

# Success comes with consistency in hard times: foraging repeatability relates to sex and breeding output in African penguins

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**ABSTRACT:** The concept of individual behavioural consistency has received a great deal of attention in the past 2 decades. However, the fitness benefits of being consistent in varying environmental conditions remain poorly explored. Such information is strongly relevant to our understanding of ecological processes, but also for predicting how some individuals and populations cope with environmental changes. We investigated short-term consistency in foraging behaviours of African penguins *Spheniscus demersus* at population and individual levels on Bird Island (Algoa Bay, South Africa) between 2015 and 2017, and related individual levels of consistency to reproductive outputs. Short-term overall consistency in foraging behaviour across individuals of the same population (population level) was generally moderate, although it was high for bearing (i.e. direction) towards the furthest point of the foraging trip. At the individual level, foraging consistency differed between years and was higher when environmental conditions were less profitable. Females were more flexible in their foraging behaviours than males. Overall, these results suggest that both intrinsic and extrinsic factors are responsible for inter-individual differences in foraging consistency in African penguins. Chicks of parents that were consistent in their foraging trip duration had higher growth rates than those of more flexible individuals when conditions were poor. It is not clear whether penguins adapt their level of short-term consistency at sea to the changing conditions or maintain their strategy across years. However, our results have revealed a reproductive advantage of individual foraging consistency during a year when resources were poor. For the first time, we have identified a potential mechanism to explain why some African penguins may cope better than others during poor environmental conditions.

**KEY WORDS:** Flexibility · Chick growth · Trip duration · Seabirds

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## 1. INTRODUCTION

The marine environment is a highly dynamic system, in which individuals must cope with environmental variability (e.g. Reed et al. 2009). However, in the current context of global changes, they face rapid local transformations which modify the environmental selective pressures acting on them (e.g. Lescroël et al. 2014). During the breeding season, many predators are constrained to find food within a restricted

range (e.g. Hamer et al. 2007), increasing the pressure they face. It is therefore necessary to understand how individuals adjust their behavioural response to their environments, and how this affects their fitness, in order to predict potential consequences of current or future changes on their population dynamics.

Individuals routinely search for food over various spatial (Ceia et al. 2012, Baylis et al. 2015, Camprasse et al. 2017a) and temporal scales (Pichegru et al. 2012, Sherley et al. 2013a, Arthur et al. 2015) throughout

their life cycle. Optimal foraging theory suggests that they should adapt their strategies to maximize foraging efficiency, and therefore, fitness (Pyke et al. 1977). Although flexibility is described as a mechanism that increases foraging efficiency in a variable environment (e.g. Grémillet et al. 2012), accumulating evidence indicates that individual specialisation and behavioural consistency may also be adaptive (Wakefield et al. 2015, Patrick & Weimerskirch 2017). It is therefore crucial to understand inter-individual differences in behaviour (Ceia & Ramos 2015), since the population response may conceal individual reactions (Potier et al. 2015). The recent emphasis in ecological research towards an individual approach (as opposed to a traditional population approach) has revealed the potential importance of individual variability in population processes (e.g. López-López 2016).

Individual specialisation, i.e. the use of a subset of the resources exploited by the population (Bolnick et al. 2003), is widespread in many taxa, including marine species (reviewed by Araújo et al. 2011). Similarly, individual consistency in foraging or diving behaviour, which reflects individual specialisation in space use (Ceia & Ramos 2015), exists over short- and long-term periods in turtles (Schofield et al. 2010), marine mammals (Kernaléguen et al. 2012, Arthur et al. 2015) and seabirds (Ceia et al. 2012, Wakefield et al. 2015). Individual specialisation has received increasing attention over the past 2 decades (e.g. Ceia & Ramos 2015), and findings suggest that this strategy potentially impacts population dynamics. Specialisation, through diet, consistency in foraging or migration, has been related to intrinsic (e.g. sex; Müller et al. 2014 or body mass; Ratcliffe et al. 2013) and extrinsic factors (e.g. breeding site; Camprasse et al. 2017a or environmental conditions; Ceia et al. 2014a). However, other factors such as personality (i.e. consistent individual differences in behaviour which persists through time; Bell et al. 2009) have not yet been related to individual consistency in foraging behaviour or diet in marine predators. Indeed, there is growing evidence that personality traits, foraging consistency and individual specialisation may covary in the wild (Toscano et al. 2016). Testing the effect of personality traits on individual specialisation might clarify how personality influences fitness. Certainly, in the wild, breeding success can differ between personality types and personality assortment within a pair (e.g. Patrick & Weimerskirch 2014a). Individual specialisation may potentially be a proximate mechanism through which personality influences reproductive success.

Woo et al. (2008) suggested that the fitness benefits of being a specialist may vary temporally as prey availability and predictability fluctuate. This hypothesis potentially explains why consistent and flexible strategies are maintained in a population (e.g. Abrahms et al. 2018). For example, in northern elephant seals *Mirounga angustirostris*, the relationship between mass gained and site fidelity fluctuated between years of positive or neutral phases of the Pacific Decadal Oscillation (Abrahms et al. 2018). However, some research has suggested that some strategies are consistently advantageous. For example, Golet et al. (2000) found that prey specialisation in pigeon guillemots *Cepphus columba* enhanced chick growth. Similarly, Patrick & Weimerskirch (2017) found that site-faithful, black-browed albatrosses *Thalassarche melanophrys* exhibited high breeding success over short- and long-term scales. Nonetheless, the impact of behavioural consistency on breeding success over fluctuating environmental conditions remains poorly studied in top predators.

Colonial seabirds are of major interest for individual-based studies because these predators are central place foragers, and therefore are easily accessible when breeding (e.g. tracking using global positioning system [GPS] loggers). During the breeding season, African penguins are restricted to foraging within limited distances from their nesting ground (ca. 45 km; Pichegru et al. 2010, 2012, 2013), so that availability of forage resources in proximity to the colony is necessary for reproductive success (Sherley et al. 2013b). In this species, individuals feed primarily on small pelagic fish, sardines *Sardinops sagax* and anchovies *Engraulis encrasicolus* (Crawford et al. 2011), and are therefore considered a specialist species. Consequently, strategies reducing intra-specific competition during the breeding season would be advantageous. The foraging behaviour of African penguins has been well studied (Pichegru et al. 2013, Sherley et al. 2013a, van Eeden et al. 2016). For example, African penguins adjust their strategy at sea according to their boldness and sex (Traisnel & Pichegru in press). However, little is known about individual short-term consistency in their foraging strategies (i.e. trip characteristics) over consecutive days, its link to intrinsic and extrinsic factors and its potential effect on reproductive output in this species. As African penguins are endangered, an understanding of their behaviour and ecology is needed to maximise the benefits of conservation management.

In this study, we examined inter-individual differences in consistency of foraging metrics (e.g. trip duration, maximum distance to the colony) on a

short-term scale at the population (i.e. overall consistency across individuals of the same population) and individual level (i.e. within individual consistency). We tested whether intrinsic (sex and boldness) and extrinsic (year) factors influenced individual consistency in foraging behaviour over a breeding season. We expected sex and boldness to affect individual consistency in foraging behaviour, as they have been found to influence different aspects of foraging behaviour in this species (Pichegru et al. 2013, Traisnel & Pichegru in press). By combining data based on GPS loggers over 3 yr (2015–2017), we explored whether individual consistency differed with environmental conditions. Finally, we related individual foraging consistency over consecutive trips to breeding success using chick growth rates, as benefits of behavioural consistency have been shown to fluctuate between years in other marine predators (Abrahms et al. 2018).

## 2. MATERIALS AND METHODS

### 2.1. Data collection

Foraging behaviour was assessed using miniature GPS devices (CatTrack/I-gotU 44.5 × 28.5 × 13 mm, ~20 g; Perthold Engineering/Mobile Action, <1.5% of adult body mass) on African penguins *Spheniscus demersus* rearing chicks 1–3 wk old. During this period, males and females alternate nest protection and foraging (Randall & Randall 1981). The loggers were deployed for consecutive trips (mean ± SD: 2.85 ± 0.98 trips) between April and June (peak of the brooding period) on Bird Island, Algoa Bay, South Africa (33° 50' S, 26° 17' E) during 3 consecutive years (2015–2017). The devices recorded latitudinal and longitudinal locations every 1 min (accuracy of <10 m) and were placed in a sealed, heat-shrink tube (EPS3248; Hellermann Tyton). Birds were captured prior to a departure, weighed and equipped with a logger taped to their lower back feathers (Tesa® tape, 4651). Devices were removed after several days (mean ± SD: 4.38 ± 1.21 d), and additional morphometric measurements (bill depth and length, flipper, weight) were taken to assess gender (see Pichegru et al. 2013, Campbell et al. 2016, and details of protocol in Traisnel & Pichegru 2018). Overall, we tracked 59 breeding adults for a total of 168 tracks (2–6 trips ind.<sup>-1</sup>; Table 1) between 2015 and 2017. Individuals were not tracked repeatedly across years.

In 2015 and 2017, we assessed boldness in nest defence for all tracked penguins during a standard

Table 1. Sample size associated with the number of individuals ( $N_{ind}$ ) and trips ( $N_{trip}$ ) recorded during the chick-rearing period by GPS devices deployed on adult African penguins between 2015 and 2017 on Bird Island, Algoa Bay (South Africa). Number of trips recorded per penguin ranged from 2 to 6; therefore, we summarised the number of individuals ( $N_{ind}$ ) that were successfully tracked over 2, 3, 4, 5 or 6 trips each year

	Year			Total
	2015	2016	2017	
$N_{ind}$ (trip = 2)	3	11	14	28
$N_{ind}$ (trip = 3)	5	4	8	17
$N_{ind}$ (trip = 4)	5	2	3	10
$N_{ind}$ (trip = 5)	2	1	–	3
$N_{ind}$ (trip = 6)	1	–	–	1
$N_{ind}$ total	16	18	25	59
$N_{trip}$ total	57	47	64	168

human approach to the nest (e.g. Brommer et al. 2014, Pichegru et al. 2016): one experimenter slowly approached the nest when only one of the parents was attending to avoid bias due to the presence of a partner (Schuett & Dall 2009). The experimenter crouched 1 m away from the nest for 30 s, holding a wooden pole a few cm from the penguin's head (a standard protocol to mark adults in this species), and the bird's response was filmed. From the videos, we extracted the total number of attacks (reaching towards or pecking the pole) and the total number of threats (head rotation from side to side alternately and irregularly from a forward-facing position; see Traisnel & Pichegru 2018 for details) during the experiment. These behaviours were previously determined as a proxy for boldness (Traisnel & Pichegru 2018), a personality trait, as they are repeatable within and between breeding seasons (Traisnel & Pichegru 2018).

We assessed breeding success from chick growth rates, as faster growing chicks are more likely to fledge at a greater mass in this species (Cooper 1977), therefore increasing their probability of survival (Wolfaardt et al. 2008). We measured chicks' mass for 3–5 wk during the linear phase of the growth (i.e. head length >65 mm, see Fig. S1 in Supplement 1 at [www.int-res.com/articles/suppl/m0608p279\\_supp.pdf](http://www.int-res.com/articles/suppl/m0608p279_supp.pdf)). The measurements were separated by at least 5 d. We determined growth increments (GI, in g d<sup>-1</sup>) using:

$$GI = (\text{Mass } 2 - \text{Mass } 1) / (\text{Date } 2 - \text{Date } 1) \quad (1)$$

Growth increments were then averaged to obtain an estimate of growth rate chick<sup>-1</sup>. Information on chick growth rates was collected for 47 penguins

tracked with GPS loggers: 15 in 2015, 13 in 2016 and 19 in 2017. Overall, growth rates were estimated for 72 chicks: 33 first-hatched (double brood clutch), 25 second-hatched (double brood clutch) and 14 single chicks.

## 2.2. Data extraction

All analyses were performed using ArcMap 10.5 and R Studio version 3.3.2. For each individual, the different trips recorded were visually separated using ArcMap. 'Trip' and 'argosfilter' packages were used to apply a speed filter of 12.4 km h<sup>-1</sup> to remove erroneous data exceeding the maximum swimming speed of African penguins (Pichegru et al. 2017). Any incomplete trip for which the last location was the furthest from the colony was discarded. Similarly, we excluded any trip with gaps > 2 h (due to signal loss), unless the gap occurred in the inbound phase of the trip, when signal loss can occur due to a bird's high traveling speed. In that case, the track was interpolated as a straight line. To approximate the most probable path used during signal loss (trips with gaps < 2 h), we interpolated the tracks at 2 min intervals using a non-stop correlated random walk model from the 'crawl' package (Johnson et al. 2008). We then extracted the following parameters from the data: maximum distance from the colony (km), trip duration (h), path length (sum of the distances between all consecutive locations during a foraging trip, km), bearing from the colony to the furthest point of the trip (degrees, ranging from 0 to 360°) and a straightness index reflecting search effort (Benhamou 2004), calculated using:

$$SI = (\text{Maximum distance} \times 2) / \text{Path length} \quad (2)$$

## 2.3. Population level consistency

We assessed short-term foraging consistency at the population level by assessing the penguins' repeatability over consecutive trips during the breeding season. We estimated a repeatability index ( $R$ ) and associated p-value for 4 of the foraging parameters (maximum distance, trip duration, path length, straightness index) using the 'rptR' package (Stoffel et al. 2017). Repeatability indices were estimated from generalised linear mixed models (GLMMs) fitted by a restricted maximum likelihood (REML) with penguin ID as random factor. We specified year as a fixed effect to control for environmental variability, as prey abundance differed between years (Fig. S3,

Table S1 in Supplement 2). All models were performed using a Gaussian error and maximum distance was log transformed to approximate normality. We estimated the different indices of repeatability ( $R$  for maximum distance, trip duration, path length and straightness index) with 2 methods. First, we calculated  $R$  controlling for year (fixed effect) and then removing the phenotypic variance of this fixed parameter (adjusted repeatability). Secondly, we determined  $R$  using non-adjusted repeatability, a technique which includes the phenotypic variance of the fixed effect to the denominator of the repeatability equation; therefore, we did not lose the variance explained by year. As year did not explain a substantial amount of phenotypic variance, we only present the results for non-adjusted repeatability. Bearing was analysed using a circular ANOVA from the 'circular' package. For this parameter,  $R$  was calculated using the between- ( $S^2_A$ ) and within-group ( $S^2$ ) variance (see Lessells & Boag 1987):

$$R = S^2_A / (S^2 + S^2_A) \quad (3)$$

where  $S^2_A = (\text{mean square}_{\text{between-groups}} - \text{mean square}_{\text{within-groups}}) / \text{coefficient reflecting the average number of trips per individual}$ , and  $S^2 = \text{mean square}_{\text{within-groups}}$ .

Mean squares both between- and within-groups were obtained from the output of the circular ANOVA. We considered consistency in foraging behaviour during consecutive trips high when  $R > 0.50$ , moderate when  $0.25 < R < 0.50$  and low when  $R < 0.25$  (Potier et al. 2015).

## 2.4. Individual level consistency

To compare consistency between individuals over a short period of time (consecutive trips), we calculated an index of foraging consistency ( $R_{\text{ind}}$ , using Eq. 3) for each penguin using that individual's residual variance, which was extracted from the models used to estimate population-level consistency in foraging behaviours following Potier et al. (2015). Penguin ID was set as a random effect in each model. To calculate  $R_{\text{ind}}$ , we used the between-individual variance ( $S^2_A$ ) of the combined 3 yr, as year did not explain a substantial amount of phenotypic variance when estimating foraging consistency at the population level.  $R_{\text{ind}}$  was assessed from maximum distance, trip duration, path length and straightness index, and ranged from 0 to 1, with a value of 0 representing a very flexible bird. Because bearing was a circular variable, we could not extract a residual variance

from the analyses. We tested whether the number of trips recorded per individual would affect individual repeatability in this study (Table S2 in Supplement 3), but as it did not ( $p \geq 0.100$  for all foraging parameters, see Supplement 3), we included all parameters in our analyses.

We collected information on boldness (attack and threats), sex and foraging behaviour from a total of 41 individuals (22 females and 19 males). Then, we determined whether sex, year, attacks or threats influenced individual consistency ( $R_{ind}$ ) of the 4 foraging variables using generalised linear models (GLMs; ‘lme4’ package). The numbers of attacks and threats were weakly and negatively correlated (Traisnel & Pichegru in press); therefore, both variables were included in the models. Using the ‘MuMIn’ package, we applied the small sample size correction of Akaike’s information criterion ( $AIC_c$ ) and estimated probabilities by averaging the different models. This technique accounts for model uncertainty by ranking the combinations of several models (Grueber et al. 2011). Normality and heteroscedasticity of the residuals were checked for each model. Individual consistency in straightness index was log transformed to approximate normality of the residuals. Boldness data were not available in 2016; therefore, this year was not included in these analyses.

### 2.5. Breeding success

To estimate whether individual consistency in foraging influenced breeding success, we fitted chick growth rates with the different indices of consistency (maximum distance, trip duration, path length and straightness index) using GLMMs and the technique of model averaging described in Section 2.4. Adult ID was set as random effect to control for repeated values, since some nests contained 2 chicks. We included an interaction between individual foraging consistency and year in the models, as individual consistency varied between years. The relationship between chick growth rates and hatching order is not uniform (it changes between years; Sherley 2010) on Bird Island (Algoa Bay), but recent works suggest that clutch size (1 or 2 offspring) and chick rank (first-, second-hatched or single brood) does not influence chick growth rates (Spelt & Pichegru 2017, Traisnel & Pichegru 2018, A. McInnes unpubl. data) on this island. Nevertheless, to control for this parameter, we included rank as a fixed effect in our model. Prior to the analyses, we also tested for collinearity between the different indices of foraging consistency ( $R_{ind}$ )

using Spearman’s method (Table S3 in Supplement 4). Because individual consistency in trip duration and path length were highly correlated ( $r = 0.73$ ), we decided to only keep trip duration, as this variable is the most commonly used to analyse individual consistency (Patrick et al. 2014, Baylis et al. 2015, Potier et al. 2015), facilitating comparisons with other species. The remaining variables ( $R_{ind}$  in maximum distance and straightness) were also included in the model.

## 3. RESULTS

### 3.1. Population level consistency

African penguins were generally consistent in their foraging behaviour, as consistency was significant for all foraging parameters (Table 2). Repeatability was high for bearing ( $R = 0.55$ ) and moderate for maximum distance, trip duration and path length ( $0.31 < R < 0.33$ ; Table 2). Only the straightness index showed limited consistency ( $R = 0.14$ ). The confidence interval was wide for 4 of these foraging parameters (Table 2), possibly indicating relatively high variability in individual levels of foraging consistency within the population. Confidence intervals were not available for bearing because the method used to determine repeatability for this variable did not allow for such estimation.

### 3.2. Individual level consistency

One female was removed from the analyses, since the high number of threats she displayed (36 in total) strongly influenced the data.

Individual consistency in foraging behaviours differed significantly between sexes, with females being more flexible than males in their maximum distance

Table 2. Population level of behavioural consistency observed for adult African penguins during the breeding season on Bird Island, South Africa. Repeatability index ( $R$ ), confidence interval (CI) and associated p-value (**bold** values represent significant results at  $p < 0.05$ ) are given for each foraging parameter. Sample sizes: individuals = 59; trips = 168

Foraging parameters	$R$	CI	p
Maximum distance (km)	0.33	0.17–0.49	<b>&lt;0.001</b>
Trip duration (h)	0.33	0.17–0.49	<b>&lt;0.001</b>
Path length (km)	0.31	0.14–0.46	<b>&lt;0.001</b>
Straightness index	0.14	0.01–0.30	<b>0.022</b>
Bearing	0.55		

Table 3. Statistical results from generalised linear models (GLMs) relating individual level consistency ( $R_{\text{ind}}$ ) of 4 foraging parameters to intrinsic (sex, attack and threat) and extrinsic (year) parameters. Sample size = 40; significant results ( $p < 0.05$ ) are shown in **bold**

Factors	$R_{\text{ind}}$ maximum distance		$R_{\text{ind}}$ trip duration		$R_{\text{ind}}$ path length		$R_{\text{ind}}$ straightness index	
	<i>z</i>	<i>p</i>	<i>z</i>	<i>p</i>	<i>z</i>	<i>p</i>	<i>z</i>	<i>p</i>
Year	1.09	0.276	<b>2.37</b>	<b>0.018</b>	0.67	0.505	<b>2.25</b>	<b>0.024</b>
Attack	1.16	0.245	1.10	0.269	1.16	0.248	0.79	0.427
Threat	0.32	0.748	0.20	0.843	0.35	0.724	0.19	0.846
Sex	<b>2.02</b>	<b>0.045</b>	1.03	0.305	1.73	0.083	0.97	0.333

( $R_{\text{ind}} = 0.71 \pm 0.23$  and  $R_{\text{ind}} = 0.84 \pm 0.14$  for females and males, respectively;  $z = 2.02$ ,  $p = 0.045$ ) and their path length, although the latter was not significant ( $R_{\text{ind}} = 0.67 \pm 0.26$ ,  $R_{\text{ind}} = 0.81 \pm 0.20$  for females and males, respectively;  $z = 1.73$ ,  $p = 0.083$ ). Individual consistency in foraging also differed between years, with individuals being more consistent in their trip duration ( $z = 2.37$ ,  $p = 0.018$ ) and straightness index ( $z = 2.25$ ,  $p = 0.024$ ) in 2017 than in 2015. However, boldness degree (numbers of attacks or threats) did not influence individual consistency in any of the foraging parameters (all  $p \geq 0.245$ ; Table 3).

### 3.3. Individual consistency and breeding success

As expected, chick rank did not influence growth rates (second-hatched:  $z = 1.40$ ,  $p = 0.163$ ; single brood:  $z = 0.85$ ,  $p = 0.398$ ; Table 4). However, growth rates varied between years, with offspring growing

Table 4. Statistical results obtained from averaging models that related chick growth rates to year, chick rank (single brood, Chick S; second-hatched chick from a double brood, Chick B) and individual level of consistency ( $R_{\text{ind}}$ ) of 3 foraging parameters (maximum distance, trip duration and straightness index) and their interaction with year. Sample size of chicks = 72; significant results ( $p < 0.05$ ) are shown in **bold**

Factors	Chick growth		
	<i>z</i>	<i>p</i>	
Year	2016	<b>2.17</b>	<b>0.030</b>
	2017	0.46	0.648
Rank	Chick B	1.40	0.163
	Chick S	0.85	0.398
$R_{\text{ind}}$ maximum distance		0.41	0.682
$R_{\text{ind}}$ trip duration		0.38	0.704
$R_{\text{ind}}$ straightness index		0.29	0.768
$R_{\text{ind}}$ maximum distance $\times$ year	2016	1.41	0.159
	2017	0.49	0.622
$R_{\text{ind}}$ trip duration $\times$ year	2016	<b>2.25</b>	<b>0.024</b>
	2017	0.24	0.807
$R_{\text{ind}}$ straightness index $\times$ year	2016	0.76	0.449
	2017	0.27	0.786

more slowly in 2016 ( $z = 2.17$ ,  $p = 0.030$ ; Fig. 1). Individual consistency in trip duration influenced growth rates only in 2016 ( $z = 2.25$ ,  $p = 0.024$ ); chicks from consistent adults grew faster in this year (Fig. 2a). Growth rates also seemed to increase with individual consistency in maximum distance in 2016, but this relationship was not significant ( $z = 1.41$ ,  $p = 0.159$ ; Fig. 2b). Neither consistency in straightness index nor its interaction with year influenced offspring growth rates (all  $p > 0.449$ ; Table 4).

## 4. DISCUSSION

This study is one of the few which relates behavioural consistency of 4 foraging metrics to breeding success. We demonstrated that individual differences in the consistency of a foraging parameter were related to chick growth rate (a proxy for breeding success) in African penguins in 2016, when environmental conditions were poor. We also showed that individual consistency varied annually and with sex, suggesting that both intrinsic and extrinsic factors

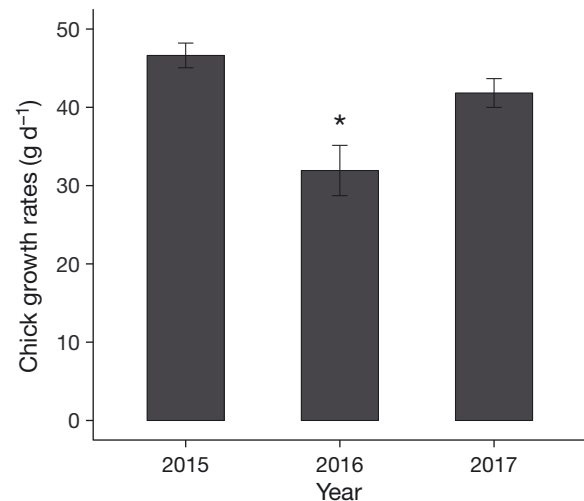


Fig. 1. Average ( $\pm$ SE) growth rates of African penguin chicks raised on Bird Island, South Africa, in 2015, 2016 and 2017. Star: significant difference in growth rates

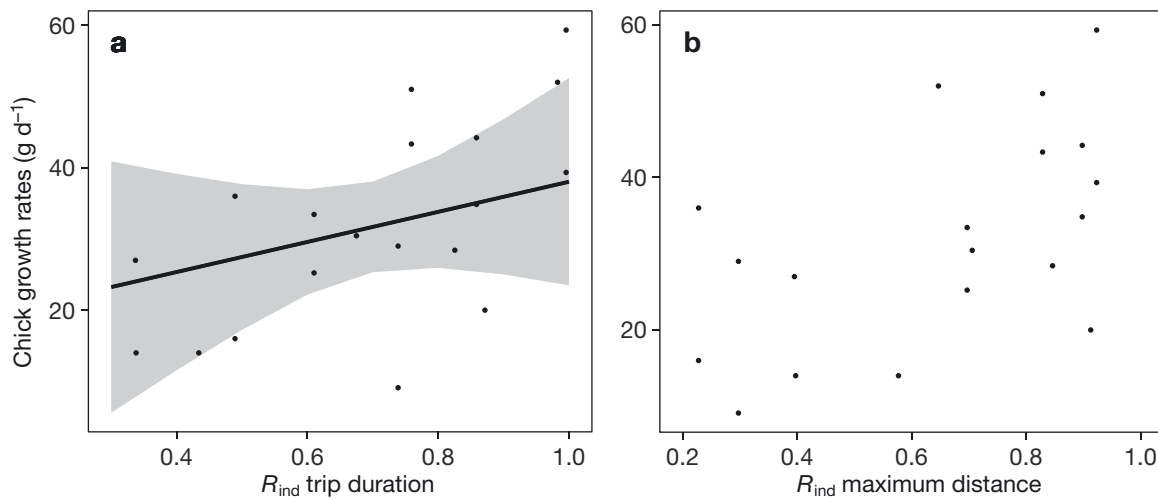


Fig. 2. African penguins' chick growth rate versus adults' consistency ( $R_{\text{ind}}$ ) in (a) trip duration and (b) maximum distance during the 2016 breeding season on Bird Island, Algoa Bay. Regression line and 95 % confidence intervals associated with the line in (a) were extracted from the model

may predict inter-individual differences in behavioural consistency in African penguins.

Foraging consistency is widely observed in marine species (guillemots, Woo et al. 2008; albatrosses, Ceia et al. 2012; gannets, Wakefield et al. 2015; fur seals, Arthur et al. 2015; elephant seals, McIntyre et al. 2017), as a possible mechanism to reduce competition (Ceia & Ramos 2015), minimise predation risks and adapt to resource availability (i.e. ecological opportunity, Araújo et al. 2011). However, consistency may differ between species (Phillips et al. 2017), colonies (Camprasse et al. 2017a), individuals (Potier et al. 2015) and even among the behavioural parameters considered (Müller et al. 2014). Overall, behavioural consistency in breeding African penguins was moderate, except for the bearing taken to the furthest point from the colony, which was highly repeatable ( $R = 0.55$ ). Our results are consistent with previous works on gannets (Patrick et al. 2014) and cormorants (Potier et al. 2015) but contrast with findings on little penguins *Eudyptula minor* (Camprasse et al. 2017a), a species with foraging ranges similar to those of African penguins and also a specialist feeder on small pelagic fish. Despite exploring the ocean at different spatial scales, African penguins, northern gannets *Morus bassanus* and great cormorants *Phalacrocorax carbo* exhibited low to moderate levels of consistency in trip duration, maximum distance and path length at population levels, indicating flexibility in foraging behaviours within the population. However, all these species exhibited higher levels of consistency in the bearing (departure bearing or bearing to the furthest location), indicating that the

birds were relatively faithful to their foraging sites (Patrick et al. 2014). By contrast, little penguins were not consistent in bearing between consecutive trips, probably reflecting the variability in local abundance and distribution of their prey (Camprasse et al. 2017a). Although bearing is highly dependent on the geography of the area, the high consistency in bearing demonstrated by African penguins here may reflect a predictable supply of forage fish in the eastern part of Algoa Bay (i.e. where the colony is situated). Indeed, the Woody Cape coast is known for the regular occurrence of upwelling cells (Goschen et al. 2012), which boost local productivity. African penguins may make use of oceanographic features to orientate and forage (van Eeden et al. 2016). Indeed, they target cold surface waters associated with upwelling cells that are mainly located east and south of Bird Island, Algoa Bay (van Eeden et al. 2016). Such oceanic features may predict availability of food resources, and a good knowledge of their surrounding environment may ensure that seabirds consistently head towards such productive areas (Weimerskirch 2007). Although African penguins remain mainly within 45 km of their colony during the breeding season (Pichegru et al. 2010, 2012, 2013), they exhibit high flexibility in their foraging routes and time spent at sea (Table 2). By doing so, they might adjust their behaviour to fine-scale changes in oceanographic conditions (Weimerskirch 2007) or to the needs of their offspring (physiological constraints; Potier et al. 2015).

In the present study, African penguins exhibited sex-specific differences in behaviour, as males and females contrasted in their level of individual con-

sistency in some foraging parameters. Overall, males were more consistent in the maximum distance at which they foraged from their colony. Although the results were not significant, they also exhibited higher levels of foraging consistency than females in their total distance travelled (path length). Sex differences in consistency exist in shags (Ratcliffe et al. 2013, Harris et al. 2014, Camprasse et al. 2017b), shearwaters (Müller et al. 2014) and albatrosses (Patrick & Weimerskirch 2014b). For all 3 species of shags, females were more consistent than males in diving behaviour (Ratcliffe et al. 2013, Camprasse et al. 2017b) and in their spatial use of habitat (Harris et al. 2014), possibly reflecting sexual dimorphism in some species. Female imperial shags *Phalacrocorax atriceps* are smaller than males and therefore may be constrained to reduce their plasticity (Harris et al. 2014). Indeed, by being smaller, females potentially exhibit higher metabolic rates per unit mass compared to males (Halsey et al. 2006), which could constrain their capacity to increase their behavioural flexibility. In contrast, male black-browed albatrosses *Thalassarche melanophrys* have a narrower feeding niche width compared to females. These differences potentially arise from sexual selection: male albatrosses forage closer to the colony where competition is high, so that selection towards specialized individuals may be strong (Patrick & Weimerskirch 2014b). Finally, sex differences of individual consistency in Scopoli's shearwaters *Calonectris diomedea* seem to depend on the behavioural parameter considered and may reflect differences in reproductive investment (Müller et al. 2014). Together, these studies indicate that sex differences in individual consistency might be species-dependent (Phillips et al. 2017), and to a further extent, behaviour-dependent. Sexual dimorphism is limited in African penguins (Pichegru et al. 2013); therefore, it may not be responsible for the different levels of individual consistency in maximum distance observed here. Instead, the difference between males and females may arise from contrasting investment in the chick-rearing period (Spelt & Pichegru 2017, Traisnel & Pichegru in press). Indeed, female African penguins, within Algoa Bay, generally exhibit higher foraging effort than males during the breeding season (Pichegru et al. 2013) and adjust their nest attendance behaviour to the brood's needs (e.g. with chick age; Spelt & Pichegru 2017). Our results support such findings, as females were more flexible than males, thereby possibly adjusting their behaviour to the current needs of their brood.

Along with predation, ecological opportunity (i.e. diversification of lineages under specific environmental conditions; Yoder et al. 2010), intra- and inter-specific competition (Araújo et al. 2011), as well as personality may drive individual specialisation and behavioural consistency (Toscano et al. 2016). While boldness (number of attacks and threats) was previously shown to relate to foraging and diving strategies in African penguins (Traisnel & Pichegru in press), it did not influence individual consistency in foraging behaviour here. Other factors could also have contributed to the observed individual differences in foraging consistency, such as age/experience (Phillips et al. 2017), although they were not examined in the present study.

Interestingly, individual behavioural consistency varied between years, and penguins were more consistent in trip duration and straightness index when environmental conditions were less profitable (Supplement 2). Likewise, Ceia et al. (2014b) and Camprasse et al. (2017a) found individual consistency to vary between years in Cory's shearwaters *C. diomedea* and little penguins *E. minor*, respectively. These variations are likely to reflect availability and predictability of resources (Woo et al. 2008) around the colony. As mentioned previously, it is possible that although Algoa Bay is considered to be a fluctuating system, resources may be relatively predictable due to the regular presence of upwelling cells (Goschen et al. 2012), even when these are less strong. Indeed, along with availability, resource predictability may increase individual consistency and reduce the energetic cost of foraging (i.e. creating a selective advantage; Arthur et al. 2015, Phillips et al. 2017).

In 2016 only, when chick growth rates were the lowest of our sampling period (Fig. 1), chicks raised by parents that were more repeatable in their trip durations grew faster, regardless of their rank (Fig. 2a). These results must be interpreted with caution, as only 1 adult from each nest was considered here. African penguins share parental care duties during the brooding period (Randall & Randall 1981); therefore, considering the behaviour of the 2 parents in relation to breeding success could have strengthened our conclusions about their breeding ecology. Nonetheless, our results agree with those reported for black-browed albatrosses (Patrick & Weimerskirch 2014b, 2017) and pigeon guillemots (Golet et al. 2000), for which repeatable individuals had higher fitness. However, they do contrast with previous studies on Brünnich's guillemot *Uria lomvia* (Woo et al. 2008), for which diet specialisation did not affect breeding success. As suggested by Woo et al. (2008),



specialist and generalist strategies may balance themselves on a long-term scale, as each strategy may increase fitness under variable levels of prey availability and predictability. Such changes may occur at different time scales throughout the different ecosystems, thereby reflecting the diversity of findings observed in the literature. In our study, the benefits of foraging consistency were only visible in one year and for one behaviour. In 2016 and 2017, prey availability around the island was low in comparison to 2015, but the benefits of consistency only paid off in 2016, when resources were the lowest recorded (Supplement 2). Two hypotheses arise: (1) penguins may increase their consistency in foraging to face poor resource conditions and potentially increase their breeding success. Indeed, Weimerskirch et al. (2000) demonstrated that chicks fed more regularly by adult albatrosses had higher growth rates than chicks fed less regularly. We could also assume that (2) poor conditions may select for consistent individuals in trip duration which exhibit higher success when resource availability is extremely poor. While we suggested that individual consistency could be advantageous, the relatively high variability of strategies observed may suggest that benefits of being consistent or flexible vary with environmental conditions. Although we did not find evidence that flexible penguins were advantaged in our study, the second hypothesis would explain the persistence of both consistent and flexible strategies in the population, as suggested by Woo et al. (2008). As demonstrated in northern elephant seals, the fitness advantages of being site-faithful vary with environmental conditions (Abrahms et al. 2018). In their study, site-faithful individuals exhibited a higher mass gain in the neutral phase of the Pacific Decadal Oscillation, but this relationship was reversed in positive phases. It is not clear at this stage whether individual African penguins adapt their level of short-term consistency in foraging to the changing conditions or maintain their strategy across years. Further studies investigating the behaviour of the same individual across years would be necessary to answer that question. However, in an environment with extremely poor resources (i.e. in 2016; Supplement 2), consistency in foraging seems to increase breeding success in African penguins. By being flexible when resources are possibly predictable but of low availability, penguins may increase the energetic cost of changing foraging sites (Arthur et al. 2015) and reduce energy available to maintain their offspring.

This study is one of few to test the impact of individual foraging consistency on breeding success in a

marine species. We demonstrated that in poor foraging conditions, endangered African penguins that showed a high level of consistency in their foraging behaviour were more successful than less consistent parents. Although our results bring new insight into the field of repeatability, other aspects of African penguin ecology (e.g. experience/age, social interaction) that could predict inter-individual variations in foraging consistency still need to be considered. In addition, as breeding success depends on both members of a pair, studying individual consistency in relation to the partner's behaviour would offer a closer look into the breeding ecology of this seabird. Long-term consistency monitoring could clarify or confirm whether individual consistency in trip duration is advantageous in years of poor environmental conditions. Finally, such monitoring may also help in understanding if African penguins can switch between consistency and flexibility on short- and long-term scales to increase their chances of coping with environmental variability, and, to a further extent, climate change.

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