Sex-specific foraging over space and time in Cape gannets during chick rearing

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ABSTRACT: Sex-specific foraging strategies have been documented in a range of seabird species, but the underlying mechanisms remain poorly understood. We aimed to assess spatial and temporal differences in the foraging behaviour of Cape gannets *Morus capensis* at Bird Island, Algoa Bay, South Africa. In total, 79 birds attending chicks younger than 50 d were fitted with GPS loggers over 2 consecutive years (2011/12, 2012/13). Furthermore, 95 additional birds were equipped with VHF tags to automatically record the temporal component of sex-specific foraging patterns over 3 consecutive years (2011/12, 2012/13, 2013/14). Using home range analysis and linear models, we found limited evidence for sex-specific differences over spatial dimensions. However, a slight extension in the foraging range of females during a year of lower prey availability was evident. This suggests a possible sex-specific response to prey limitation, which could reflect intraspecific competition or differences in nutritional requirements. Using a binomial generalized linear mixed effects model, applied to the VHF data, a clear pattern in temporal foraging behaviour emerged. In general, females were more likely to be on a foraging trip during the morning and midday hours, with the probability of males being on a foraging trip increasing towards late afternoon. These results provide insight into sex-specific behaviour in a monomorphic seabird, suggesting a marginal degree of spatial segregation, but provide the first support for sex-related temporal foraging segregation in gannets. Such separation could potentially reflect resource partitioning. In addition, synchronized foraging may also carry benefits in terms of chick provisioning and nest defence.

KEY WORDS: Foraging segregation · Foraging distributions · Time-activity budgets · Resource partitioning · Sulidae

INTRODUCTION

Understanding differences in resource utilisation amongst individuals is central to the study of ecology (Pianka 1969, Polito et al. 2015). In this respect, segregation patterns may occur at both the community (Weiss et al. 2009, Cáceres & Machado 2013, Méndez-Fernandez et al. 2013) and population level (Masello et al. 2010, Wakefield et al. 2013). Such segregation has often been attributed to the role of resource or niche partitioning in reducing inter- or intraspecific competition (Grémillet et al. 2004, Cherel et al. 2008, Weiss et al. 2009, Masello et al. 2010, Wakefield et al. 2013).

Gender-based differences in resource utilisation have been well studied across various taxa (Selander 1966, Encarnacao 2012, Leung et al. 2012, Levin et al. 2013, Drago et al. 2015). Amongst seabirds, sex-specific differences in foraging distribution and diet are common, particularly in sexually dimorphic species (Gilardi 1992, Bearhop et al. 2006, Weimerskirch et al. 2009). This is often thought to be linked to differential abilities and size-related competitive advantages of one sex over the other (González-Solís et al. 2000,

Lewis et al. 2005). However, weakly dimorphic and non-dimorphic seabirds may also show sex-specific differences in foraging behaviour (Peck & Congdon 2006), spatial use (Pinet et al. 2012) and prey preferences (Elliott et al. 2010). In addition, temporal differences in foraging behaviour are also known to occur between females and males (e.g. Wanless et al. 1995, Cook et al. 2007, Harris et al. 2013), although this has largely been unexplored in monomorphic species. Despite the many documented cases of sex-specific segregation in seabirds, the underlying mechanisms remain poorly understood in both dimorphic and monomorphic species. However, current thinking suggests that sex-specific segregation may facilitate resource partitioning to reduce intraspecific competition (González-Solís et al. 2000, Elliott et al. 2010). Under these scenarios, it would be reasonable to expect elevated levels of resource partitioning during periods of diminished resource availability. However, as an alternative to segregation, individuals of both sexes could also increase the amount of effort invested into foraging during periods of low prey abundance (Angel et al. 2015). In addition, gender-based segregation could also result from displacement through competitive exclusion (Peck & Congdon 2006, Stauss et al. 2012) or may reflect sex-specific differences in nutritional requirements or parental investment strategies (Lewis et al. 2002, Welcker et al. 2009).

Our study species, the Cape gannet *Morus capensis*, is a monomorphic seabird endemic to the coast of southern Africa. The species breeds on 6 islands, 5 of which are located within the Benguela Upwelling Region off the west coast of southern Africa, whilst the sixth and eastern-most colony is located at Bird Island in Algoa Bay on the south coast of South Africa (Crawford et al. 1983, 2007). Currently, the species is listed as Vulnerable on the IUCN Red List (IUCN 2016). Care is shared by both parents throughout the breeding season (Nelson 2005). Cape gannets feed primarily on sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*, both of which are of commercial importance to the South African purse-seine fishery (Berruti et al. 1993, Adams & Klages 1999, Green et al. 2015a). Both the diet and foraging distribution of Cape gannets reflect variations in the distribution and availability of these prey species (Moseley et al. 2012, Green et al. 2015a,b). Sex-specific differences in foraging trip duration and distance have been documented for Cape gannets on the west coast, with females undertaking longer foraging trips than males (Mullers & Tinbergen 2009, Mullers & Navarro 2010). In addition, the foraging trip duration of females increased significantly towards the late stages of chick-

rearing at Bird Island (Rishworth et al. 2014b, Pistorius et al. 2015). However, there is currently no evidence for sex-specific differences in spatial distribution at sea, although this has been observed in both northern (Stauss et al. 2012, Cleasby et al. 2015) and Australasian gannets (Angel et al. 2016). Furthermore, temporal sex-specific foraging patterns have largely remained unexplored in gannets.

Understanding sex-related foraging segregation is important when managing species of conservation concern (Pinet et al. 2012, Stauss et al. 2012, Pichegru et al. 2013). Furthermore, with attention focussed on the use of seabirds as ocean sentinels (Cairns 1987, Le Corre & Jaquemet 2005, Piatt & Sydeman 2007), there is a clear need to understand how intrinsic factors such as sex influence foraging behaviour (e.g. Rishworth et al. 2014b). In this study, we aimed to determine whether sex-specific differences in foraging distribution and behaviour occur in Cape gannets breeding at Bird Island. Using GPS data from 2 consecutive years, we tested for sex-specific differences in foraging distribution. We further assessed whether males and females show temporal separation in their foraging activities using an extensive dataset on time-activity budgets obtained through an automated VHF-based monitoring system.

MATERIALS AND METHODS

Data collection

Data were collected at Bird Island (33° 50′ 26″ S, 26° 17′ 10″ E), Algoa Bay, South Africa, over 2 consecutive years (2011/12 and 2012/13) during the Cape gannet breeding period. During each year, a total of 40 and 39 respective adult Cape gannets attending small chicks were fitted with GPS loggers weighing 39 g (I-gotU, Mobile Action, or CatLog-S, G117) (Green et al. 2015b). Following nest change-overs, the departing partner was captured using a 3 m pole with a crook on the end, after which the GPS unit was attached to the base of the central tail feathers using waterproof Tesa® tape. Each individual was tracked over a single foraging trip. Nests were monitored at hourly intervals between sunrise and sunset until the individual returned, after which it was captured and the device removed. Handling time was no longer than 7 min. In 2011/12, the devices were programmed to record positions at 10 s intervals when speed exceeded 10 km h^{-1}, otherwise every 5 s, whilst in 2012/13, fixes were recorded every 10 s irrespective of speed. In addition, a total of 39 individuals from 20

nests and 56 individuals from 28 nests were captured in 2011/12 and 2012/13, respectively, and fitted with VHF transmitters (NTQB-6-2; Lotek Wireless). The VHF transmitters weighed 4.5 g and were attached to PVC leg rings (Rishworth et al. 2014c). When birds were at their nests, a coded signal was transmitted every 39–40 s to a fixed receiver station (DataSika-C5, BioTrack) on the island. These signals were recorded for each individual as a unique identity code, date and time stamp. For a total of 20 individuals (11 females, 9 males), VHF transmitters continued to transmit a signal into a second breeding season. These data were included in our analyses, allowing for a third year (2013/14) of VHF data collection. Concerns have been raised regarding the negative effects of handling and attaching devices to seabirds (Durant et al. 2009, Evans 2012, Vandenabeele et al. 2012). However, previous studies of a similar nature reported no adverse effects associated with the above-mentioned activities (Grémillet et al. 2004, Pichegru et al. 2007, Rishworth et al. 2014c).

In addition to the attachment of devices, body mass (to the nearest 25 g), culmen length (to the nearest 0.1 mm) and wing cord length (to the nearest 1 mm) of all handled birds were recorded. Adult body condition was calculated as body mass over wing cord length (Lewis et al. 2006). Breast feathers were collected from all birds fitted with devices and used to determine sex by means of genetic analyses, following the Chelex® extraction method (see Rishworth et al. 2014a for further details). Chicks of all equipped birds were removed from their nests, and mass, wing cord length and culmen length were measured. This lasted no longer than 5 min, and all chicks were safely returned to their nest. Chick age at the time of GPS or VHF deployment on the adult was calculated following Mullers et al. (2009): chick age (days) = $\ln[(89.782b/6.156b)/0.086] + 0.5$ (when wing cord length was <40 mm) or chick age (days) = $1.395 - \ln[\ln(588.8/w)/0.0264] + 0.5$ (when wing cord was >40 mm), where b and w represent culmen and wing cord length (mm), respectively.

Data processing and statistical analysis

GPS data were inspected in ArcMap 10.3, and all points at the colony were removed. Following this, all further processing and analyses of tracking data were conducted in R (R Core Team 2015). Irregular fix frequencies were corrected by regularising all tracks to 10 s intervals by means of linear interpolation using the package 'adehabitatLT' (Calenge 2006).

Summary statistics representative of foraging effort were derived from GPS data. Total distance travelled, maximum distance from the colony, trip duration and mean flight speed were calculated for each track using the 'geosphere' package (Hijmans 2015). Activities of the Cape gannets at sea were considered to be flying, sitting on the water or foraging. Flying was identified as all fixes corresponding to speeds greater than 10 km h^{-1}. When speed was less than 10 km h^{-1}, birds were assumed to be sitting on the water (Grémillet et al. 2004, Mullers & Navarro 2010, Green et al. 2015b). We used area-restricted search (ARS) as a proxy for the identification of foraging areas (Kareiva & Odell 1987). To reduce the potential effect of birds sitting on the water on the identification of ARS, we removed all points with speeds of less than 10 km h^{-1}. Positions of ARS were isolated using a path straightness index (Batschelet 1981) calculated as the ratio between displacement between the first and last point over 4 fixes and the cumulative distance covered over these 4 fixes (Zavalaga et al. 2011, Green et al. 2015b). Straightness values lower than 0.3 were considered to represent foraging behaviour (Mullers & Navarro 2010, Green et al. 2015b). Possible feeding events associated with gannets tracking fishing vessels and foraging on discards could not be accounted for using this approach. However, recent diet studies suggest that fishery discards contribute only a small proportion to the diet of Cape gannets at Bird Island (Green et al. 2015a). Once ARS locations were identified, the mean and maximum distances from the colony were calculated. Furthermore, the proportion of time allocated to flying, sitting on the water and foraging were computed.

Spatial distributions of male and female Cape gannets in each respective year were computed using a kernel home range analysis in the 'adehabitatHR' package (Calenge 2006) with the ad hoc method as a smoothing parameter and a grid cell size of 200 m^2. Home ranges were computed using all locations of the GPS track. To account for different sample sizes between sexes and years, 18 GPS tracks for each sex in each year were randomly selected. Furthermore, incomplete GPS tracks were also included to reduce any bias of including only shorter, complete trips during 2011/12. Home ranges were represented as the 95% (total range) and 50% (core activity areas) volume contours, and subsequently the areas of each volume contour were calculated. To quantify the amount of overlap between females and males in each year, a utilisation distribution overlap index (UDOI) was used (Fieberg & Kochanny 2005).

Data downloaded from the VHF receiver were processed using a purpose-built interface (Y. Tremblay unpubl.) in MATLAB (R2011a, MathWorks) and converted to trip durations at a 10 min resolution (Rishworth et al. 2014c). To aid interpretation of temporal features, data were further grouped to hourly time stamps, and a binomial response variable was coded to indicate whether the bird was at the nest (0) or on a foraging trip (1). All data included for the purpose of this study were limited to the breeding period, and specifically to the guard-phase, when chicks were younger than 50 d. Chick age for birds monitored over consecutive years was calculated based upon hatching dates inferred from the clear shift in parent nest attendance patterns between incubation and brooding (Pistorius et al. 2015).

All data were tested for normality using Shapiro-Wilk's test. Morphometric measurements and body condition were normally distributed and were compared between males and females using Student′s 2-sample t-tests. Summary statistics derived from GPS data were each included into a linear model, with predictor variables of sex, year and the interaction of sex with year. All summary statistics, with the exception of time allocation parameters, were skewed and were therefore log-transformed before being incorporated into the model. In general, only complete GPS tracks were included into the models. However, for ARS distances, both complete and incomplete tracks were included into the model to reduce any potential bias associated with including only complete (shorter duration) tracks. Residuals for all linear models appeared normally distributed. The probability of birds being at the nest or on a foraging trip, derived from VHF data, was modelled using a binomial generalized linear mixed effects modelling (GLMM) framework using the 'lme4′ package (Bates et al. 2015). The model included sex, year, chick age, time (per hour) and the interaction between sex and time (per hour) as predictor effects. Individual identification, nested within nest site, was included as a random effect to account for repeated measures per individual and per breeding pair as both partners of each breeding pair were sampled (Zuur et al. 2009). A significance level of $\alpha = 0.05$ was assumed, and all results are presented as mean ± standard error (SE), unless stated otherwise.

RESULTS

A total of 79 GPS tracks (43 female and 36 male) were collected over the study period (see Table S1 in the Supplement at www.int-res.com/articles/suppl/ m579p157_supp.pdf). Of these, 40 were collected during the first year, but unfortunately 18 of these tracks were incomplete as a result of battery failure before completion of the trip (likely resulting from the high fix rate at which the devices were programmed). The VHF receiver station at Bird Island recorded a total of 3133 foraging trips (1598 female and 1535 male) from 95 individuals (47 female and 48 male) rearing chicks younger than 50 d over the study period (Table S2). A comparison of morphometric measurements obtained from all handled birds (n = 174) revealed no significant sex-linked differences in adult mass ($t_{2, 0.05} = -0.12$, p = 0.9), wing cord length ($t_{2, 0.05} = -0.01$, p = 0.99) and body condition ($t_{2, 0.05} = -0.11$, p = 0.91). However, a significant difference in culmen length was apparent ($t_{2, 0.05} = 5.2$, p < 0.001), with average culmen length of males being 2.42 mm longer than that of females.

Sex-specific foraging effort and spatial distribution

Total distance travelled, maximum distance from the colony and foraging trip duration were best predicted by year and an interaction between sex and year (Table 1, Table S3). Males, on average, travelled further and remained at sea for longer than females in 2011/12, whilst the opposite trend was evident in 2012/13 (Table 1). Females showed a clear annual difference in foraging trip distance and duration, undertaking longer foraging trips in 2012/13, whereas the foraging trips of males were similar in distance and duration between the 2 years. Flight speed was not affected by any of the 3 predictor variables, with birds, on average, travelling at speeds ranging from 42 to 45 km h^{-1} (Table 1).

Home ranges of female and male Cape gannets covered an area of 12 798 and 12 103 km^2, respectively, in 2011/12. The sexes showed a high degree of overlap (UDOI: 0.79) in their total range (95% contours), while core activity areas (50% contours) overlapped considerably less (UDOI: 0.12). Comparatively, the home range of females was noticeably larger in 2012/13 (18 841 km^2), whilst the home range of males remained similar in size to the previous year (11 153 km^2) (Fig. 1). Evident was that both the total and core activity areas of females extended further west than that of males in 2012/13 (Fig. 1). However, barring this extension, there was still a substantial degree of overlap in the total range of females and males (UDOI: 0.76). Similar to the previous year, females and males showed a lower degree of overlap in their core activity areas (UDOI: 0.14). The mean and max-

Table 1. Summary statistics (mean ± SE, range in parentheses) of female and male Cape gannet *Morus capensis* foraging trips during 2011/12 and 2012/13. The significance of each fixed effect used in the linear model is indicated—non-significant (ns) $p \geq 0.05$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Sample size (n) = 10 or 19 and 12 or 18 for females and males, respectively, for 2011/12 and 2012/13 for all trip parameters except mean and maximum foraging distances, where n = 22 or 21 and 18 or 18, respectively. ARS: area-restricted search

| Trip parameter | 2011/12 | | 2012/13 | | Significance | | |
	Females	Males	Females	Males	Sex	Year	Sex: Year
Total distance (km)	174.8±28.9 (79.3–361.3)	313.3±57.6 (59.4–655.1)	397.7±50.1 (111.9–861.3)	293.7±38.5 (107.7–644.9)	ns	**	*
Maximum distance (km)	45.8±5.9 (23.5–75.6)	96.3±18.7 (15.4–201.2)	117.9±17.5 (26.9–243.1)	77.2±12.6 (22.9–183.2)	ns	**	*
Duration (h)	10.3±2.5 (2.8–27.5)	20.7±4.4 (4.0–50.9)	25.3±2.6 (7.5–53.0)	19.9±2.4 (5.3–46.6)	*	***	**
Time flying (%)	43.3±4.7 (19.5–64.0)	34.5±3.1 (23.3–55.5)	31.4±1.5 (22.7–43.4)	31.7±1.9 (21.9–46.5)	*	**	ns
Time sitting on the water (%)	56.2±4.8 (35.2–79.8)	65.2±3.1 (44.2–76.5)	68.2±1.5 (56.4–77.0)	67.8±1.9 (53.1–77.0)	*	**	ns
Time associated with ARS (%)	0.5±0.1 (0.2–1.0)	0.3±0.1 (0.1–0.7)	0.4±0.04 (0.2–0.8)	0.5±0.1 (0.2–1.2)	*	ns	**
Mean flight speed (km h^{-1})	43.8±1.0 (39.2–47.1)	44.7±1.4 (38.1–56.8)	43.4±1.4 (34.5–59.9)	42.0±0.9 (35.4–52.9)	ns	ns	ns
Mean foraging distance (km)	67.4±10.8 (16.4–220.4)	63.5±9.4 (11.5–179.5)	89.3±14.2 (13.1–200.2)	55.6±10.4 (15.3–146.9)	ns	ns	ns
Maximum foraging distance (km)	87.7±12.3 (22.2–239.8)	87.8±13.1 (12.9–197.5)	120.2±17.8 (26.3–270.6)	73.6±12.4 (22.1–181.5)	ns	ns	ns

imum distances of ARS patches from the colony were similar for females and males in 2011/12 (Table 1, Fig. 2). During the second year, ARS patches of females extended beyond that of males, particularly in the area to the west of Cape Recife (Table 1, Fig. 2). Despite this, there was no significance in the effect of sex, year and the interaction between these on the mean and maximum foraging distances (Table 1).

Sex-specific differences in at-sea time-activity budgets

The proportion of time spent flying and sitting on the water during a foraging trip was influenced by

Fig. 1. Kernel home ranges of female (red) and male (blue) Cape gannets *Morus capensis* in (a) 2011/12 and (b) 2012/13 at Bird Island, Algoa Bay, South Africa. Both 95% (solid lines) and 50% (solid filled kernels) volume contours are represented for kernel home ranges. The red and blue striped area indicates the overlap of female and male core (50%) foraging areas. Bird Island is indicated by a yellow star. Sample sizes for each year consisted of 18 individuals randomly selected per sex
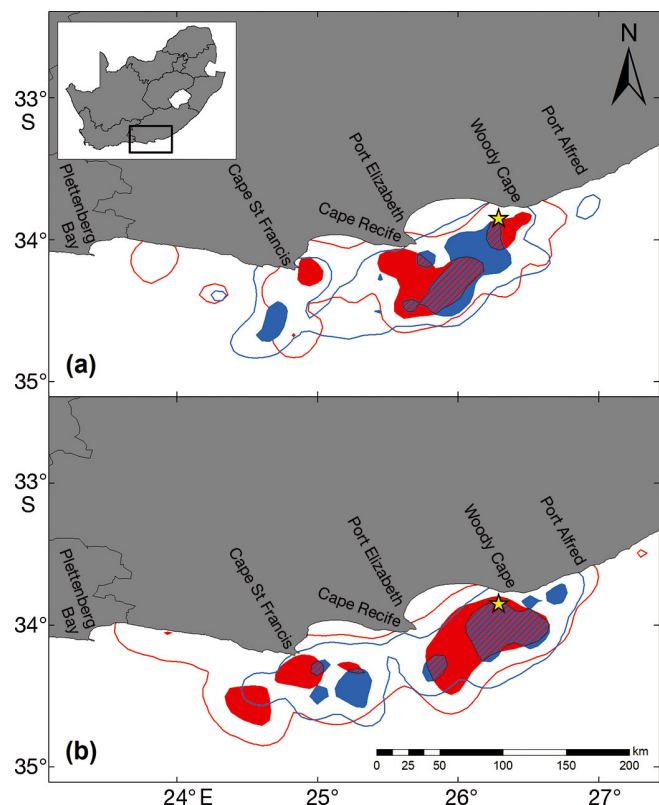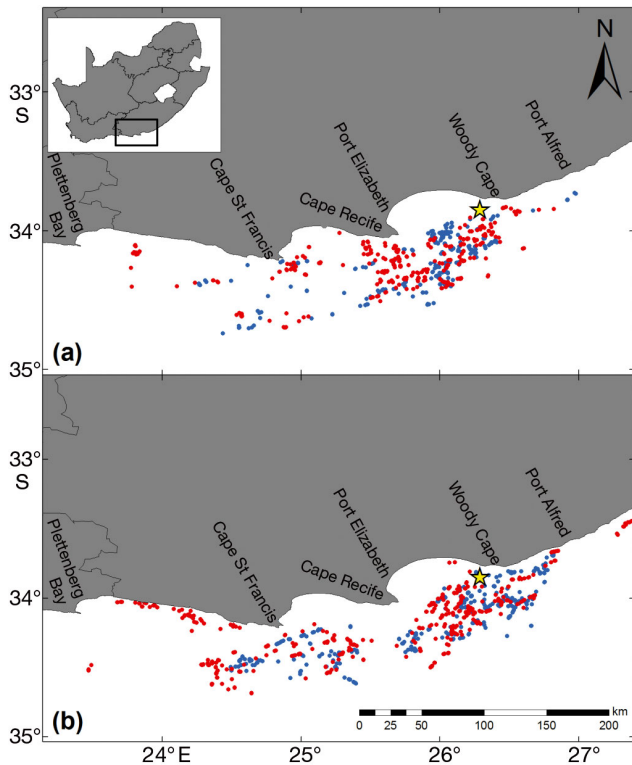
Fig. 2. Locations of area-restricted search (ARS) for female (red) and male (blue) Cape gannets *Morus capensis* in (a) 2011/12 and (b) 2012/13 at Bird Island, Algoa Bay, South Africa. Bird Island is indicated by a yellow star. Sample sizes for 2011/12 are 22 females and 18 males. Sample sizes for 2012/13 are 21 females and 18 males

sex and year (Table 1, Table S3). Birds spent more time flying and less time sitting on the water in 2011/12 compared to 2012/13. The effect of sex was most apparent during the first year, where males spent a greater proportion of time sitting on the water and a lower proportion of time flying than females. In comparison, the proportion of time allocated to these respective activities was similar for males and females in 2012/13. The proportion of the foraging trip associated with ARS was best predicted by sex and sex interacting with year (Table 1). Again, the effect of sex was more apparent in 2011/12, as females allocated a greater proportion of the trip to ARS, whilst this was similar for males and females in 2012/13.

Sex-specific temporal foraging patterns

The probability of birds being on a foraging trip was significantly affected by the time of day and sex interacting with the time of day (Table 2, Fig. 3a). In general, all birds were more likely to be at sea during

daylight hours (Fig. 3a). However, females were more likely to be at sea during the morning to midday hours (07:00–14:00 h), while males were more likely to be at sea during the late afternoon (Fig. 3). Males also showed a greater tendency to be at sea during nighttime hours (Fig. 3). Chick age had an effect on the probability of being on a foraging trip, as birds with older chicks were more likely to be away from the nest (Table 2). An inter-annual effect was also apparent, in that birds spent less time at sea in 2012/13 than in 2011/12 (Table 2)

DISCUSSION

The present study investigated sex-specific foraging segregation in a largely monomorphic species, the Cape gannet *Morus capensis*, over 2 consecutive years. A marginal degree of spatial segregation was apparent during the second year, with the foraging range of females extending well beyond that of males. In addition, clear differences in the timing of foraging bouts were evident between females and males. This study therefore identified a degree of sex-specific foraging in a monomorphic seabird, and provides the first account of temporal segregation in the foraging behaviour of gannets.

Sex-specific foraging effort and spatial distribution

Differences in foraging effort between sexes have been documented previously in Cape gannets (Mullers & Navarro 2010, Rishworth et al. 2014b). The results of the present study indicated that such differences may vary between years as females travelled further than males only during the second year. This could,

Table 2. Binomial generalized linear mixed effects model of male and female Cape gannet *Morus capensis* foraging trip probability as a function of sex, time of day (1 h bins), the interaction between sex and time of day, chick age and year. Coefficients (C), test statistics (z) and significance (p) are indicated. M: coefficients reflecting male behaviour

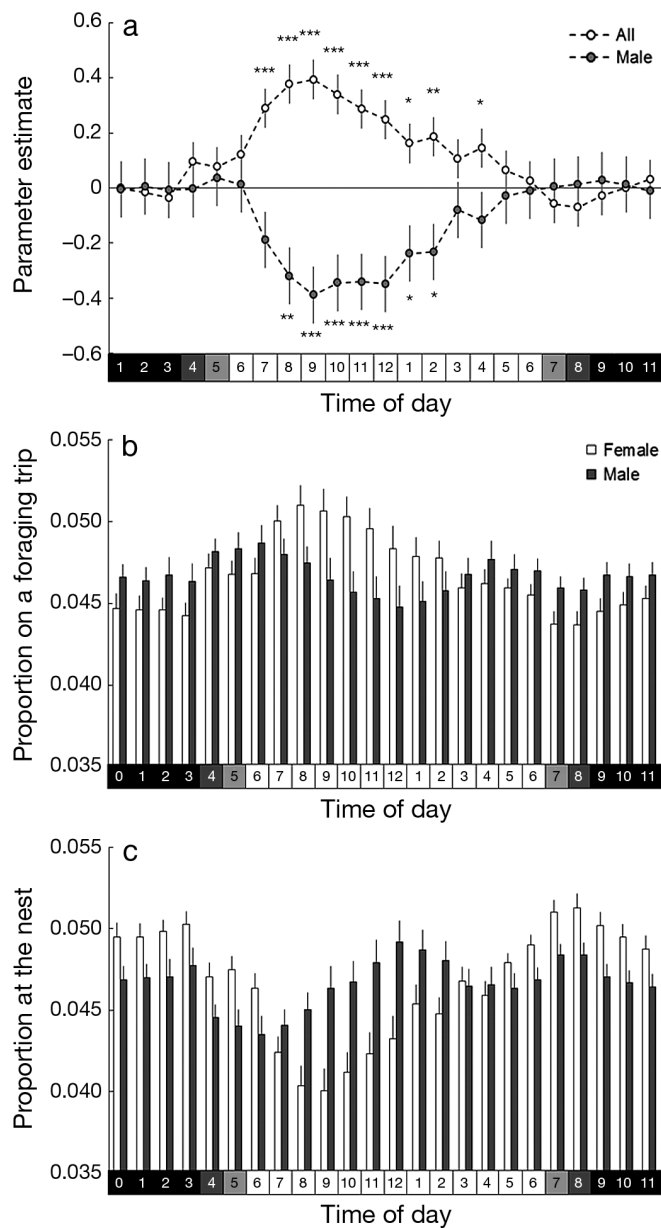| Predictor variable	C (SE)	z	p
Sex_M	−0.05 (0.15)	−0.32	0.75
Time	Refer to Fig. 3		
Sex_M:Time	Refer to Fig. 3		
Chick age	0.02 (0.00)	28.20	<0.001
Year_2012/13	−0.17 (0.07)	−2.56	<0.05
Year_2013/14	0.14 (0.07)	1.88	0.06

Fig. 3. (a) Probability of Cape gannets *Morus capensis* being on a foraging trip in relation to the time of day indicated for all birds and males only as obtained from the binomial generalized linear mixed effects model. The significance of time of day is indicated as: *p < 0.05, **p < 0.01, ***p < 0.001. Also shown are the proportions of female and male Cape gannets (b) on a foraging trip or (c) at the nest, in relation to time of day

however, be an artefact of using only complete tracks, which might have biased the results towards shorter forging trips, particularly for females, in 2011/12. Indeed, no significant differences in the distances of ARS (which included both complete and incomplete trips) were apparent between the 2 years for both sexes, although on average, females did appear to

forage slightly further from the colony than males during the second year.

We noted a westward propagation in the foraging range of females, which extended beyond that of males, in 2012/13 (Fig. 1b). Home range analysis is sensitive to sample size and the variation in individual contribution to the data (Soanes et al. 2013). As such, the apparent extension in the foraging range of females in 2011/12 may well have been caused by 1 or 2 females which extended their range. Indeed, only 2 females extended their foraging activity to the area east of Plettenberg Bay. However, at least 4 more individual females extended their range beyond Cape St Francis, suggesting that 33% of females extended their foraging distributions (see Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m579p157_suppl.pdf). In comparison, only 2 males (11%) foraged in the area west of Cape St Francis, while the remainder of male foraging activity was limited to the east of this region (Figs. S1 & S2). Therefore, the results suggest that, although subtle, there was a tendency for females to increase their range in 2012/13. Green et al. (2015b) identified a progressive westward shift in the foraging distribution of Cape gannets (without sex differentiation) at Bird Island during this year which appeared to be driven by relatively low prey biomass. The results of the present study indicate that this may have been a sex-specific response, whereby only females were largely responsible for the observed range shift, with little spatial adjustment observed for males. Interestingly, Mullers & Tinbergen (2009) also found an almost immediate increase in foraging trip durations of female Cape gannets in response to reduced food availability, whereas the increase in trip duration of males lagged behind. Inter-annual variability in the overlap of female and male home ranges has also been documented in northern gannets (Cleasby et al. 2015).

During periods of resource limitation, changes in foraging behaviour may alleviate the effects of increased levels of competition amongst conspecifics (Lewis et al. 2001). Individuals foraging further from the colony could avoid competition and gain access to higher densities of profitable prey resources (Ropert-Coudert et al. 2004). Under these conditions, sex-specific differences in foraging behaviour and diet may reflect niche and/or risk partitioning strategies to reduce intraspecific competition and ensure adequate levels of chick provisioning (Elliott et al. 2010, Castillo-Guerrero & Mellink 2011, Rishworth et al. 2014b). However, barring the westward extension of the female foraging range in 2012/13, foraging

ranges were not mutually exclusive between sexes. This suggests that competition is an unlikely driving force underlying the apparent segregation (Lewis et al. 2002). It is possible that a few females may have been tracking the contraction of high-quality prey species in an attempt to meet the greater energetic requirements associated with an energy deficit carried over from egg production (Lewis et al. 2002, Catry et al. 2009, Pinet et al. 2012, Machovsky-Capuska et al. 2016). A range shift in response to nutritional requirements could also imply sex-specific differences in diet (e.g. Stauss et al. 2012), but this has not previously been apparent in Cape gannets (Mullers & Navarro 2010).

Sex-specific differences in at-sea time-activity budgets

Sex-specific differences in time-activity budgets have been assessed previously in gannets. In northern gannets, females spend a greater proportion of time sitting (resting) on water than males (Lewis et al. 2002). However, the same behaviour does not appear to be reflected in Australasian and Cape gannets (Mullers & Navarro 2010, Angel et al. 2016). We found a significant effect of sex on at-sea behaviour in that males appeared to allocate more time to sitting on the water and less time to flying and foraging than females. However, this was only true for the first year, as both sexes showed a remarkably similar pattern of time allocation in 2012/13. This may reflect a bias due to including only complete tracks in the calculation of time-activity budgets. The greater number of incomplete tracks (particularly for females) in 2011/12 resulted in a greater number of single-day foraging trips which would involve a greater proportion of flying in comparison to overnight trips when birds sit on the water at night. The present study did not consider sex-specific differences in diving behaviour, which has been documented in several sulids (Lewis et al. 2002, Weimerskirch et al. 2006, Zavalaga et al. 2007, Cleasby et al. 2015). Therefore, although at-sea time-activity budgets are probably similar, the foraging strategies of female and male Cape gannets may still differ, which warrants further investigation using detailed diving data.

Sex-specific temporal foraging patterns

Although largely unexplored in seabirds, sex-specific differences in the timing of foraging have been documented in several species of the blue-eyed shag species assemblage (Bernstein & Maxson 1984, Wanless et al. 1995, Kato et al. 1999, Cook et al. 2007, Harris et al. 2013). These temporal foraging differences between females and males are usually thought to reflect differences in prey type (Cook et al. 2007), or sex-specific roles in nest attendance, provisioning and defence (Harris et al. 2013). Additionally, temporal differences in foraging behaviour may also serve as a means of reducing intraspecific competition (Bernstein & Maxson 1984). We found that female Cape gannets were more likely to be at sea between 07:00 and 14:00 h, whilst males were more likely to be at the nest during those hours. Males, in turn, were more likely than females to be foraging during the late afternoon hours and had a greater tendency to be at sea during night-time hours.

Sex-specific differences in the timing of foraging bouts could reflect a resource partitioning strategy between males and females (Bernstein & Maxson 1984). However, the timing of foraging bouts was not exclusively sex-specific, with both sexes, to some extent, still foraging throughout the day. Therefore, it is unlikely that competition is the sole driving force underlying the observed patterns of diurnal foraging. Additionally, sex-specific roles in nest defence and chick provisioning or protection could be implicated (Wanless & Harris 1986, Wojczulanis-Jakubas et al. 2009, Harris et al. 2013). Most seabirds exhibit biparental care, but the degree of care is not always shared equally between partners. Sex-specific differences in chick provisioning and nest attendance occur in a number of seabirds and appear to be linked to inter-specific reproductive strategies and the breeding stage (Harding et al. 2004, Thaxter et al. 2009, Elliott et al. 2010, Rishworth et al. 2014b). For example, prior to egg laying, male common guillemots *Uria aalge* spend more time at the nest site than females (possibly to guard nest sites and ensure paternity), whilst females invest more effort into chick feeding during the brooding period (Wanless & Harris 1986). Cape gannets do appear to show sex-specific differences in parental investment, as males visit the nest site more often, and for longer periods than females, and also make more frequent foraging trips as chicks age (Mullers & Tinbergen 2009, Rishworth et al. 2014b). Differences in the timing of foraging bouts may also reflect temporal patterns in the movement, aggregation and subsequently the availability of pelagic prey species. However, most studies have described diel variation in the movement patterns of pelagic fishes (Wilson et al. 1993, Zwolinski et al. 2007, Kaltenberg & Benoit-Bird 2009), with little

evidence of diurnal variation. Furthermore, quantifying the relationship between temporal segregation in foraging activity and diurnal patterns of prey accessibility would require detailed data on diving behaviour, which were not available for this study. In addition to sex-specific differences, we found that Cape gannets were more likely to be away from the nest, spending longer periods at sea, as chicks aged. These results are consistent with previous studies (Rishworth et al. 2014b, Pistorius et al. 2015), possibly reflecting a local depletion of prey as the breeding season progresses or changes. Alternatively, this could also reflect changes in the fasting and defence capabilities of older chicks, which may allow adults to travel further and remain away from the nest for longer periods.

CONCLUSION

We have provided evidence for sex-specific foraging in Cape gannets, but note that the observed spatial differences were not consistent over years. This highlights the dynamic nature of sexual foraging segregation and the importance of multi-year studies in this field of investigation. Furthermore, we identified a sex-specific pattern in the timing of foraging and nest-attendance bouts, a behaviour which has not been previously documented in gannets. Given the large size of the Cape gannet breeding colony at Bird Island, strategies of resource partitioning may be expected to avoid intraspecific competition, particularly when resources are limited (Lewis et al. 2001, Wakefield et al. 2013). Additional factors such as sex-specific differences in nutritional requirements as well as sex-specific roles in parental care and nest defence may also be implicated. This would warrant further investigation of potential sex-linked differences in diet as well as detailed data on diving behaviour (e.g. Lewis et al. 2002). Furthermore, previous studies have shown a substantial increase in foraging trip duration of females during the later stages of the breeding cycle (Rishworth et al. 2014b, Pistorius et al. 2015). Thus spatial differences between males and females as the breeding season progresses require further exploration.

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