

Protection and provisioning: the role of parental behaviour in terms of chick growth and survival in a pelagic seabird

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ABSTRACT: Long-lived organisms maximise lifetime reproductive output by shifting the negative effects of temporal environmental variability onto their offspring while maintaining adult survival. Amongst seabirds, chick growth and survival could be influenced by a range of factors, including prey delivery and parent behaviour as well as predation and exposure to adverse weather conditions. In this study, an automated method of recording adult Cape gannet *Morus capensis* time-activity budgets by means of new generation VHF technology was used to relate their behaviour to chick growth and survival at Bird Island, Algoa Bay, South Africa, across 2 breeding seasons (2011–2012 and 2012–2013). Using one of the most comprehensive datasets of breeding seabird foraging effort, we showed that, although chick growth was predominantly associated with age, parents which made shorter foraging trips clearly raised chicks which grew faster. Chick survival varied greatly between the 2 seasons (40 versus 97%), which was explained by different levels of nest non-attendance by parents. Chicks in the 2011–2012 season which were exposed to longer periods of non-attendance were particularly vulnerable to unseasonal storms and they were also more vulnerable to kelp gull *Larus dominicanus* predation while young. In contrast to Cape gannets in the declining west coast populations, chick survival at Bird Island was primarily related to parental protection rather than food provisioning rate, which probably reflects favourable foraging conditions along the southern coast of South Africa. This study highlights the importance of understanding the interplay between factors affecting chick growth and survival for the effective conservation of threatened seabird populations.

KEY WORDS: Automated monitoring · Cape gannet · Chick provisioning · Foraging effort · Parental roles · Survival · Time-activity budget · VHF

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INTRODUCTION

Life-history theory predicts that long-lived organisms maximise their lifetime fitness by prioritising self-maintenance over reproduction when conditions are unfavourable or resources scarce (Stearns 1989, Weimerskirch et al. 2001). While breeding, animals must adapt their behaviour to meet the requirements of their developing offspring, therefore placing limits on their foraging range, resource acquisition strategy, foraging duration and the time which parents can leave their progeny unattended (Humphreys et

al. 2006). Exceeding these limits (e.g. reduced provisioning or increased non-attendance) as a response to decreased prey availability or external pressures would be expected to result in negative effects on offspring growth and survival (Stearns 1989, Ronconi & Burger 2008). Consequently, adult survival in seabirds is relatively constant across variable prey availabilities, unless these are severely depleted (e.g. Harding et al. 2011), while chick survival and growth are more variable (Weimerskirch et al. 2001, Ronconi & Burger 2008). However, flexible time-activity budgets of seabirds can generally buffer against the

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effects of moderately scarce prey and thus maintain reproductive effort (Harding et al. 2007).

Amongst seabirds, chick growth and survival is generally closely associated with local prey availability (Piatt et al. 2007), with seabirds often abandoning their breeding attempt under poor prey conditions. This is well-demonstrated in black-legged kittiwakes *Rissa tridactyla* where tight coupling between breeding success and prey (sand lance *Ammodytes marinus*) availability informs and guides management on the state of fish stocks and temporal closure of the fishery (Frederiksen et al. 2008). Aspects of the prey themselves can affect chick growth and survival. For example, pigeon guillemot *Cepphus columba* chicks fed on nutrient-rich or larger prey tend to grow faster and have a higher chance of survival than those whose parents forage on a generalist diet of low-lipid demersal prey (Litzow et al. 2002).

In addition to being driven by prey availability, the allocation of resources to developing chicks rather than to self-maintenance (Weimerskirch et al. 1997) is influenced by environmental conditions such as sea-ice extent (Yoda & Ropert-Coudert 2007) or wind patterns (Weimerskirch et al. 2012). Furthermore, intraspecific variation in adult foraging behaviour may affect chick growth and survival. For example, the foraging ability and efficiency associated with adult body size influences chick growth and fledging mass in snow petrels *Pagodroma nivea* (Barbraud et al. 1999). Inter-colony differences in the allocation of provisioned resources to body mass also potentially drive differences in chick growth between populations despite similar prey conditions, as found in wedge-tailed shearwaters *Puffinus pacificus* (McDuie et al. 2013).

The Cape gannet *Morus capensis* was used as a model species in this study. This monomorphic seabird is a breeding endemic to southern Africa where it is restricted to 6 islands (Crawford et al. 2007). Its diet consists mostly of commercially important sardine *Sardinops sagax*, and anchovy *Engraulis encrasicolus* (Green et al. 2015). Cape gannets nest colonially, usually commencing breeding around August of each year. A single offspring is guarded by both parents from egg-laying until the chick is at least 3 wk old; thereafter the chick is periodically left unattended (Bijleveld & Mullers 2009, Rishworth et al. 2014b). At breeding locations on the west coast, local forage conditions largely determine chick survival and growth (Mullers et al. 2007, Mullers & Navarro 2010), with decreased prey availability resulting in increased chick starvation. Breeding success varies in Cape gannets but is around 60% on average (Green

& Pistorius 2013); however, it can be much lower when local prey availability is poor (2% at Malgas Island in the 2005–2006 season; Pichegru et al. 2010).

The Cape gannet is listed as 'Vulnerable' to extinction (IUCN 2015), largely due to population declines associated with commercial over-fishing and distributional shifts in its main prey, particularly amongst populations on southern Africa's west coast (Crawford et al. 2007). However, the south coast population at Bird Island, Algoa Bay, has either increased or been stable over the past few decades (Crawford et al. 2009). Annual survival amongst Cape gannets is generally high (approximately 85%), and birds are faithful to their nesting grounds (Pichegru et al. 2010, Distiller et al. 2012). Adults can maintain body condition, but not reproductive success, by supplementing their diet with fishery discards when natural prey is scarce (Mullers et al. 2009). Despite this association with the fishing industry, unlike many threatened seabirds (Lewison et al. 2012), they are not often caught as bycatch (e.g. Watkins et al. 2008).

As the population trend of Cape gannets seems to be largely driven by chick survival and consequent juvenile recruitment into adult colonies (Distiller et al. 2012), this study aimed to investigate the extent to which parent time-activity budgets affect chick growth and fledging success in Cape gannets. The following hypotheses were tested: (1) chick growth is inversely related to foraging trip duration/effort; (2) higher nest provisioning rates from both parents increase chick growth and fledging success; and (3) fledging success is positively related to levels of nest attendance. These were tested using data from an extensive, continuous set of parent time-activity budgets obtained by means of new generation automated VHF technology (Rishworth et al. 2014c).

MATERIALS AND METHODS

Data collection

Pairs of Cape gannets breeding on Bird Island, Algoa Bay (33° 50' S, 26° 17' E), from 20 nests in the 2011–2012 (10 to 15 December 2011) and 30 nests in the 2012–2013 breeding seasons (5 to 12 December 2012) were fitted with leg-ring-attached VHF transmitters (NTQB-6-2, Lotek Wireless) to automatically record their presence at the island (Rishworth et al. 2014c). These transmitted a coded signal every 39 to 40 s at 150.38 MHz which was recorded by a Yagi antenna attached to a 12 V solar-powered receiver (DataSika-C5, BioTrack) as a unique coded identity,

together with a date, time and signal strength, when the birds were on the island. Together with the leg-ring, transmitters weighed ~10 g, approximately 0.4% of an average Cape gannet's mass. Data from the VHF transmitters were downloaded on a monthly basis during the breeding season, with parent attendance patterns recorded until each chick either fledged or died.

All Cape gannets equipped with a VHF transmitter were attending a chick. At the time of transmitter deployment, adult body mass (to the nearest 25 g) and wing chord length (to the nearest 1 mm) were measured. A few breast feathers were also plucked to allow for subsequent DNA sexing of this monomorphic species through Chelex[®] extraction (Rishworth et al. 2014a). Chicks were carefully removed from their nests (between 08:00 and 10:00 h) at 4 to 5 d intervals for the periods 8 to 28 December and 27 January to 6 February 2011–2012 and 5 to 13 December and 15 to 27 January 2012–2013. Nest observations, adult VHF deployments and repeated chick weighing were unlikely to have affected chick growth or survival (Einoder et al. 2011, Rishworth et al. 2014c). Basic morphometric measurements were recorded from each chick: culmen length (to the nearest 0.1 mm), wing chord length and body mass (to the nearest 10 or 25 g). Each chick was safely returned to its nest within 3 min after removal. Chick measurements were taken prior to the attachment of parents' VHF transmitters. When the tarsus of each chick was sufficiently developed (at approximately 3 wk old), a unique coloured PVC leg-ring was fitted. Coinciding with growth measurement periods, any chick mortalities were recorded. During the visit to the island (22 March 2012 and 27 February 2013), when all chicks would have been >100 d old, the average age of fledging (Rishworth et al. 2014b), chick survival was assessed (absent chicks were assumed to have fledged, and all chick carcasses at the colony were inspected for PVC leg-rings).

Chick age was determined following Mullers et al. (2009): when wing chord length was <40 mm, $\text{age} = -\ln[(89.78 - b/6.15 \times b)/0.086] + 0.5$, and when wing chord length was >40 mm, $\text{age} = 1.395 - \ln[\ln(588.8/w)/0.0264] + 0.5$, where b is culmen length (in mm) and w is wing chord length (in mm).

Data analysis

Data downloaded from the VHF receiver were converted into trip durations using a purpose-built MatLab (R2011a; MathWorks) interface (Y. Tremblay un-

publ.). Data were imported at a 10 min resolution into MatLab. Other adult behavioural parameters including nest attendance duration, trip frequency per day (hereafter referred to as provisioning rate) and the duration of nest non-attendance (when both partners were absent from the nest) were also calculated.

Chick growth rate was calculated as the change in body mass per day. Each chick growth measurement was associated with mean values of all respective adult behavioural parameters during the time interval of that measurement. To account for partner behavioural interplay (Bijleveld & Mullers 2009, Rishworth et al. 2014b), maternal and paternal behavioural parameters were pooled as a single predictor variable. Chick growth was incorporated into a linear mixed-effects model (LMM; 'lmer' in the 'lme4' package) fitted by restricted maximum likelihood (REML) using R (R 2.15.1; R Foundation for Statistical Computing) with the following predictor variables: foraging trip duration, nest attendance duration, nest non-attendance duration, daily provisioning rate, adult body condition at the time of transmitter deployment (measured as forewing length over mass; Rishworth et al. 2014b) and chick age. Mixed-effects models have the advantage of being able to account for repeated measures using specified random effects (see below, Zuur et al. 2009).

The probability of chick survival to fledging was analysed by logistic regression using a generalised linear mixed-effects model (GLMM; 'glmer' in the 'lme4' package, with a binomial distribution and logit link specified) fitted by the Laplace approximation (Zuur et al. 2009). Chick age, the aforementioned adult behavioural parameters and adult body condition were used as predictors. Chick survival was modelled by combining data from both parents as well as for maternal and paternal data separately.

Seasonal effect was considered as a predictor in all models. To account for the potential effects of repeated measures, multi-level models were used for both chick growth (individual was specified as a random effect) and survival (progression into the breeding season [per 2 wk category] was specified as a random effect). Models incorporated only those fixed-effect predictor variables with low variance inflation factors (VIFs ≤ 3) in order to overcome the potential problem of collinearity (Zuur et al. 2009). Deviance information criterion (DIC) scores, a generalisation of Akaike's information criterion (AIC) which are more suitable for multi-level model comparisons when the number of observations in the data is not necessarily greater than the number of parameters in the models, were used for model

selection (Spiegelhalter et al. 2002). As for AIC, the model with the lowest DIC is selected, with $\Delta\text{DIC} \leq 2$ representing analogous models (Spiegelhalter et al. 2002). A pseudo- R^2 was calculated to estimate the variance explained by the fixed-effect predictors in each of the most parsimonious models (Nakagawa et al. 2013). The significance of the effect of predictor variables on chick growth and survival for the most parsimonious models were tested using F - or z -tests, respectively, using Satterthwaite's approximation for denominator degrees of freedom (ImerTest package in R; Kuznetsova et al. 2012). Age-specific growth rate was compared between 2 wk chick age categories from model slope coefficients for separate LMMs of each category. Differences in parent behavioural parameters respective to chick survival were additionally compared for each 2 wk chick age category using logistic regression models. A significance level of $\alpha = 0.05$ was used, and all results are presented as means \pm 95% CI of the mean.

RESULTS

In the 2011–2012 Cape gannet breeding season at Bird Island, 12 monitored nests failed (60%) compared to the 1 failed nest (3%) in 2012–2013. On average, the last measurement for those chicks that died during the first season was recorded at 52.8 ± 11.7 d. The 1 nest failure during the following season was at a chick age of 24 d. An average of 8 and 5 growth measurements were recorded from chicks that fledged and 3.7 ± 0.9 and 2 from those that died for both seasons, respectively (247 in total). Following a rainstorm during 1 to 5 February 2012, 5 chicks died (average age of last measurement: 74.3 ± 8.6 d), whereas the other 7 chicks died prior to the storm

(average age of last measurement: 37.4 ± 5.6 d). Initial chick age differed in the 2011–2012 breeding season compared to the following season (24.8 ± 2.7 versus 18.6 ± 2.6 d; $t_{(2,48)} = 3.14$; $p < 0.05$) as nest monitoring began 5 d earlier in the 2012–2013 season. A total of 4563 foraging trips and 4463 nest attendance bouts were recorded across the 2 breeding seasons from chick-provisioning parent Cape gannets (Rishworth et al. 2014b).

Chick growth

Chick growth was best predicted by chick age and adult foraging trip duration, although there was also support for nest attendance duration and nest non-attendance as important predictor variables (Table 1). Neither provisioning rate nor parental body condition were included in the most parsimonious models. There did not appear to be differences between the 2 seasons in terms of growth rates of chicks either ($p = 0.25$; Table 2).

Chick age had the greatest influence on growth rate ($p < 0.001$; Table 2). Body mass gain was at a maximum at 28 to 41 d following hatching (60.0 ± 7.6 g d⁻¹; $t_{(2,50)} = 10.49$; $p < 0.001$), thereafter decreasing and becoming negative prior to chicks reaching 100 d of age (Fig. 1). Additionally, parent trip duration (Fig. 2a) was inversely related to chick growth rate ($p < 0.01$; Table 2). Nest attendance and non-attendance duration were not significantly related to chick growth rate (both $p > 0.05$; Table 2, Fig. 2). Although not included in the most parsimonious model, provisioning rate appeared positively related to chick growth, especially for young chicks (Fig. 2). Residual errors for the most-parsimonious models (Models 1 to 4; Table 1) appeared to be normally distributed.

Table 1. Linear mixed-effects models of Cape gannet *Morus capensis* chick growth rate as a function of several predictor variables: chick age, adult foraging trip duration, nest attendance duration, nest non-attendance duration, provisioning rate and season (2011–2012 or 2012–2013). Deviance information criterion (DIC) scores and the number of parameters used in each model (np) are shown. Dots (•) indicate included predictor variables for each model

Model	Chick age	Nest attendance	Nest non-attendance	Provisioning rate	Trip duration	Season	np	DIC	ΔDIC
1	•				•		5	1933.6	0.0
2	•		•		•		6	1933.7	0.1
3	•	•	•		•		7	1934.4	0.8
4	•	•			•		6	1934.5	0.9
5	•		•		•	•	7	1937.8	4.2
6	•				•	•	6	1938.0	4.3

Table 2. Linear mixed-effects model (Model 3, Table 1; season included) fitted by restricted maximum likelihood of Cape gannet *Morus capensis* chick growth rate at Bird Island, Algoa Bay, South Africa, as a function of chick age and adult behavioural parameters. Coefficients (C) represent the directional effect of the predictors. Marginal $R^2 = 0.26$ (variance explained by fixed effects; Nakagawa et al. 2013).

Predictor effects were considered significant at $p < 0.05$

Predictor variable	df	Chick growth (g d^{-1})		
		C (SE)	F-value	p
Intercept	1	102.74 (13.33)	7.71	<0.001
Chick age	1	-0.64 (0.19)	3.35	<0.001
Trip duration	1	-1.10 (0.35)	3.17	<0.01
Nest attendance duration	1	-0.37 (0.68)	0.54	0.59
Nest non-attendance duration	1	-0.66 (0.62)	1.06	0.29
Season ^a	1	-7.62 (6.55)	1.16	0.25

^aCoefficient reflective of the 2011–2012 breeding season

Chick survival

Due to the contrast in chick mortality between seasons and high survival in the 2012–2013 season, chick survival was only modelled for the 2011–2012 season. When modelling the probability of survival to fledging, the most-parsimonious model included all of the predictor variables except adult body condition (Table 3).

As expected, and indicated by the positive coefficient of chick age in relation to survival for the most-parsimonious model, older chicks had a greater probability of survival to fledging ($p < 0.001$; Table 4). When combining behavioural data from both parents, chick age and nest non-attendance were the only significant predictors of chick survival ($p < 0.001$; Table 4).

Table 3. Generalised linear mixed-effect models for Cape gannet *Morus capensis* chick survival during the 2011–2012 breeding season as a function of chick age, nest attendance duration, nest non-attendance duration, provisioning rate and adult foraging trip duration. Deviance information criterion (DIC) scores and the number of parameters used in each model (np) are shown. Dots (•) indicate included predictor variables for each model

Model	Chick age	Nest attendance	Nest non-attendance	Provisioning rate	Trip duration	np	DIC	Δ DIC
1	•	•	•	•	•	7	379.9	0.0
2	•	•	•		•	6	380.0	0.1
3	•	•	•	•		6	381.2	1.3
4	•	•	•			5	381.3	1.4
5	•		•	•	•	6	381.8	1.9
6	•		•		•	5	383.1	3.2

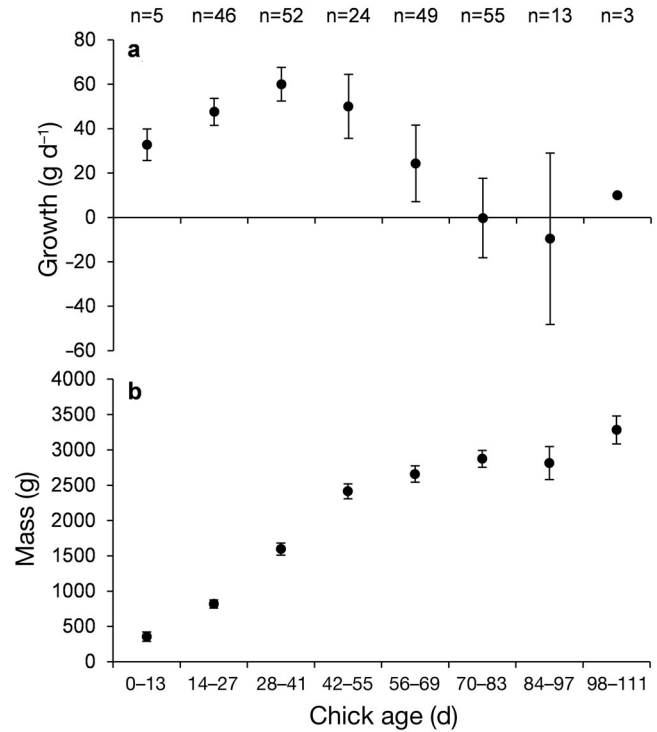


Fig. 1. (a) Growth rate and (b) body mass of Cape gannet *Morus capensis* chicks at Bird Island, Algoa Bay, South Africa, as a function of their age, grouped into 2 wk bins. Total numbers of measurements (n) per chick age category are represented above the figure. Data are means ($\pm 95\%$ CI)

The durations of nest non-attendance bouts increased with chick age (LMM: $F_{(1,1290)} = 436.1$, $p < 0.001$; Table 5) and were noticeably longer amongst those chicks which died, specifically in the 42 to 55 chick age category (GLM: $z = 2.38$, $p < 0.05$; Table 5). Nest non-attendance during the 2012–2013 season was shorter on average than during the previous season (LMM: $F_{(1,50)} = 4.05$, $p < 0.05$); however, when comparing between those nests where the chicks successfully

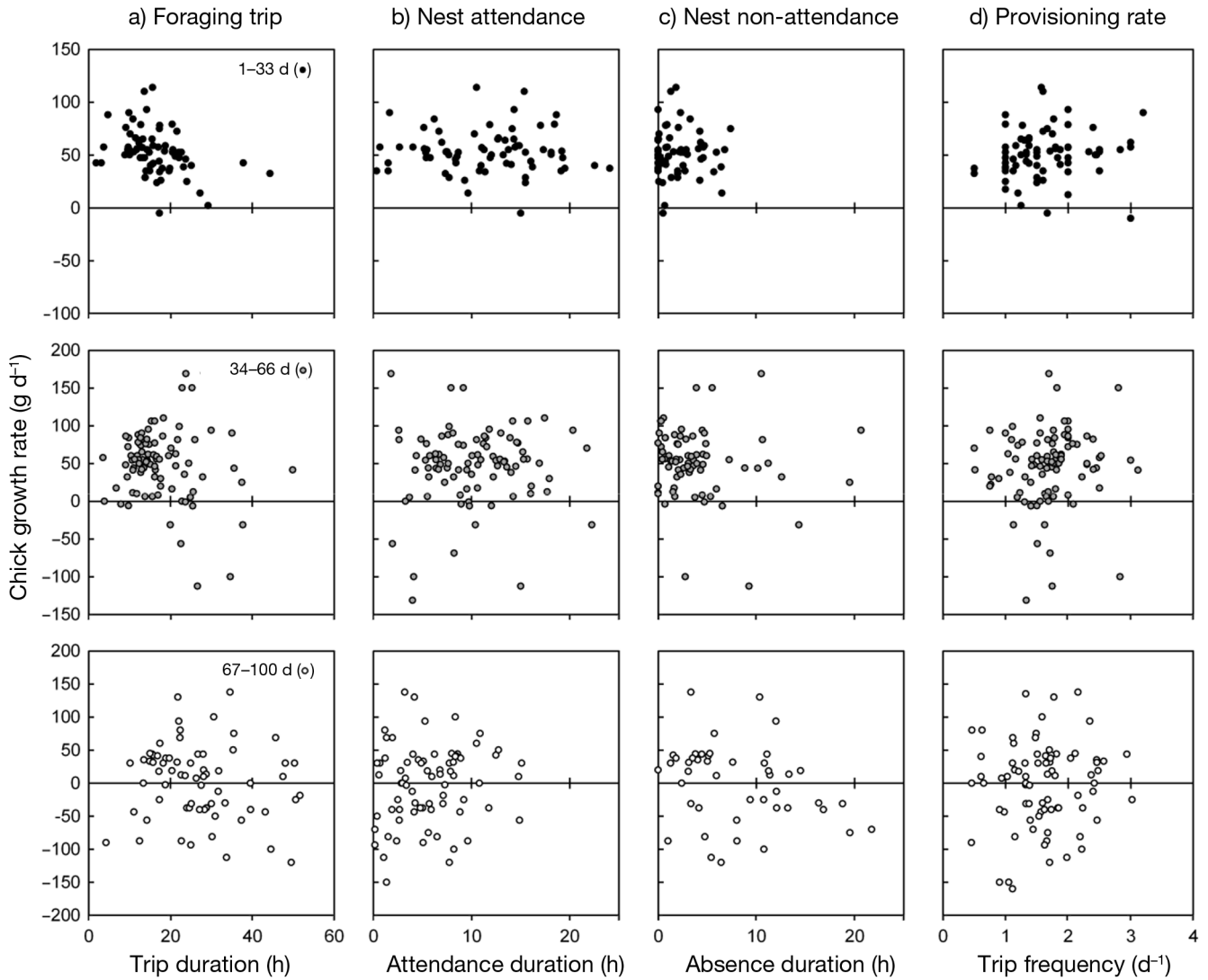


Fig. 2. Relationship between age-specific (1 to 33 d, top graphs, black circles; 34 to 66 d, centre graphs, grey circles; 67 to 100 d, bottom graphs, white circles) chick growth rate and parent Cape gannet *Morus capensis* behavioural parameters at Bird Island, Algoa Bay: (a) foraging trip duration, (b) nest attendance duration, (c) nest non-attendance duration and (d) provisioning rate. Foraging trips are shown up to 60 h and nest non-attendance up to 25 h, thereby excluding 3% of all records

Table 4. Generalised linear mixed-effects models fitted by Laplace approximation of Cape gannet *Morus capensis* chick survival at Bird Island, Algoa Bay, during the 2011–2012 breeding season as a function of chick age, adult behavioural parameters and parent body condition. Coefficients (C) represent the directional effect of the predictors. Three models are presented: chick survival in relation to combined, maternal and paternal parent parameters. Marginal R² for the combined model = 0.47 (variance explained by fixed effects; Nakagawa et al. 2013). Predictor effects were considered significant at p < 0.05

Predictor variable	df	Combined			Maternal			Paternal		
		C (SE)	z-value	p	C (SE)	z-value	p	C (SE)	z-value	p
Intercept	1	-3.80 (0.72)	5.28	<0.001	-18.93 (2.70)	7.01	<0.001	-55.49 (7.15)	7.76	<0.001
Chick age	1	0.10 (0.01)	7.82	<0.001	0.09 (0.01)	5.97	<0.001	0.12 (0.03)	3.50	<0.001
Trip duration	1	-0.005 (0.01)	0.80	0.42	-0.02 (0.01)	2.27	<0.05	-0.02 (0.02)	0.84	0.40
Provisioning rate	1	-0.07 (0.21)	0.33	0.74	-0.52 (0.30)	1.76	0.08	-0.46 (0.51)	0.91	0.36
Nest attendance duration	1	0.03 (0.02)	1.39	0.17	-0.01 (0.02)	0.47	0.64	-0.02 (0.03)	0.70	0.48
Non-attendance duration	1	-0.05 (0.01)	3.42	<0.001						
Body condition	1				2.92 (0.44)	6.68	<0.001	9.01 (1.15)	7.83	<0.001

Table 5. Age of Cape gannet *Morus capensis* chicks that fledged ($n = 8$) and died ($n = 12$) during the 2011–2012 breeding season at Bird Island, Algoa Bay, as a function of parental foraging trip duration, provisioning rate, nest attendance duration and nest non-attendance duration. Chick ages are grouped into 2 wk bins and are represented from 14 to 97 d old. The total proportion of chicks from failed nests which had died by the end of each respective age category is shown. Parental behaviour specific to chick age which significantly predicted chick survival is also indicated. Data are means ($\pm 95\%$ CI). Significance: * $p < 0.05$

	Chick age (d)					
	14–27	28–41	42–55	56–69	70–83	84–97
Proportion of all failed nests (%)	8	42	58	75	92	100
Trip duration (h)						
Died	18.4 \pm 4.7	24.1 \pm 18.7	69.3 \pm 78.1	39.7 \pm 24.2	32.9 \pm 16.3	–
Fledged	17.0 \pm 7.7	15.1 \pm 1.7	18.0 \pm 3.2	37.0 \pm 8.1	37.5 \pm 10.4	38.4 \pm 12.3
Provisioning rate (trips d ⁻¹)						
Died	1.1 \pm 0.2	1.1 \pm 0.2	0.9 \pm 0.2	1.3 \pm 0.4	0.8 \pm 0.5	–
Fledged	1.1 \pm 0.2	0.9 \pm 0.1	1.1 \pm 0.2	0.7 \pm 0.2	0.9 \pm 0.3	1.0 \pm 0.3
Nest attendance duration (h)						
Died	13.7 \pm 3.1	11.5 \pm 1.7	10.4 \pm 2.2	3.4 \pm 1.5	1.6 \pm 0.9	–
Fledged	10.2 \pm 4.6	13.7 \pm 1.6	10.5 \pm 1.5	6.7 \pm 1.7	5.5 \pm 2.3	6.6 \pm 1.8
Nest non-attendance duration (h)						
Died	2.3 \pm 1.1	1.8 \pm 0.6	14.8 \pm 7.5	21.0 \pm 14.0	23.5 \pm 11.2	–
Fledged	1.2 \pm 1.0	1.5 \pm 0.9	3.7 \pm 1.1*	13.9 \pm 5.2	15.1 \pm 5.3	18.8 \pm 8.7

fledged, there was no significant difference (LMM: $F_{(1,35)} = 0.11$, $p = 0.74$). Overall foraging trip duration, nest attendance duration and provisioning rate did not influence chick survival (Tables 4 & 5; all $p > 0.05$), but this differed between parents. Females which made longer trips significantly decreased the probability of their chicks' survival ($p < 0.05$; Table 4). Furthermore, chick survival probability was significantly improved when either the male or female parent was in better body condition (Table 4; both $p < 0.001$).

DISCUSSION

Chick growth and survival amongst seabirds is influenced by several factors, including prey availability (Litzow et al. 2002, Elliott et al. 2010), parent requirements and resource allocation (Weimerskirch et al. 1997), meteorological conditions (Yoda & Ropert-Coudert 2007, Weimerskirch et al. 2012), predation (Mullers & Tinbergen 2009) and life-history plasticity (McDuie et al. 2013). An adult seabird's time-activity budget can be used as a measure of some of these factors (e.g. Chivers et al. 2012), and this approach was adopted to investigate its influence on chick growth and survival, using the Cape gannet as a model. This study showed that chick growth is largely a function of age and parental provisioning, while chick survival is mostly affected by nest attendance levels, female provisioning rate and parent body condition.

Prey quantity or quality delivered to the nest was not accounted for in the analyses of this study. However, anchovy dominated Cape gannet diet samples at Bird Island during the 2012–2013 breeding season, whereas anchovy and sardine in equal proportions and a smaller contribution of saury constituted the diet samples in 2011–2012 (Green et al. 2015). When there is a large proportion of fishery discards in Cape gannet diet, chicks have reduced growth rates and lower survival (Pichegru et al. 2007, Mullers et al. 2009). There were, however, few discards found in the diet of gannets during the course of the current study (Green et al. 2015). Therefore, it is unlikely that their diet contributed to the reduced breeding success in 2011–2012.

Chick growth

As expected, chick growth amongst Cape gannets was driven predominantly by their age. However, irrespective of chick age, adult Cape gannets that made shorter foraging trips enabled their chicks to grow faster, a relationship that Chivers et al. (2012) showed for breeding success of black-legged kittiwakes. Similarly, amongst Cape gannets, Mullers & Tinbergen (2009) demonstrated that when foraging behaviour varies, between seasons of variable prey states or within a season, chick growth and survival are affected. Parents that spent more time foraging had reduced provisioning rates and raised chicks with

relatively slow growth rates (Mullers & Tinbergen 2009), which accords with the results of the present study. Shorter foraging trips, which can be related to an increased availability of local prey (Pichegru et al. 2007), translate to greater provisioning rates, allowing for faster growth. More broadly, Bijleveld & Mullers (2009) used the Cape gannet as a model to investigate the trade-off between self- and chick-provisioning in seabirds by artificially handicapping one partner of a breeding pair, thereby increasing the other partner's reproductive effort while not affecting its foraging or flying ability. They showed that birds from handicapped nests demonstrated increased overall foraging trip duration, decreased nest attendance and decreased provisioning rate, which resulted in chicks with slower growth and lower survival rates (Bijleveld & Mullers 2009). The Cape gannet therefore shows foraging flexibility, but the potential effects of reduced prey abundance are passed onto its chicks as a result of increased foraging effort reflected by longer trips and decreased provisioning rates.

Chick survival

The lower survival probability of chicks that were attended less at their nests suggests that a factor on the island contributed to this. There were more kelp gulls in the vicinity of Bird Island during the 2011–2012 breeding season compared to 2012–2013 as reflected in a higher weekly colony perimeter count of Cape gannet eggs predated by kelp gulls (200 vs. 50; G. M. Rishworth unpubl. data). Kelp gull predation is an important cause of chick mortality among Cape gannets (Green & Pistorius 2013) and explains why reduced nest attendance affected chick survival, especially for those chicks that died at a younger age. Other factors such as heat stress (Hochscheid et al. 2002) or exposure, particularly during the adversely cold and rainy storm in early February 2012, may have contributed to the lower survival of unattended chicks. During this storm >100 mm of rain fell (South African Weather Service 2013) which is far more than the average rainfall usually recorded during February (Stewardson et al. 2012). Furthermore, adult foraging trip durations were significantly longer during this 5 d storm than they were 5 d before or after (53.5 ± 20.1 h compared to 28.3 ± 8.7 h and 21.6 ± 7.8 h, respectively; $F_{(2,117)} = 7.04$, $p < 0.01$). As a result, many chicks were left unattended and exposed to the cold and rain (G. M. Rishworth pers. obs.), and this was probably a major contributor to the observed mortality amongst older chicks.

In addition to nest non-attendance, it is interesting that chick survival was significantly affected by maternal, but not paternal, behaviour in terms of foraging trip duration (Table 4). Sex-specific partitioning in reproductive investment between parents is fairly common amongst seabirds (Lewis et al. 2002, Elliott et al. 2010, Sommerfeld et al. 2013). The costs of egg development to the female are sometimes reflected in increased relative reproductive effort during chick provisioning by male parents (Weimerskirch et al. 1997, Elliott et al. 2010, Rishworth et al. 2014b). These observations are consistent with life-history theory amongst long-lived animals, whereby self-maintenance is favoured over reproduction (Stearns 1989). Male Cape gannets generally have shorter foraging trips than females (Rishworth et al. 2014b), and the present study demonstrates that the costs incurred by some females in making longer foraging trips are reflected in chicks which have a lower probability of survival. Furthermore, the positive effect of male and female body condition in predicting chick survival highlights the importance of adults achieving favourable body condition prior to the breeding season (Pinaud & Weimerskirch 2002). Adult body condition at the time of transmitter deployment was significantly poorer in the 2011–2012 breeding season compared to 2012–2013 (5.7 ± 0.1 vs. 6.0 ± 0.1 g mm⁻¹; $t_{(2,98)} = 3.39$, $p < 0.01$). Therefore, pre-breeding foraging conditions, in addition to shorter mean nest non-attendance durations in 2012–2013, might have contributed to the seasonal difference in chick survival.

West versus south coast Cape gannets

The demographic dichotomy between west and south coast Cape gannet populations (declining versus increasing/stable; Crawford et al. 2007) has been attributed to juvenile recruitment rather than adult survival (Distiller et al. 2012). Breeding success is low at west coast populations due to a combination of scarce natural prey and predation (Crawford et al. 2007, Mullers et al. 2007). The current study demonstrates that Cape gannet chick growth is largely a function of both developmental stage and prey delivery rate. Chick growth and survival on the west coast are negatively influenced by chicks being fed large amounts of fishery discards (Mullers et al. 2009). At Bird Island, Algoa Bay, fishery discards are uncommon in Cape gannet diet (Pichegru et al. 2007, Green et al. 2015), which could, to some extent, explain differences in population status. Furthermore, chick survival on the west coast can be predicted by both

parent nest attendance and provisioning rate (Ichaboe Island: Mullers & Tinbergen 2009). In the current study, nest attendance was clearly important, with provisioning rate bordering on significant, but only in female parents. At both locations unattended young chicks are predated upon by kelp gulls (Mullers & Tinbergen 2009, Green & Pistorius 2013). Adult Cape Gannet diet and pelagic fish surveys, however, suggest that foraging conditions are more favourable for maintaining reproductive success on the south coast (Green et al. 2015).

CONCLUSIONS

The continuous data generated by the automated VHF system (Rishworth et al. 2014c) allowed for a confident description of the way adult Cape gannet time-activity budgets affect their chicks. Chick growth, specifically, was clearly a function of prey delivery. Both quantity and quality of food delivered to chicks have been shown to influence chick growth in other seabird studies (Litzow et al. 2002). The present study supported other work on Cape gannets which has shown that chick survival depends on an interplay of several factors including nutritional input (Pichegru et al. 2007), predation (Mullers & Tinbergen 2009) and exposure (Hochscheid et al. 2002), which contribute on varying scales depending on chick age and local prey conditions. However, this study clearly demonstrates the inter-colony differences which can exist in terms of the drivers of chick growth and survival in a seabird. As a long-lived species, Cape gannets, specifically the adults, can buffer against variable prey through flexible foraging behaviour (Pichegru et al. 2007) or by targeting fishery discards (Grémillet et al. 2008). However, effective conservation of seabirds such as the Cape gannet requires the protection of all life-history stages (Crawford et al. 2007, Lewison et al. 2012). Understanding the factors which affect chick development and survival at the nest will aid the management of this Vulnerable species.

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