et al. 2009, 2013, Machovsky-Capuska et al. 2011, 2014). Northern gannets have been shown to be sexually dimorphic, with larger females foraging further offshore and on different prey than the smaller males (Stauss et al. 2012, Cleasby et al. 2015). A recent study has also documented the Australasian gannet to be sexually dimorphic, with females larger than males (Angel et al. 2015b). However, it is not known whether the species displays similar patterns of sexual segregation in diet or foraging habitat to that observed in the northern gannet, or if environmental conditions play a role in such segregation.

The aims of the present study, therefore, were to determine, in 2 neighbouring colonies experiencing divergent oceanographic regimes, whether differences exist in (1) foraging behaviour, (2) habitat use and (3) dietary niche at the colony and/or sex level.

MATERIALS AND METHODS

Study sites and animal handling

The study was conducted between October 2012 and January 2013 at Point Danger (38° 23' 36" S, 141° 38' 54" E; 3500 breeding pairs including Lawrence

Rocks) and Pope's Eye (38° 16' 42" S, 144° 41' 48" E; 330 breeding pairs including other colonies in Port Phillip Bay) colonies in northern Bass Strait, south-eastern Australia (Fig. 1). These 2 adjacent colonies are <300 km apart; a third, larger colony (12 300 individuals) is situated 250 km south of Pope's Eye in southern Bass Strait (Fig. 1). Individual gannets were captured at the nest during the incubation period; the egg was covered for protection while the adult was being processed. Where possible, both adults of a breeding pair were sampled to ensure equal sex ratios. Individuals were weighed using a suspension balance (± 25 g; Salter Australia). Tarsus length was measured using Vernier callipers (± 0.1 mm) and wing ulna length was measured using a slide ruler (± 1 mm).

A total of 29 birds were measured at Point Danger (5 males, 7 females) and Pope's Eye (8 males, 9 females). Individuals were equipped with a GPS data logger (IgotU GT-600, Mobile Action Technologies; 26.50 g) that recorded location (± 10 m) every 2 min, and a tri-axial accelerometer data logger (X8, Gulf Coast Data Concepts; 14.12 g) measuring at 25 Hz to determine at-sea movements and foraging behaviours, respectively. Devices were encapsulated in heat-shrink plastic (whole package: 52.56 g; <3% body mass; Phillips et al. 2003) and attached with water-proof tape (Tesa® 4651, Beiersdorf) to the central tail feathers following the methods of Wilson et al. (1997). Device positioning ensured the logger was covered by the wings during a plunge dive in an attempt reduce drag (Hamer et al. 2000). In most cases, individuals were recaptured after a single foraging trip. A single blood sample (0.1 ml) was then collected by venipuncture of a tarsus vein for genetic sexing (DNASolutions) and stable isotope analysis before the bird was released.

Data processing, environmental variables and statistical analyses

Body mass (BM; kg), tarsus (T; mm) and wing ulna (WU; mm) length were used to estimate body condition (i.e. percent total body fat, TBF%) based on the equation of Angel et al. (2015b):

$$\text{TBF \%} = 24.43 + 1.94 \times (\text{BM} \div \text{WU}) - 0.58 \times \text{T} \quad (1)$$

GPS locations were processed using a speed filter (McConnell et al. 1992) and summary statistics calculated using the 'adehabitatHR' package (Calenge 2006) in the R statistical environment (R Core Team 2015). Trip parameters indicative of effort were cal-

culated (i.e. maximum distance from colony, total distance and duration and average speed) for the first foraging trip for each individual. Foraging area overlap was quantified by calculating the colony home range (95% contour) and core foraging area (50% contour) for each sex based on dive locations. A kernel density estimation, with an ad hoc smoothing parameter and cell size of 250 m², was calculated for each contour and a utilization distribution overlap index used to estimate overlap (Fieberg & Kochanny 2005).

Tri-axial accelerometers were positioned to measure surge (longitudinal axis), heave (dorso-ventral axis), and sway (lateral axis). Data from the accelerometers were visually assessed for behaviour in IGOR Pro (version 6.34; WaveMetrics) based on previous studies of plunge diving species (Ropert-Coudert et al. 2004, 2009, Weimerskirch et al. 2005). Five key behaviours were identified: (1) resting at the sea surface; (2) flapping flight; (3) gliding flight; and foraging (including [4] plunge diving and [5] surface foraging; Warwick-Evans et al. 2015). The 'Ethographer' package was used to perform a *k*-means algorithm clustering analysis following the methods of Sakamoto et al. (2009). Behaviours were identified using an unsupervised continuous wavelet transformation (1 s window). The proportion of time spent performing each behaviour during a foraging trip was then calculated. The range and proportion of behaviours observed during foraging trips were similar to that recorded by animal-borne video data loggers in a recent study of Australasian gannets from the 2 colonies in the present study (Wells et al. 2016).

From the behavioural data, the total number of plunge dives and surface foraging events performed were used to calculate plunge and surface dive rates (dives h⁻¹) averaged over the entire foraging trip. Since the accelerometers could not be positioned near the animal's centre of the gravity (Vandenabeele et al. 2014), mean vectorial body dynamic acceleration (VeDBA; *g*) and total VeDBA were used as indices of energy expenditure following the methods outlined in Qasem et al. (2012).

The major habitat differences between the 2 study colonies are in the depth of the waters available for foraging and their proximity to the seasonally productive Bonney Upwelling (Fig. 1). Due to the limitations of remote-sensed data in shallow inshore regions (Sathyendranath et al. 1989, Miller & McKee 2004), and the fact that the Bonney Upwelling's influence on prey availability has been shown to lag by months (Kämpf 2015), relationships between the foraging behaviour of Australasian gannets and concurrent sea surface temperature and chlorophyll *a* (chl *a*)

concentration were not investigated in the present study.

To determine if wind conditions influence foraging behaviour differently at each colony, average monthly wind speed and direction were extracted from areas in which individuals were observed to frequent during the study (i.e. along the Bonney Upwelling coast, northern central Bass Strait and Port Phillip Bay). Data were obtained from the National Centre for Environmental Prediction/National Centre for Atmospheric Research (NCEP/NCAR) Reanalysis Project (Kalnay et al. 1996). NCEP values were extracted for daily wind speed and direction and averaged for the duration of the breeding season for the 3 respective areas (Bonney Upwelling: 39°–38° S, 136°–142° E; Bass Strait: 40° 12'–38° 30' S, 144° 5'–146° 48' E; Port Phillip Bay: 38° 23'–37° 47' S, 144° 18'–145° 11' E).

In order to investigate whether differences in the diet of Australasian gannets occurs between colonies and sexes, nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotopes in whole blood samples were analysed. Nitrogen has an average enrichment of 3 to 4‰ at each trophic step and is used to determine a consumer's trophic position (Deniro & Epstein 1981). While carbon also increases slightly with trophic level (enrichment of 1 to 2‰; Hobson & Welch 1992), variation in $\delta^{13}\text{C}$ gradients can be caused by foraging inshore/offshore or in benthic/pelagic zones (Hobson et al. 1994). As such, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ can be used together to infer the diet of a consumer. Additionally, the turnover rate of protein varies between body tissues, reflecting different temporal scales (Kelly 2000). In the present study, whole blood was used since it is indicative of the previous 2 wk (Hobson & Clark 1992) and, thus, provides a longer time-scale to compare between the colonies than the tracking data.

Blood samples were ground up and lipids extracted following the methods of Ehrlich et al. (2011). Samples were processed through a CHN elemental analyser (CE1110; Carlo Erba) and analysed with an interfaced Fisons isochrom continuous-flow isotope ratio mass spectrometer (GV Instruments). Replicate measurements for internal laboratory standards found a precision of 0.1 and 0.3‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. The C:N mass ratio for males (3.24 ± 0.02) and females (3.26 ± 0.02) was less than 3.5, indicating lipids in the samples were sufficiently extracted as to not influence the results (Post et al. 2007).

As the behavioural variables were proportional, they were arcsine transformed for statistical analysis. Assumptions for independence and normality of data were tested using a chi-square and Shapiro-Wilk's

test, respectively. For all foraging metrics where the assumptions were not met, a log₁₀ transformation was performed to provide a better approximation of normality. Data were analysed using 2-way ANOVAs with sex and colony as factors, followed by Tukey's post hoc test. Results are reported as mean ± SE, unless otherwise stated.

RESULTS

Body mass of Australasian gannets was significantly lower for both males and females at Point Danger (2.30 ± 0.08 and 2.46 ± 0.07 kg, respectively) than at Pope's Eye (2.50 ± 0.10 and 2.67 ± 0.08 kg, respectively; 2-way ANOVA, $F_{1,25} = 5.84$, $p = 0.02$), although wing length at Point Danger (males: 206.0 ± 2.4, females: 208.4 ± 2.2 mm) was longer than at Pope's Eye (males: 201.8 ± 0.9, females: 202.4 ± 2.0 mm; $F_{1,25} = 6.00$, $p = 0.014$). Tarsus length did not differ significantly between Point Danger (males: 71.9 ± 1.5, females: 68.9 ± 1.2 mm) and Pope's Eye (males: 68.3 ± 1.1, females: 67.4 ± 1.3 mm; $F_{1,25} = 3.48$, $p = 0.07$). Furthermore, body condition (TBF%) did not differ between Point Danger (males: 17.2 ± 0.9%, females: 15.5 ± 0.7%) and Pope's Eye (males: 15.2 ± 0.6%, females: 14.6 ± 0.8%; $F_{1,25} = 3.49$, $p = 0.07$). No sex effect was found in body mass ($F_{1,25} = 3.29$, $p = 0.818$), wing length ($F_{1,25} = 1.16$, $p = 0.28$), tarsus length ($F_{1,25} = 1.59$, $p = 0.22$) or body condition ($F_{1,25} = 1.60$, $p = 0.22$), potentially due to the small sample sizes ($n = 29$) and high variability between individuals. Indeed, a power analysis revealed a sample size of 45 birds at Pope's Eye and 22 birds at Point Danger would be needed to detect a significant difference ($\alpha = 0.8$).

larger foraging home range (41.1×10^3 and 70.7×10^3 km², respectively) than birds from Pope's Eye (2.6×10^3 and 1.2×10^3 km², respectively). Comparison between the sexes found that females and males had similar foraging ranges ($F_{1,25} = 2.11$, $p = 0.16$), total distance ($F_{1,25} = 0.57$, $p = 0.46$) and total duration ($F_{1,25} = 0.21$, $p = 0.66$) during a foraging trip.

Furthermore, the average travelling speed for males and females was much greater at Point Danger (14.0 ± 0.9 and 11.2 ± 0.8 km h⁻¹, respectively) compared to Pope's Eye (6.9 ± 1.0 and 7.6 ± 1.2 km h⁻¹, respectively; $F_{1,25} = 21.56$, $p < 0.001$). No sex differences in travelling speed were detected at either colony ($F_{1,25} = 0.01$, $p = 0.91$). To determine whether the different travelling speeds were related to flying conditions around the colonies, wind speed and direction was assessed in areas used by the birds. No significant difference was found for average wind speed ($F_{2,8} = 0.50$, $p = 0.62$) between colonies, with birds from Point Danger foraging along the Bonney Coast (8.2 ± 1.3 km h⁻¹) facing similar wind conditions to birds from Pope's Eye foraging in Port Phillip Bay (9.5 ± 2.2 km h⁻¹) and Bass Strait (10.8 ± 2.3 km h⁻¹). Similarly, the predominant wind direction experienced by birds at both colonies was not significantly different (Bonney Coast: $256.2 \pm 3.3^\circ$; Port Phillip Bay: $242.0 \pm 11.8^\circ$, Bass Strait: $258.6 \pm 7.9^\circ$; $F_{2,8} = 1.30$, $p = 0.32$).

Point Danger individuals spent significantly more time in gliding flight (males: $24.4 \pm 1.7\%$, females: $28.4 \pm 3.2\%$) than Pope's Eye birds (males: $14.2 \pm 2.8\%$, females: $18.3 \pm 2.8\%$; $F_{1,22} = 10.56$, $p = 0.004$), although no significant difference was found in flapping flight ($F_{1,22} = 3.23$, $p = 0.09$; Table 1). The proportion of time spent resting on the sea surface was 10 to 15% less at Point Danger than at Pope's Eye ($F_{1,22} = 6.43$, $p = 0.02$; Table 1). While no difference was

Foraging effort

During the study period, birds from Point Danger travelled 77% further from the colony than those breeding at Pope's Eye ($F_{1,25} = 27.01$, $p < 0.01$; Table 1). A significant difference between colonies was also observed in the total trip distance ($F_{1,25} = 25.64$) and duration ($F_{1,25} = 14.50$, $p < 0.001$ in both cases; Table 1). Hence, males and females from Point Danger had a

Table 1. At-sea movements and behaviour of Australasian gannets foraging from 2 colonies in Bass Strait, Australia. Mean ± SE; *significant difference between colonies ($p < 0.05$)

	Point Danger		Pope's Eye	
	Male (n = 5)	Female (n = 7)	Male (n = 8)	Female (n = 9)
Distance from colony (km)*	172.5 ± 58.3	238.2 ± 42.0	38.5 ± 7.4	54.4 ± 18.6
Total distance (km)*	679.7 ± 232.2	772.5 ± 115.4	193.9 ± 31.9	214.5 ± 52.7
Trip duration (h)*	48.7 ± 15.7	55.2 ± 6.6	27.3 ± 3.4	25.7 ± 3.2
Average speed (km h ⁻¹)*	14.0 ± 0.9	11.2 ± 0.8	6.9 ± 1.0	7.6 ± 1.2
Time resting (%)*	49.7 ± 1.9	46.9 ± 2.6	64.4 ± 4.7	56.6 ± 4.8
Time flapping (%)	20.9 ± 2.2	19.9 ± 2.0	14.8 ± 1.7	18.0 ± 1.9
Time gliding (%)*	24.4 ± 1.7	28.4 ± 3.2	14.2 ± 2.8	18.3 ± 2.8
Time foraging (%)	5.0 ± 0.6	4.8 ± 0.7	6.6 ± 0.9	7.1 ± 1.2
Plunge dives h ⁻¹ *	4.8 ± 0.5	3.5 ± 0.8	2.0 ± 0.6	1.5 ± 0.7
Surface dives h ⁻¹	2.5 ± 0.3	2.2 ± 0.1	2.4 ± 0.8	1.4 ± 0.6

detected in the proportion of time spent foraging ($F_{1,22} = 3.24$, $p = 0.09$) or in the rate of surface foraging events ($F_{1,22} = 0.43$, $p = 0.52$; Table 1), birds from Point Danger were found to have a higher rate of plunge dives (males: 4.8 ± 0.5 , females 3.5 ± 0.8 dives h^{-1}) than Pope's Eye birds (males: 2.5 ± 0.3 , females 2.2 ± 0.1 dives h^{-1} ; $F_{1,22} = 10.33$, $p = 0.004$). For all behaviours and foraging rates, no significant difference was found between the sexes ($p > 0.05$ in all cases).

Mean VeDBA was significantly greater at Point Danger (males: 0.45 ± 0.03 g, females: 0.43 ± 0.03 g) than Pope's Eye (males: 0.32 ± 0.03 g, females: 0.40 ± 0.03 g; $F_{1,22} = 5.07$, $p = 0.04$). Total VeDBA was also much greater at Point Danger (males: $25.6 \times 10^5 \pm 7.4 \times 10^5$ g, females: $21.6 \times 10^5 \pm 4.3 \times 10^5$ g) than Pope's Eye (males $7.9 \times 10^5 \pm 0.9 \times 10^5$ g, females $6.6 \times 10^5 \pm 1.4 \times 10^5$ g; $F_{1,22} = 28.20$, $p < 0.001$), suggesting both a greater rate and total amount of energy expenditure at Point Danger. Males and females were found to have a similar rate of mean VeDBA ($F_{1,25} = 2.23$; $p = 0.15$) and total VeDBA ($F_{1,25} = 0.97$, $p = 0.36$), regardless of colony.

Foraging segregation

Calculations of core foraging area (50% contour) and home range (95% contour) were conducted to predict the overlap between colonies and sexes within each colony from a small sample of the population. Point Danger birds covered a home range of 8619.9×10^3 km² and a core area of 1705.8×10^3 km², a much greater area compared to Pope's Eye birds,

who covered a home range of 261.6×10^3 km² and a core area of 33.1×10^3 km². The core foraging areas of the 2 colonies did not overlap, and minimal overlap (0.005%) in the home range occurred (Fig. 2).

Although no sex differences were detected in any metric of foraging effort (potentially due to the small sample size), sexual segregation in foraging areas was clearly evident at each colony. At Point Danger, home ranges overlapped 46.3%, with males foraging predominantly to the west of the colony and females foraging both east and west of the colony. Furthermore, core foraging areas overlapped only 4.2%, occurring in the waters immediately around the colony (Fig. 2a). A greater overlap in foraging area was found at Pope's Eye, where home range overlapped 73.7% and core foraging area overlapped 18.4%. The overlap of the core and home range foraging areas was concentrated around the entrance to Port Phillip Bay, south of Pope's Eye—an area where birds leaving the colony need to traverse to access open waters (Fig. 2b). Only males were observed to forage inside Port Phillip Bay (north of Pope's Eye).

Dietary segregation

Stable isotope analysis of whole blood indicated males and females at Point Danger were significantly less enriched in $\delta^{15}N$ (12.5 ± 0.1 and 12.6 ± 0.2 ‰, respectively) than males and females from Pope's Eye (14.3 ± 0.3 and 14.2 ± 0.1 ‰, respectively; $F_{1,51} = 34.33$, $p < 0.001$). These results indicate that birds at Pope's Eye foraged at a higher trophic niche. Fur-

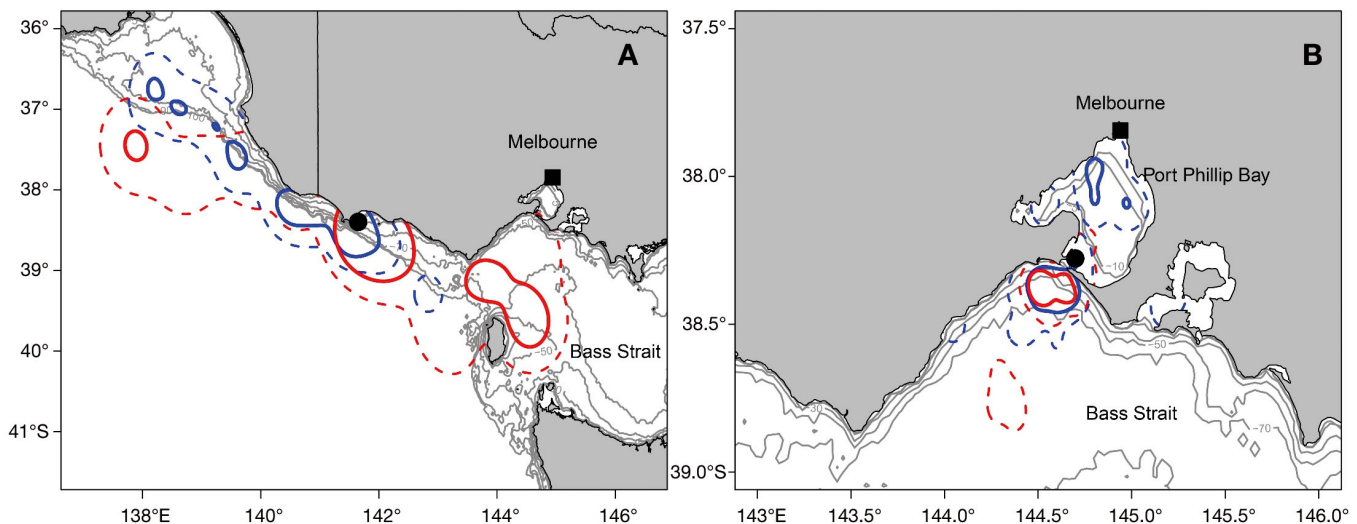


Fig. 2. Male (blue) and female (red) Australasian gannet foraging ranges using kernel density based utilization distributions at 95% (dotted lines) and 50% (solid lines) contours during the incubation stage of breeding at (A) Point Danger and (B) Pope's Eye colonies. Black circles: breeding colony locations

thermore, males and females at Point Danger had lower $\delta^{13}\text{C}$ values (-20.3 ± 0.1 and $-20.0 \pm 0.2\text{‰}$, respectively) than birds at Pope's Eye (-18.3 ± 0.3 and $-19.6 \pm 0.3\text{‰}$, respectively; $F_{1,51} = 22.05$, $p < 0.001$), indicating a different geographic origin of prey.

Significant differences were found between the sexes in $\delta^{15}\text{N}$ ($F_{1,51} = 4.421$, $p = 0.04$) and $\delta^{13}\text{C}$ ($F_{1,51} = 4.73$, $p = 0.03$). However, within colonies, Tukey's post hoc comparison indicated no significant difference between males and females in $\delta^{15}\text{N}$ (Point Danger males vs. females: $p = 0.95$; Pope's Eye males vs. females: $p = 0.20$), indicating the prey items they consumed were of a similar trophic level. While no difference in $\delta^{13}\text{C}$ values were found between sexes at Point Danger ($p = 0.99$) and Pope's Eye ($p = 0.06$), an enrichment difference of 1.3‰ between the sexes (in the case of Pope's Eye) could be considered biologically significant. In addition, the standard deviation in $\delta^{13}\text{C}$ values was greater at Pope's Eye for both sexes in comparison to Point Danger, indicating a greater degree of variation in the geographic origin of prey at Pope's Eye than at Point Danger. Furthermore, there was a significant difference in $\delta^{13}\text{C}$ between males from Pope's Eye and males ($p < 0.001$) and females ($p = 0.001$) from Point Danger, but not for females from Pope's Eye ($p = 0.12$; $p = 0.19$). These results suggest geographic variation in the origin of prey for males at Pope's Eye when compared to females at Pope's Eye and both sexes at Point Danger (Fig. 3).

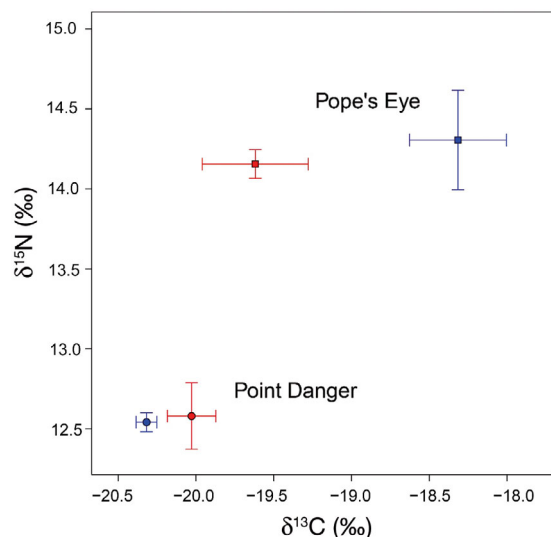


Fig. 3. Whole blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm SD) for breeding male (blue) and female (red) Australasian gannets at Point Danger (females, $n = 6$; males, $n = 6$) and Pope's Eye (females, $n = 9$; males, $n = 7$)

DISCUSSION

The present study investigated the foraging behaviour, habitat use and dietary niche during the incubation stage of the breeding period of Australasian gannets from 2 adjacent colonies with fundamental habitat differences. Birds from Point Danger, despite being located in a productive region, were found to forage further from the colony and spend significantly less time resting on the sea surface during a foraging trip. In addition, minimal overlap in habitat use was observed between the 2 colonies despite their relatively close proximity, supported by a segregation in the dietary niche. Comparison between sexes within the colonies indicated no difference in foraging behaviour. However, a spatial sexual segregation was observed at both colonies. Core foraging areas overlapped very little between the sexes at Point Danger yet similar isotopic niches were observed between the sexes. A greater overlap in core area was observed at Pope's Eye, although the dietary niche suggested that the species of prey consumed increased sexual segregation.

Foraging effort

Birds from Point Danger were found to weigh less than those from Pope's Eye. However, geographical variation in a species' body size is common and can reflect differences in food availability or inter-population growth patterns (Lovich & Gibbons 1992). Although no sex differences were detected in the present study due to a small sample size, females have been found to be on average 180 g heavier throughout the breeding season and between years at both colonies (Angel et al. 2015b). Interestingly, there were no differences in body condition between colonies for either sex, despite individuals from Point Danger travelling faster, further and having a greater home range than those from Pope's Eye. This suggests that Point Danger individuals are either more efficient foragers or the prey being consumed is of a higher quality, allowing for the similar body condition observed between colonies.

Australasian gannets predominantly forage on small schooling prey such as pilchards *Sardinops sagax* and anchovy *Engraulis australis* (Bunce 2001, Schuckard et al. 2012). These prey are found in neritic waters on the continental shelf (Fletcher & Tregonning 1992) with a greater abundance associated with the enriched primary productivity produced by the Bonney Upwelling (Nieblas et al. 2009). The

greater foraging range of the Point Danger colony could reflect the narrowness of the continental shelf, requiring individuals to fly further to locate sufficient prey resources. In addition, Point Danger (660 pairs) and the nearby (2 km) Lawrence Rocks (3100 pairs) colonies are considerably larger than Pope's Eye (180 pairs) and its nearby colonies in Port Phillip Bay (330 pairs; Bunce et al. 2002). Consequently, local prey resources might be depleted much faster at Point Danger due to intra-colony competition. Competition can result in individuals travelling further and covering a greater area in search of prey, as has been observed in northern gannets where foraging trip duration and distance travelled was influenced by colony size (Lewis et al. 2001).

Birds from Point Danger were found to maintain greater average travelling speeds during a foraging trip. As gannets use a combination of flapping and gliding flight, they are sensitive to wind speed and direction (Amélineau et al. 2014). There was little difference in the mean direction (west-southwest, 242 to 258°) and speed of the wind between the 2 colonies. However, due to the location of the colonies relative to their respective foraging areas, at Point Danger the wind direction was perpendicular to the coast and the foraging routes taken by individuals feeding along the narrow continental shelf. Consequently, these birds are likely to have tacked with the wind (Weimerskirch et al. 2000) which may explain the higher proportion of their trip spent gliding. In contrast, birds at Pope's Eye commuted to and from feeding zones with a head or tail wind, respectively, similar to that found for northern gannets (Amélineau et al. 2014). The difference in wind direction relative to foraging areas may also have consequences for the energy expended to reach profitable prey patches.

Point Danger birds spent 10 to 15% less time during a foraging trip resting on the sea surface than Pope's Eye birds. Furthermore, birds from Point Danger had twice as many plunge dives per hour compared to those from Pope's Eye. However, the total time spent foraging did not differ between the colonies. This could be due to Pope's Eye birds performing more U-shaped plunge dives, which are known to be more frequent in coastal areas and of a longer duration (Machovsky-Capuska et al. 2011, Cleasby et al. 2015). Furthermore, the greater density of birds breeding at Point Danger and Lawrence Rocks could also be a contributing factor to the greater plunge dive rate observed from Point Danger birds, with more dives required to successfully out-compete conspecifics (Thiebault et al. 2014).

Mean and total VeDBA have been found to be positively correlated with the rate and total amount of energy expenditure, respectively, in Australasian gannets (L. P. Angel et al. unpubl. data) and were, therefore, used to compare foraging energy expenditure between the colonies. The results suggest a higher energy expenditure rate in Point Danger birds, which is likely due to their higher plunge dive rate. While the cost of a plunge dive is minimal due to its short duration, the take-off from the sea surface incurs a high energetic cost (Green et al. 2009). Point Danger birds also had a higher total VeDBA, suggesting a greater total energy expenditure which is likely due to their significantly longer foraging trips. Despite the higher energy expenditure, body condition was similar between the 2 colonies, suggesting that birds from Point Danger forage with greater efficiency or experience greater food availability. Interestingly, no significant differences were detected in any foraging parameter or metric of foraging effort between the sexes, for either colony. This is consistent with there being no difference in body condition between the sexes (Angel et al. 2015b, this study).

Foraging segregation

The mean distances gannets have been found to travel from their colony ranges from 185 to 520 km in a single foraging trip (Grémillet et al. 2004, Stauss et al. 2012, Machovsky-Capuska et al. 2014). In the present study, the adjacent colonies were located <300 km apart, and thus, a small amount of overlap could be expected (Lewis et al. 2001, Grémillet et al. 2004, Wakefield et al. 2013). However, the potential establishment of mutually exclusive foraging areas, observed in a small number of individuals in the present study, may result in a restriction in the type of habitat available to each colony. At Point Danger, the narrowness of the continental shelf requires birds to travel a greater distance from the colony to cover the same area as those from Pope's Eye. However at Pope's Eye, birds have 2 habitats in which to forage: an embayment (Port Phillip Bay) or in the open waters of Bass Strait.

Interestingly, the maximum distance Pope's Eye birds ranged into Bass Strait was only 20% of the distance from the colony covered by birds from Point Danger. This seemingly restricted foraging range for Pope's Eye birds may be due to the smaller size of their colony resulting in less intra-colony competition. However, in years of poor prey availability, and hence increased competition, Pope's Eye birds did

not increase this range (Angel et al. 2015a). Therefore, it is more likely that this restriction is due to competitive exclusion caused by individuals from Point Danger and another, much larger gannet colony (Black Pyramid) in southern Bass Strait (12 300 breeding pairs; Bunce et al. 2002) (Fig. 1).

Similar to what has been observed in northern gannets (Stauss et al. 2012), the findings in the present study clearly reveal a degree of sexual segregation at both colonies investigated, despite the small sample size. At Point Danger, females foraged both east and west of the colony whereas males exclusively travelled west in search of prey. Furthermore, females' foraging efforts extended beyond the continental shelf, whereas males appeared to remain closer inshore. At Pope's Eye, while the degree of segregation was smaller than that observed at Point Danger, females and males diverged in their focal foraging habitats. The majority of females foraged in northern Bass Strait, concentrating their feeding near the entrance to Port Phillip Bay (see Fig. 2). In contrast, half the males foraged within the shallow waters of Port Phillip Bay while the other half foraged in northern Bass Strait in the same area as the females. Due to the small sample sizes observed in the present study, further data is needed to determine the extent of this segregation. However, these results are similar to those of Wells et al. (2016), who documented 2 distinct foraging strategies (inshore and pelagic) for birds from the Pope's Eye colony, with primarily males foraging within Port Phillip Bay targeting demersal/benthic fish species.

Foraging in mainly inshore areas has previously been observed in northern gannets (Lewis et al. 2002, Stauss et al. 2012, Cleasby et al. 2015), and is consistent with males of other sulid species making shorter foraging trips (Gilardi 1992, Weimerskirch et al. 2006, Weimerskirch et al. 2009). This behaviour may be residual territorial defence in males due to the need to establish nesting sites at the start of the breeding season (Nelson 1978, Matthews et al. 2008). Alternatively, sexual segregation may be due to different nutritional needs (Lewis et al. 2002) or competitive displacement between the sexes (Stauss et al. 2012, Cleasby et al. 2015), factors commonly related to the presence of sexual dimorphism (Ruckstuhl & Clutton-Brock 2005). Similar to other sulid species, Australasian gannets display reversed sexual dimorphism, with females being heavier than males (3.1% at Pope's Eye and 7.3% at Point Danger; L. P. Angel et al. unpubl. data). The sexual segregation in habitat use observed at both colonies in the present study, therefore, may be due to sexual dimorphism.

Dietary segregation

The degree of segregation in the diet of the 2 colonies was inferred from stable isotope analysis of whole blood samples. Differences between the 2 colonies were found in $\delta^{15}\text{N}$ values, with Point Danger birds feeding at an enrichment 1.6 to 1.8‰ lower than those from Pope's Eye. The higher trophic position of Pope's Eye birds may reflect feeding at higher trophic levels (Kelly 2000). Alternatively, as inshore water tends to have longer food-chains, and hence greater nitrogen absorption through the trophic levels (Hobson & Clark 1992, Hobson et al. 1994, Chérel & Hobson 2007), the results could indicate that they are feeding on more inshore species than those at Point Danger. Indeed, a previous analysis of regurgitate samples found that individuals from Point Danger fed on pelagic clupeoids more frequently than those from Pope's Eye (Barker 2012). In addition, using animal-borne video cameras, Wells et al. (2016) documented that individuals foraging within Port Phillip Bay fed predominantly on the demersal/benthic species of the shallow embayment.

Intra-colony comparisons for males and females found no segregation in $\delta^{15}\text{N}$, despite the niche segregation in foraging areas. As Australasian gannets forage by plunge diving and surface foraging, they are typically limited to feeding on schooling fish concentrated by other predators (i.e. tuna, dolphins and fur seals) brought near the sea surface (Machovsky-Capuska et al. 2011). Hence, the similarity of the trophic position between the sexes is possibly due to the limited number of such prey species available within their range.

Tissue $\delta^{13}\text{C}$ values are influenced by spatial gradients in marine phytoplankton, whereby coastal/inshore communities are more enriched in $\delta^{13}\text{C}$ than pelagic/offshore communities (Hobson et al. 1994, Kelly 2000, Chérel & Hobson 2007). As Pope's Eye is situated in a semi-enclosed embayment, individuals feeding on prey originating from the region would be expected to have higher $\delta^{13}\text{C}$ values. Indeed, Pope's Eye males were observed to forage inside the bay. The enriched carbon from inshore waters tends not to transport more than a few km offshore (Gearing 1988). Females from Pope's Eye feed almost exclusively in Bass Strait, and their lower $\delta^{13}\text{C}$ values were reflective of the more offshore waters than the males. In contrast, Point Danger is located near the continental shelf and is greatly influenced by deep oceanic waters (Cai & Lennon 1993). The observed carbon values for Point Danger males and females match those reported for offshore environments in

previous studies (Hobson et al. 1994, Cherel & Hobson 2007). Hence, a decreasing $\delta^{13}\text{C}$ gradient can be seen from the inshore males at Pope's Eye, to the off-shore females at Pope's Eye, to the open water prey consumed by birds from Point Danger.

In summary, Australasian gannets foraging in Bass Strait were found to differ in foraging effort, habitat use and dietary niche between 2 colonies. Birds from Point Danger appear to tack the wind in search of prey, resulting in a larger foraging range; however, this may cause a hemmed-in effect on Pope's Eye birds due to competitive exclusion (Wakefield et al. 2013). Although no difference in foraging behaviour or effort was found between the sexes, spatial and dietary niche segregation was apparent within the colonies. Consequently, the influence of future environmental variability on the foraging behaviour and success of Australasian gannets may differ in relation to this inter- and intra-colony variation.

Acknowledgements. We thank Hilary Stuart-Williams for assistance with the stable isotope analysis and Laëticia Kernaléguen for her invaluable advice when interpreting the results. Thank you to Alastair J. Hobday and Jason R. Hartog (CSIRO Oceans and Atmosphere, Hobart) for their assistance with the environmental data. Logistical support for the project was provided by the Victorian Marine Science Consortium, Sea All Dolphin Swim, and Parks Victoria. The assistance of the many field work volunteers who made this work possible is gratefully acknowledged. The research was financially supported by the Holsworth Wildlife Research Endowment and conducted under approval from Deakin University's Animal Welfare Committee [A86/2010] and Department of Sustainability and Environment Victoria Wildlife Research [Permit 0005745].

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*Editorial responsibility: Scott Shaffer,
San Jose, California, USA*

*Submitted: November 13, 2015; Accepted: July 20, 2016
Proofs received from author(s): August 22, 2016*