



Intrinsic and extrinsic controls on foraging effort in an iconic Benguela seabird

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ABSTRACT

Seabirds are upper trophic level predators and as such reflect bottom-up changes in the conditions of their prey species through behavioural or demographic changes. This is especially useful in fisheries management where seabirds can act as biomonitors of commercially-important prey species, potentially providing an attractive, albeit coarse, supplementation to expensive and labour-intensive conventional stock surveys. The Cape gannet *Morus capensis* is an important predator of both sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* within the Benguela upwelling region, and has been shown to be a useful biomonitor of these fish stocks. A recently-developed automated monitoring system that measures foraging trip durations (a reflection of foraging effort and prey availability) in Cape gannets using VHF technology was used in this study to explore a range of intrinsic and extrinsic drivers of foraging effort that potentially need to be accounted for when relating foraging effort to availability of prey resources. Data from three seasons (2011/2012, 2012/2013 and 2013/2014) representing 5470 foraging trips from 50 chick-provisioning pairs were used for this purpose. Using a linear mixed-effects modelling approach, Cape gannet foraging trip behaviour was shown to be influenced by chick age, parent sex, meteorological conditions (barometric pressure, rainfall and wind) and ambient light conditions. These factors ideally need to be accounted for when foraging effort in seabirds is used as a proxy for prey availability.

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1. Introduction

Global climate change and increasing fisheries pressures present an escalating threat to the health and sustainability of marine ecosystems (Hoegh-Guldberg and Bruno, 2010; Poloczanska et al., 2013). Monitoring the state of marine systems is therefore important, yet often challenging because of the large spatial scales travelled by animals (Einoder, 2009), and the large costs involved in ocean surveys (Scott et al., 2006). As such, focusing research effort on select marine top predator species can be rewarding as their behavioural and demographic responses are often reflective of ecosystem changes, providing a simplistic and cost-effective monitoring tool (Durant et al., 2009).

Seabirds are particularly useful in this regard. Breeding colonially on land, individuals are monitored with relative ease and sample sizes can be large, an important consideration for the statistical and informative power of observations made (Furness and Camphuysen, 1997; Piatt et al., 2007). Seabirds often cover a broader area in their foraging distribution than what would be economically feasible in fisheries surveys (Einoder, 2009; Montevecchi, 1993; Sydeman et al., 2017) and thereby provide a continuous sample of prey availability in their foraging range

(Furness and Camphuysen, 1997). As seabirds often amplify changes in the lower trophic levels (Litzow and Piatt, 2003; Piatt et al., 2007), they make ideal indicators of the current health of ecosystems because of their apex trophic position (Durant et al., 2009; Einoder, 2009; Lyday et al., 2015; Scott et al., 2006).

Being long-lived species, seabirds maximise long-term rather than annual reproductive effort by favouring self-maintenance in years when conditions are poor (Monaghan et al., 1992). Seabirds buffer against prey that is patchily-distributed and sometimes unpredictably available (Weimerskirch, 2007) by having flexible time-activity budgets, spending less time foraging when prey is readily available (Burger and Piatt, 1990; Cairns, 1987; Litzow and Piatt, 2003). As such, foraging behaviour is sensitive to prey conditions and has been demonstrated to be a useful bioindicator proxy of the state of prey stocks (Cairns, 1987; Davoren, 2000; Jacobs et al., 2013; Litzow and Piatt, 2003; Montevecchi, 1993).

The Cape gannet *Morus capensis* has long been recognised as an important biomonitor of South African epipelagic fish stocks (Crawford et al., 1983; Lewis et al., 2006). This monomorphic, biparental seabird is restricted in its breeding distribution to six islands along the southern African coastline falling within the Benguela upwelling region (Crawford et al., 2007). The Cape gannet's diet primarily consists of sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* (Green et al.,

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2015b), both of which are commercially- and ecologically-important fish stocks (Coetzee et al., 2008; van der Lingen et al., 2005). Particularly in the Benguela upwelling ecosystem, Cape gannets and other top predators compete with purse-seine fisheries for these prey species (Okes et al., 2009; Pichegru et al., 2009). Several authors have demonstrated some degree of foraging flexibility in the Cape gannet and have linked this to changes in prey conditions (Mullers and Tinbergen, 2009; Pichegru et al., 2007; Ropert-Coudert et al., 2004). However, other factors such as wind (Grémillet et al., 2004; Pistorius et al., 2015) or sex-specific requirements (Bijleveld and Mullers, 2009; Rishworth et al., 2014b) can also influence the foraging behaviour of Cape gannets.

Recently, an automated system that uses long-term, very high frequency (VHF) transmitters has been demonstrated to continuously monitor Cape gannet behaviour in terms of nest attendance and foraging trip durations (Rishworth et al., 2014c). From a biomonitoring perspective, these data could be used to monitor prey conditions as foraging trip durations are a reflective proxy of foraging effort and prey availability (Jacobs et al., 2013; Litzow and Piatt, 2003; Rishworth et al., 2014c). Several studies have since demonstrated the important influence of intrinsic (parent sex and chick age) and extrinsic (wind and rainfall patterns) factors on foraging trip and nest attendance behaviour, and also how this transcends to chick growth and fledging success (Pistorius et al., 2015; Rishworth and Pistorius, 2015; Rishworth et al., 2014b). The aim of the current study was to further investigate the influence of a more-complete suite of intrinsic and extrinsic factors on foraging trip durations of Cape gannets during the breeding season, the period when seabirds are most-constrained in terms of self-maintenance and chick-provisioning trade-offs (Mullers and Tinbergen, 2009). This was achieved using previously published (Pistorius et al., 2015; Rishworth et al., 2014b) and additional data generated from the automated VHF monitoring system (Rishworth et al., 2014c).

2. Materials and methods

2.1. Study site

Fieldwork was conducted at Bird Island, Algoa Bay, South Africa (33° 50' S, 26° 17' E). Of the six islands that support Cape gannet populations (Crawford et al., 2007), Bird Island lies at the easternmost extent of their distribution, situated at the transition of the Agulhas current and the Benguela upwelling zone (Goschen et al., 2012). It also hosts the largest gannetry in the world, estimated at 90,000 breeding pairs (Crawford et al., 2007).

2.2. Data collection

Both partners of parents attending chicks (mean age: 22.4 ± 7.1 d) were equipped with a VHF transmitter (NTQB-6-2; Lotek Wireless Inc., Newmarket, Ontario, Canada) that transmits a unique, coded signal (every 39–40 s), which was recorded by a VHF receiver (DataSika-C5; Biotrack Ltd., Dorset, UK) when birds were at their nests or within range of the receiver (Rishworth et al., 2014c). The transmitters were attached to PVC leg-rings and together weighed ~10 g. No observable deleterious effects were recorded on chick growth, fledging success or parent behaviour following transmitter attachment (Rishworth et al., 2014c). A total of 20 and 30 Cape gannet pairs were equipped during the 2011/2012 and 2012/2013 breeding seasons, respectively. Two control transmitters were permanently located on the island to continuously establish receiver functionality and data were downloaded at approximately monthly intervals from December 2011 to September 2014. Ethics clearance was granted by the Research Ethics Committee at the Nelson Mandela Metropolitan University (reference: A10-SCI-ZOO-008).

Chick age at the time of transmitter attachment was determined by carefully removing the chick from its nest, measuring body morphometrics (mass, ± 10 g or ± 25 g; culmen length, ± 1 mm; forewing length,

± 1 mm), and then safely returning the chick within 3 min. Morphometric measurements were used to calculate chick age following Mullers and Tinbergen (2009). During subsequent seasons when chick age could not be back-calculated (nests were not disturbed the following season), known adult behavioural distinctions between incubation and chick provisioning were used to determine hatching date, as described by Pistorius et al. (2015). A few breast feathers were collected from each partner during transmitter deployment to genetically-determine parent sex (Rishworth et al., 2014a).

Available daylight was calculated as the time difference between sunrise and sunset. Moonlight was calculated as a scaled gradient based upon moon phase, with new moon representing no light (0%) and full moon maximum moonlight (100%). Meteorological parameters (atmospheric pressure, hPa; wind speed, m s^{-1} ; wind direction; rainfall, mm h^{-1}) were recorded on a permanent weather station on Bird Island and obtained from the South African Weather Service (SAWS).

2.3. Data analysis

All downloaded raw data from transmitters recorded at Bird Island were converted to foraging trip durations at a 10-minute resolution using a purpose-designed MatLab (MathWorks, Natick, MA, USA) software interface (Tremblay, unpubl.). Data were subsequently filtered to remove records from birds from which consistent signals were not received, as per Rishworth et al. (2014c).

Foraging trip durations of parents (provisioning chicks prior to fledging age: 1 to 100 d) were analysed in R (R Core Team, 2017) using linear mixed-effects models (LMMs) fitted using the 'nlme' package (Pinheiro et al., 2016). In accordance with previous studies, these data were log-transformed prior to analysis as they were right-skewed (Pistorius et al., 2015; Rishworth et al., 2014b). The following predictor variables were included in the LMM: parent sex, chick age, chick age interacting with parent sex, nest departure time (24 one-hour time bins), daylight hours, moon phase, atmospheric pressure (average on the day of nest departure), atmospheric pressure change (compared to the day prior to nest departure), rainfall, wind speed, wind direction and breeding season (nominal factor). Rainfall, wind speed and wind direction were averaged over the duration of each foraging trip, with wind direction (in degrees) being averaged using circular statistics ('circStats' package: Lund and Agostinelli, 2012), as in Pistorius et al. (2015). Independence amongst these predictor variables was tested using variance inflation factors ($\text{VIF} < 2$) and correlation coefficients ($r < 0.6$) to assess collinearity (Zuur et al., 2010; Zuur et al., 2009).

The optimal random component of the LMM, which accounts for repeated measures or individual variability amongst birds, was determined by fitting and comparing separate models fitted under restricted maximum-likelihood estimation (REML). These included a null model (no random effects), models with random intercepts per nest site, random intercepts per individual partner associated with each nest-site, and residual variability according to each nest-site strata ('varIdent'), fitted under the generalised least squares (GLS) framework. These models were then compared using log-likelihood ratio tests and Akaike information criterion (AIC) scores (Zuur et al., 2010; Zuur et al., 2009). The optimal fixed component was determined using a backwards-iteration model-selection approach based on AIC scores (Zuur et al., 2009). This fitted the full model under maximum likelihood estimation (ML), with all possible predictor variables incorporated, and compared this to separate models with single predictor terms omitted. The predictor term that most-substantially lowered the AIC score ($\Delta\text{AIC} \geq 2$) was then omitted from further analyses. This iteration procedure was repeated until no further single-term deletions improved the AIC score (Zuur et al., 2009). The most-parsimonious model was then refitted using REML estimation and residuals assessed for normality and homogeneity for all predictor variables, thereby meeting model assumptions for LMMs (Zuur et al., 2009). An a priori significance level of

$\alpha < 0.05$ was specified and all data are presented as mean \pm SD unless otherwise indicated.

3. Results

During the 2011/2012, 2012/2013 and 2013/2014 Cape gannet breeding seasons, a total of 5470 foraging trips were recorded in conjunction with all measured intrinsic and extrinsic parameters (971, 3343 and 1156 foraging trips, respectively for each of the seasons, of which 2717 were from females and 2753 from males).

The optimal random structure for the LMM of Cape gannet foraging trip duration incorporated random intercepts per individual partner associated with each nest-site, rather than as different residual variability structures per nest-site strata. All measured explanatory variables were independent from each other and were also all retained in the backwards model-selection iteration for the most-parsimonious model (Table 1). This model explained at least 20% of the residual variability in Cape gannet foraging trip duration (Table 1).

Foraging trip duration increased with chick age but this varied between sexes, with females extending their trips more than males when provisioning older chicks (Fig. 1; both $p < 0.001$, Table 1). However, irrespective of chick age, foraging trip duration was not significantly different between sexes ($p = 0.28$, Table 1). Foraging trip durations were significantly shorter during the 2012/2013 Cape gannet breeding season compared to during both the 2011/2012 and 2013/2014 seasons, with the former reflecting the longest foraging trips overall (Fig. 1; Table 1).

Cape gannets departing during the first few hours after sunrise generally had shorter trips compared to those leaving the nest later (Fig. 2a; $p < 0.001$, Table 1). Birds spent more time away on foraging trips when daylight length was relatively short ($p < 0.001$, Table 1), probably due to an increased tendency to stay at sea overnight. Nonetheless, a clear peak in activity was evident in terms of nest departure and arrival that tracked sunrise and sunset times, respectively (Fig. 3).

The amount of moonlight associated with moon phase was also included in the most-parsimonious model. Although this effect was not significant ($p = 0.178$, Table 1), in general when it was close on full

moon, Cape gannets had shorter foraging trips ($C = -0.06 \pm 0.04$, Table 1; Fig. 4), foraging on average for 20.2 ± 25.0 h during new moon compared to 18.1 ± 25.5 h during full moon.

All measured meteorological conditions had a significant effect on Cape gannet foraging trip durations (Table 1). Higher atmospheric pressures on the day of nest departure resulted in longer foraging trips ($p < 0.001$, Table 1; Fig. 5), while pressure increases compared to the day prior to departure resulted in shorter foraging trips ($p < 0.01$, Table 1). Foraging trips undertaken when there was much precipitation tended to be significantly shorter than those during which little to no rain fell ($p < 0.01$, Table 1). Stronger wind speeds resulted in shorter foraging trips ($p < 0.001$, Table 1) and this was confounded by the prevailing wind direction whereby foraging trips made during westerly to south-westerly conditions were significantly shorter than those during easterly conditions (Fig. 2b; $p < 0.001$, Table 1).

4. Discussion

Several studies have demonstrated that seabirds reflect changes in lower trophic levels and are thus often suitable as ecological indicators (Cairns, 1987; Durant et al., 2009; Harding et al., 2007; Lewison et al., 2012; Lyday et al., 2015; Montevecchi, 1993; Piatt et al., 2007). They can therefore potentially be employed in fisheries management, bearing in mind that signals can be complicated by species interactions or climate variability (Sydeman et al., 2017). For example, the breeding success of black-legged kittiwakes (*Rissa tridactyla*) has been used in sand lance (*Ammodytes marinus*) fisheries management in the North Sea, where the fishery closed during years of poor kittiwake breeding success, and reopened when this resource recovered (Frederiksen et al., 2008). Lyday et al. (2015) also demonstrated the close and predictable coupling between shearwater (*Puffinus* spp.) metrics and the catch of commercial fisheries species, for example dolphinfish (*Coryphaena hippurus*). Technological advances have driven the miniaturisation of attached data-loggers for seabirds (Ropert-Coudert and Wilson, 2005; Wilson and Vandenabeele, 2012), and these can now be deployed for long periods with little or no negative effects (Rishworth et al., 2014c). Their use can therefore be incorporated into monitoring schemes of seabird behaviour that are designed to provide information relevant to ecosystem-based management (Einoder, 2009; Le Maho et al., 1993; Montevecchi, 1993; Piatt et al., 2007). The method of leg-ring attached VHF transmitters used in this study clearly does not negatively impact Cape gannets and is therefore suitable for long-term or inter-seasonal monitoring schemes (Rishworth et al., 2014c). Furthermore, foraging effort, which is reflective of prey availability (Burger and Piatt, 1990; Davoren, 2000; Litzow and Piatt, 2003), is strongly related to Cape gannet foraging trip duration (Rishworth et al., 2014c).

In order to use seabirds as environmental indicators or to aid fisheries management it is important to understand factors other than prey availability that also influence their behaviour. Based upon our most parsimonious model (Table 1), chick age and parental sex interacting with chick age as well as climate variability (wind and rain) influence foraging trip duration, as has recently been reported (Pistorius et al., 2015; Rishworth et al., 2014b).

Chick age clearly influenced Cape gannet behaviour, as also observed elsewhere (Mullers and Tinbergen, 2009), but this only becomes pronounced during the poorly-documented post-guard stage of chick provisioning (>50 d chick age) when adults start taking longer trips. The effect of chick age on foraging behaviour may reflect local prey depletion, which would be expected to drive longer foraging trips, during the later stages of the breeding season (Rishworth et al., 2014b). There also appears to be clear segregation in reproductive investment between male and female partners during this stage. Not only do females generally spend longer periods of time foraging at sea, but this is enhanced as the chick nears fledging, indicating that females may be using this period and strategy to replenish their investment during egg development by shifting chick provisioning responsibilities to the

Table 1

The most-parsimonious linear mixed-effects model fitted by REML estimation of Cape gannet foraging trip duration in relation to intrinsic (sex, chick age and the interaction of these) and extrinsic (moon phase, daylight duration, breeding season, atmospheric pressure, rainfall, wind conditions and time of departure) factors during three breeding seasons (2011/2012 to 2013/2014) at Bird Island, Algoa Bay, South Africa. The directional effect of each parameter (coefficient: C) as well as the test significance thereof are indicated. Coefficients for "Sex" and "Season" are reflective of males compared to females and the other two seasons compared to 2011/2012, respectively. Marginal and conditional R^2 values were 0.192 and 0.203, respectively (Nakagawa et al., 2013).

Parameter	df	C	(\pm SE)	t-Value	P
Intercept	1	-15.37	(\pm 4.31)	-3.6	<0.001
Sex ^{Male}	1	0.07	(\pm 0.06)	1.1	0.28
Chick age	1	0.01	(\pm 0.001)	8.0	<0.001
Sex ^{Male} :Chick age	1	-0.005	(\pm 0.001)	-4.3	<0.001
Departure time	23	see Fig. 2a		636.8 ^a	<0.001
Daylight	1	-0.33	(\pm 0.05)	-6.2	<0.001
Moon phase	1	-0.06	(\pm 0.04)	-1.3	0.18
Pressure	1	0.02	(\pm 0.004)	5.1	<0.001
Δ Pressure	1	-0.01	(\pm 0.004)	-2.7	<0.01
Rainfall	1	-0.10	(\pm 0.04)	-2.6	<0.01
Wind speed	1	-0.03	(\pm 0.01)	-5.2	<0.001
Wind direction	7	see Fig. 2b		94.4 ^a	<0.001
Season	2				
2012/2013		-0.18	(\pm 0.05)	-3.8	<0.001
2013/2014		-0.13	(\pm 0.05)	-2.4	<0.05

^a Test statistics for the "Wind direction" and "Departure time" parameters represent the log-likelihood ratio values for the comparisons of nested models with and without the respective parameters, fitted under ML estimation.

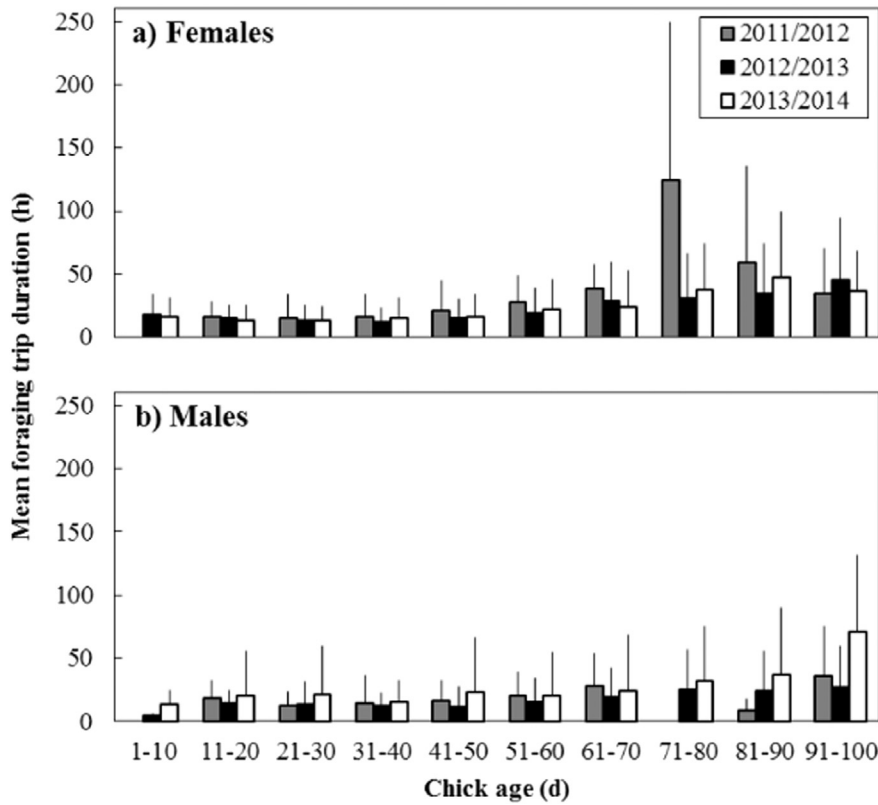


Fig. 1. Mean foraging trip durations (\pm SD) as a function of chick age of female (a) and male (b) Cape gannets during three breeding seasons (2011/2012, grey bars; 2012/2013, black bars; 2013/2014, white bars) at Bird Island, Algoa Bay, South Africa.

male (Rishworth et al., 2014b). Sex in itself is, however, not necessarily an important predictor of foraging trip duration, except when interacting with chick age (Table 1; Fig. 1). Females tended to spend longer periods on average away from the nest immediately post-hatching (hatching was calculated using the VHF activity patterns: see “Materials and Methods”) but spent similar amounts of time foraging compared to males when chicks were of an intermediate age (Fig. 1). Therefore, in addition to the period of post-guard provisioning when female Cape gannets seem to favour self-provisioning trips (Rishworth et al., 2014b), the first few days immediately post-hatching may serve a similar purpose.

Although atmospheric pressure is a tool used by meteorologists to forecast weather patterns, its direct relationship with wind and rainfall

patterns measured during this study was not collinear. It was therefore included in the LMM analysis of foraging trip duration and demonstrated that higher pressures resulted in significantly longer foraging trips (Table 1, Fig. 5). The ability to detect changing barometric pressure and thereby to anticipate future weather conditions is an evolutionary-selected means to improve on fitness through appropriate behavioural responses (Austin et al., 2014; Pellegrino et al., 2013). Birds have long been known to be able to detect changes in pressure, possibly through the inner ear paratympanic organ (von Bartheld, 1994), and this has often been contextualised around migratory strategies (Breuner et al., 2013; Kreithen and Keeton, 1974). Our data showed that breeding gannets responded to changing barometric pressure by altering their time at sea during foraging trips. The significance of this is unclear, but

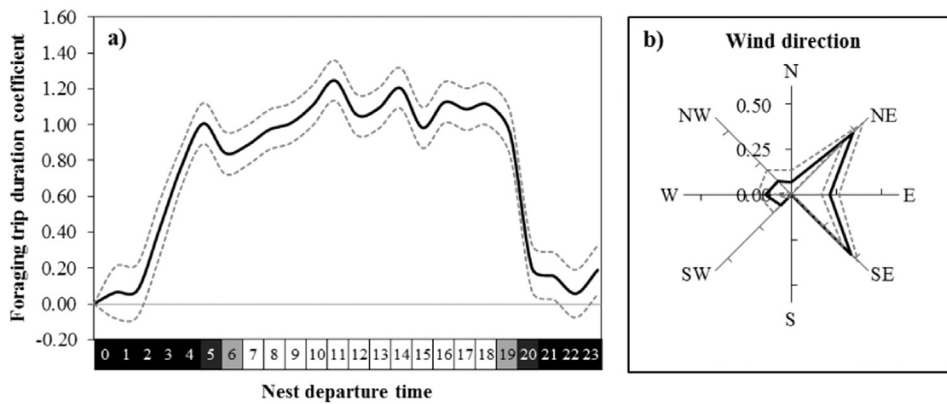


Fig. 2. Foraging trip duration coefficient estimates (dark lines) \pm SE (dotted lines) of nest departure time (a) and mean wind direction (b) (Table 1) of Cape gannets during three breeding seasons at Bird Island, Algoa Bay, South Africa. Time is modelled as 24 one-hour time bins (00:00 is the reference category) and wind according to eight prevailing directions (south is the reference category).

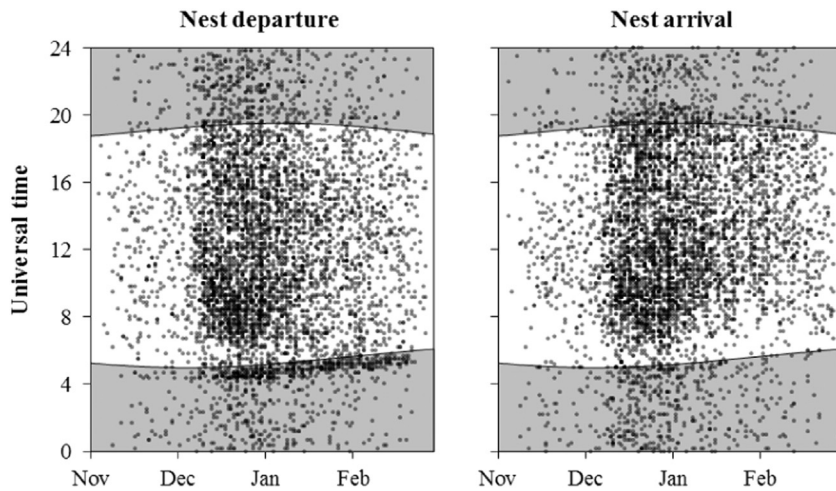


Fig. 3. Nest departure (left graph) and arrival (right graph) times for chick-provisioning adult Cape gannets equipped with VHF transmitters at Bird Island, Algoa Bay, South Africa during three breeding seasons (2011/2012 to 2013/2014). Sunrise and sunset times are indicated by the solid lines, with night hours being shaded.

it could be related to birds undertaking foraging trips closer to the island when low pressure systems are passing through to avoid being caught in storms far from the island.

Both wind and rainfall affected foraging trip durations of chick-provisioning adults, as previously demonstrated by Pistorius et al. (2015). Over and above strong winds resulting in relatively short foraging trips, probably due to wind-aided locomotion, wind direction strongly influenced foraging trip duration. Short trips were observed during westerly winds. As the primary foraging grounds of Cape gannets from Bird Island during the breeding seasons are located to the southwest of the island (Green et al., 2015a), the relatively short trips could be explained by birds taking advantage of tail winds when returning to the colony with a load of prey for provisioning chicks. Birds furthermore undertake shorter trips during rainy conditions, but also only spend brief periods at their nests when it is raining (Pistorius et al.,

2015), which consequently negatively affects chick survival and growth (Rishworth and Pistorius, 2015).

Further on meteorological influences, ambient light conditions also affected Cape gannets. Although Cape gannets are visual foragers (Ropert-Coudert et al., 2004), we found a surprising amount of nocturnal activity (Fig. 3). Moon phase, and the consequent amount of nocturnal light it emits, influenced Cape gannet foraging trip durations (Fig. 4). Birds had shorter overall foraging trips when the moon was brighter, likely because this enabled more efficient travel at night, which thereby resulted in birds reaching foraging grounds or their nests sooner. Sea-bird time-activity budget periodicity has elsewhere been shown to be dependent on the phase of the moon (Pinet et al., 2011).

Birds departing on foraging trips when there was more daylight available spent significantly shorter periods away from their nests (Table 1). Presumably the later in the day birds depart on foraging trips the lower the chances are that they will find adequate prey resources and return to the colony that same day. Lewis et al. (2004) demonstrated similar patterns in relation to daylight and time of nest departure (Fig. 2a) in boobies (*Sula* spp.), while also showing that

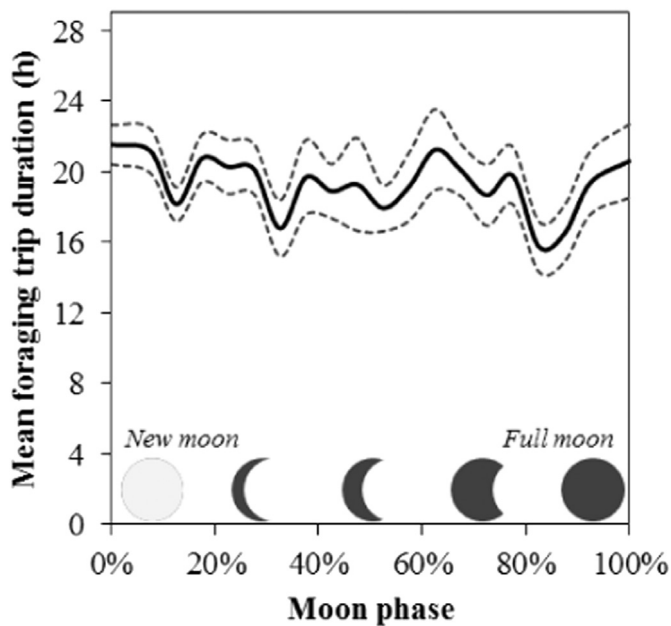


Fig. 4. Mean foraging trip duration (black line) \pm SE (dotted lines) of Cape gannets during three breeding seasons (2011 to 2014) at Bird Island, Algoa Bay, South Africa as a function of moon phase on the day of nest departure.

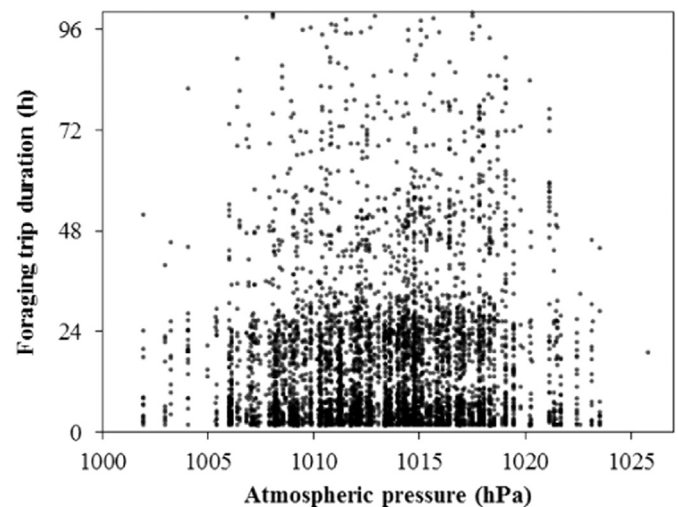


Fig. 5. Foraging trip durations of Cape gannets during three breeding seasons (2011 to 2014) at Bird Island, Algoa Bay, South Africa as a function of atmospheric pressure (hPa) during the day of nest departure. Trips shorter than 100 h (~98% of all recorded) are reflected.

parents tended to work harder, in terms of number of dives per foraging trip, when available daylight diminished.

Factors that have previously been shown to influence foraging trip durations of breeding Cape gannets (Pistorius et al., 2015; Rishworth et al., 2014b), together with additional influences highlighted in this study, (atmospheric pressure, available daylight and moon phase; Table 1), account for over 20% of residual variability in foraging trip durations. Although prey availability probably accounts for most of the remaining variability, other factors may also be important in governing foraging trip duration. Much recent work has demonstrated the importance of individual specialisation and patterns in behavioural decisions in seabirds (e.g. Patrick et al., 2014; Sommerfeld et al., 2013). A simple measure of individual or pair behaviour was used in this study (by accounting for unique residual variability structures per nest-site strata), but this did not feature in the most-parsimonious model. Nonetheless, further detailed descriptors of behavioural patterns demonstrated by individual Cape gannets, such as the well-documented regular alternation of self- and chick-provisioning foraging trips in albatrosses (e.g. Weimerskirch et al., 1997), may yet be an important variable to consider.

5. Conclusion

Estimates of the prey populations of seabirds, obtained through acoustic surveys and fisheries catch data, are essential if seabird proxies are to be accurately interpreted in relation to prey variability (Litzow et al., 2000; Monaghan, 1996). This is the next step which would need to be investigated in the Cape gannet: to what extent does prey availability relate to foraging trip duration, and how does this relationship change throughout the breeding season. This is not a simple task as it is not only prey availability but also prey type which is likely to affect Cape gannet behaviour. For instance, Mullers and Navarro (2010) showed that gannets foraging on fisheries discards had shorter foraging trips.

Faced with environmental change, phenotypic plasticity may restrict the suitability of seabirds as indicators as their range of responses may be increasing (Grémillet and Charmantier, 2010). Nevertheless, a number of seabird proxies have been shown to be a good reflection of prey state (Einoder, 2009; Furness and Camphuysen, 1997; Montevecchi, 1993) and that seabirds are useful candidates as ecological indicators (e.g. Lyday et al., 2015; Piatt et al., 2007). With the modern advancements in technology (Ropert-Coudert and Wilson, 2005; Wilson and Vandenebee, 2012), multitude of publicity and awareness campaigns for seabirds (Lewison et al., 2012), coupled with improvements in statistical techniques and modelling (Durant et al., 2009), we are now better equipped than ever to understand the dynamics of seabird-prey-fishery interactions.

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