

Does it always pay to defend one's nest? A case study in African penguin

Gwendoline Traisnel  | Lorien Pichegru

DST-NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology, Institute for Coastal and Marine Research and Department of Zoology at the Nelson Mandela University, Port Elizabeth, South Africa

Correspondence

Gwendoline Traisnel, DST-NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology, Institute for Coastal and Marine Research and Department of Zoology at the Nelson Mandela University, Port Elizabeth, South Africa.
Email: traishnel.gwendoline@gmail.com

Funding information

DST-NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology

Editor: T. Tregenza

Abstract

Throughout the animal kingdom, individual variation in reproductive success is commonly observed, even under similar environmental conditions. However, the mechanisms behind such differences remain unclear. The notion of behavioural consistency in animals has developed rapidly since the early 21st century partly as an approach to understand among-individual differences. In this context, a number of studies have highlighted the influence of pair assortment in personality on breeding success. In this study, we related breeding success to individual behaviour, specifically a risk-taking behaviour, and pair assortment per behaviour in African penguins (*Spheniscus demersus*) over two breeding seasons of contrasting food availability. On Bird Island, Algoa Bay, South Africa, we used indices of boldness and overall mobility in penguins' nest defence behaviour as a response to a standard pedestrian approach during chick-rearing. These behaviours were consistent over the trials and indicated these traits may be related to personality in African penguins. Individuals were categorized as risk-prone ("bold," "mobile") or risk-averse ("shy," "non-mobile"). We then assessed their breeding success through chick growth and survival over 4 weeks in 2015 and 2016. There was weak positive assortment of pairs in relation to nest defence behaviour. However, pair assortment did not significantly influence birds' breeding success. Shy penguins were generally the most successful (had the highest chick growth rates), which was especially apparent during a food shortage in 2016, possibly reflecting a higher energy investment when foraging. In contrast, chicks from bold parents grew significantly slower, especially in 2016. Bold parents may defend their nest successfully against predation or intra-specific aggression when food is abundant, but when predation risks are limited and food availability is low, this strategy may not be beneficial. In the context of climate change, where food shortage events may become more frequent, risk-averse individuals may be favoured and genetic diversity may be reduced in African penguins.

KEYWORDS

boldness, breeding success, environmental conditions, pair assortment, personality, risk-taking

1 | INTRODUCTION

Individual fitness can be defined by the persistence of an individual's genetic material in the population through survival and production of

viable offspring (Orr, 2009). Throughout their life, individuals must allocate their energy to (i) produce sustainable offspring and (ii) maintain their own life, therefore creating a trade-off parent/offspring (Stearns, 1989). To increase their reproductive success, some species

actively defend their nests against intrusions or aggressions from conspecifics or non-conspecifics (Betini & Norris, 2012; Kontiainen et al., 2009; Montgomerie & Weatherhead, 1988). This behaviour is considered as an anti-predator defence in both mammals and birds (Caro, 2005) and represents a costly parental investment (Trivers, 1972). Indeed, it generally requires large energetic expenses from the parents (Redondo, 1989) with an associated increased risk of mortality or injury (Montgomerie & Weatherhead, 1988), therefore participating in the trade-off survival/reproduction (Montgomerie & Weatherhead, 1988). In some species, parents showing a high intensity of nest defence have a higher breeding success (Knight & Temple, 1988; Kontiainen et al., 2009; Weatherhead, 1990). However, when re-nesting potential is high, some individuals may choose to invest less energy in nest defence in the present breeding attempt to ensure their survival and the following breeding attempt (Caro, 2005; Montgomerie & Weatherhead, 1988). These individual differences in nest defence behaviour are generally consistent over time (Kontiainen et al., 2009; Redmond, Murphy, Dolan, & Sexton, 2009; Burtka & Grindstaff 2013) and contribute to individual variations in fitness (Kontiainen et al., 2009; Montgomerie & Weatherhead, 1988), which may have important implications for population dynamics (Orr, 2009).

Behavioural variation within a population is generally attributed to individual plasticity (i.e., the ability of one genotype to express variable phenotypes in contrasting environments, Whitman & Agrawal, 2009). However, recent findings indicate that consistent inter-individual variations may also contribute to behavioural fluctuations at the population level (Dingemanse, Kazem, Réale, & Wright, 2010). Such consistent inter-individual differences in behaviours are commonly referred as personality (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). This consistency can be genetically maintained through generations as different behavioural types may lead to different fitness across contrasting environmental conditions (Wolf & Weissing, 2012). To a further extent, co-variations between certain traits (e.g., exploration and aggression, Verbeek, Boon, & Drent, 1996; Wolf, van Doorn, Leimar, & Weissing, 2007) are commonly reported under the concept of "behavioural syndrome" (Sih, Bell, Johnson, & Ziemba, 2004). However, several studies pointed out that a behavioural syndrome is not systematic and similar behavioural traits may also be un-related (reviewed by Garamszegi, Marko, & Herezeg, 2012). At an evolutionary scale, co-variations between traits (e.g., risk-taking behaviours such as aggressiveness and boldness, Wolf et al., 2007) may result from differences in strategy, whether individuals have high expectations for future reproduction (risk-averse) or not (risk-prone, Wolf et al., 2007). For example, bolder individuals may have a high reproductive success but a short lifespan while shy ones may have immediate low reproductive success but survive for longer (Smith & Blumstein, 2008).

Nest defence is associated with risk-taking, such as boldness (Brommer, Karell, Ahola, & Karstinen, 2014; Krama et al., 2012), mobility (Hollander, Van Overveld, Tokka, & Matthysen, 2008) or aggressiveness (Carrillo & Aparicio, 2001; Kontiainen et al., 2009), all three behaviours being consistent over time (Réale et al., 2007). Aggression and boldness in nest defence have been shown to increase breeding success in female Ural owls (*Strix uralensis*, Kontiainen et al., 2009),

male tree swallows (*Tachycineta bicolor*, Betini & Norris, 2012) or female tawny owls (*Strix aluco*, Brommer et al., 2014). However, pair assortment also influenced these results, with for example, aggressive female tree swallows having larger eggs only when mated with a male with a complete different personality (Rosvall, 2009).

In monogamous species with bi-parental care, individuals' choice for their partner is crucial because both parents share the responsibility of offspring survival during early stages of its life (Davies, Krebs, & West, 2012). Preference for a mate can be made through behaviour or other individual characteristics (Fargevieille, Grégoire, Charmantier, Rey Granado, & Doutrelant, 2017; Schuett, Tregenza, & Dall, 2010), which results in pairs being either assorted (i.e., similar personality trait) or dis-assorted (i.e., dis-similar personality trait). For example, in a captive experiment, proactive female zebra finches (*Taeniopygia guttata*), which were moderately or highly exploratory, preferred risk-taking males (Schuett, Godin, & Dall, 2011). Pair assortment may be context dependant, for example species or individual dependant (Schuett et al., 2010), and results in different breeding success. For example, in great tits (*Parus major*), pairs that were assorted in their exploratory behaviour (e.g., both individuals being very slow or very fast explorers) had higher fitness (Both, Dingemanse, Drent, & Tinbergen, 2005; Dingemanse, Both, Drent, & Tinbergen, 2004). It was hypothesized that positive assortment may result in better coordination between partners. However, Fargevieille et al. (2017) demonstrated in a long-term study on pair assortment that assortment may vary between years (i.e., across different environmental conditions) and, therefore, warn on the ease to generalize conclusions in short-term studies. In addition, how assortment types influence breeding success may also vary with environmental conditions. Careau, Thomas, Humphries, and Réale (2008) suggested that risk-prone individuals, which constantly exhibit higher energy expenditure, might have higher fitness in favourable food conditions, possibly by outcompeting risk-averse individuals when foraging (e.g., Patrick & Weimerskirch, 2014). By contrast, risk-averse individuals may be advantaged when food availability is more limited due to their lower energy requirement (e.g., Biro & Stamps, 2008). In the context of climate change, food shortage events may become more frequent, thereby possibly selecting for risk-averse individuals (Careau et al., 2008) and therefore reducing genetic diversity of a species.

The endangered African penguin (*Spheniscus demersus*) is a monogamous long-lived species with bi-parental care (Hockey, Dean, & Ryan, 2005). During the breeding season, both parents defend the nest but males are known to be more territorial (Hockey et al., 2005). The marine environment in South Africa is currently under an ecosystem shift (e.g., Mhlongo, Yemane, Hendricks, & van der Lingen, 2015) and impacts African penguin breeding success, which is known to fluctuate with food availability (Crawford et al., 2006; Sherley et al., 2013). However, the way individual nest defence behaviour may influence reproductive output during contrasting environmental conditions remains unknown. Understanding this relation and the influence of pair assortment may be especially important in this species because being long-lived and generally faithful to their partner (Culina, Radersma, & Sheldon, 2015), mate choice may have long-term consequences on their fitness.

In this study, we explored (i) whether boldness and mobility in nest defence (both associated with risk-taking, Réale et al., 2007) may be consistent in African penguins and could, potentially, be assimilated to personality traits in that species; (ii) if individual nest defence behaviour and pair assortment by behaviour may influence breeding success; and (iii) if this relation may vary with food conditions. We hypothesized that males would be risk-prone (bolder and more mobile) than females when defending their nests because of a potential biased sex ratio towards males in that population (Pichegru & Parsons, 2014; Spelt & Pichegru, 2017). Males will, therefore, ensure the keeping of a territory (Sundström, Petersson, Höjesjö, Johnsson, & Järvi, 2004) to maximize their chance to reproduce. In addition, female exhibiting risk-prone behaviour may not be advantage because of high physiological costs of breeding (see Betini & Norris, 2012). We also expected a dominance and a greater success of assorted pairs per nest defence behaviour, as assortment may result in an increase of coordination in parental care (Schuett, Dall, & Royle, 2011; Schuett et al., 2010), which may increase their breeding success. We predicted that bolder birds and bolder pairs would be more successful in favourable environmental conditions while at the opposite, shyer birds and pairs would be more successful during poorer conditions (Careau et al., 2008), although dis-assortment may buffer the cost on the breeding output of risk-prone behaviour (Rosvall, 2009). This research aimed to explore for the first time the potential influence of African penguin risk-taking behaviour (possibly personality) on their breeding success, and how this relation may vary with environmental conditions.

2 | METHOD

2.1 | Study site and species

Data were collected between April and June 2015 and 2016, during the peak breeding season on Bird Island (33°50'S, 26°17'E) Algoa Bay (South Africa), which hosts approximately 2,500 breeding pairs of African penguins (Pichegru et al., 2013). Their population has been stable over the past decade (Crawford et al., 2016). Around late January, male and female breeders return to the colony to initiate the breeding season (Pichegru, 2013). Males engage in ecstatic and agonistic behaviours, and while females can also do so, it is less frequent (Hockey et al., 2005). Approximately a month after copulating, females will lay generally two eggs and both parents will alternate self-maintenance and incubation for ca. 40 days (Hockey et al., 2005). Once the eggs hatched, parents will continue to share equally parental duties, alternating brood protection and foraging trips at sea (Hockey et al., 2005) for two to four months.

Environmental conditions around the island contrasted between the 2 years of our study, as was suggested by penguins' foraging effort data, collected as part of a long-term monitoring (Pichegru et al., 2012). Indeed, foraging effort of breeding adults was much higher in 2016 than in 2015 (Pichegru L. unpubl., Appendix 1), indicating possible high food availability in 2015, while 2016 was marked by a strong El Niño event (Barnard et al., 2017) and poorer environmental conditions.

All ethical permits and relevant approvals were obtained from South African National Parks, the Department of Environmental Affairs and Nelson Mandela University.

2.2 | Approach protocol

Boldness and mobility in nest defence were assessed through a standard protocol of pedestrian approach to 1 m of the nest (Betini & Norris, 2012; Kontiainen et al., 2009; Pichegru, Edwards, Dille, Flower, & Ryan, 2016). Because of the endangered status of the species on the IUCN red list (Birdlife International 2015), the experiment was designed to minimize disturbance and limit the risk of temporary nest desertion. In case of nest desertion, the experiment was terminated and the experimenter withdrew from the area.

Nests selected contained chicks 1–3 weeks old. An experimenter approached the nests at a constant pace of 0.5 m/s, then crouched 1 m away from the nest and extended a wooden pole to a few centimetres away from the penguin's head (a standard protocol in African penguin research to mark individuals without handling them) for 30 s while the behaviour of the bird was recorded by a video camera. The experiment took place when only one parent was on the nest to avoid the other parent's behaviour to influence the reaction of the targeted individual (Schuett & Dall, 2009). Each trial was conducted by the same experimenter (G. T.), and no other human was in the vicinity of the nest. Behaviours were not recorded during the approach but only when the experimenter was within one metre from the nest, and the pole was extended. Before leaving the vicinity of the nest, the experimenter marked the targeted penguin with a non-toxic animal crayon attached to the wooden pole. We could not control for the start distance of the approach due to the topography of the area. However, the videos showed that the small number of birds (19 penguins) who noticed the experimenter only when she was within 5 m of their nests did not differ from those (144 penguins) that saw the approaching human earlier (attack: $X^2 = 0.20$, $df = 1$, $p = .66$; threat: $X^2 = 2.80$, $df = 1$, $p = .09$; alertness: $X^2 = 0.74$, $df = 1$, $p = .39$; backward movements: $X^2 = 0.31$, $df = 1$, $p = .58$).

In 2016, due to technical issues, the approaches could not be recorded on video; therefore, the protocol was adapted using observations from 2015 (see details below).

2.3 | Boldness and mobility in nest defence

From the video footage, penguins' responses to a human approach were analysed using behaviours described in Pichegru et al. (2016) (Table 1). Boldness level in nest defence was estimated from four variables: counts of attacks and threats, as well as alertness and backward movements (see Table 1). In this study, individuals were termed "bold" when they displayed more attacks and threats, and less alertness and backward movements. We also calculated a mobility index by summing the total number of all movements (attacks, threats, alertness and backward movements) when the experimenter was within a metre from the nest.

TABLE 1 Behaviours used to estimate boldness and mobility in nest defence behaviour of African penguins in response to a standard pedestrian approach on Bird Island, Algoa Bay, South Africa (inspired from Pichegru et al., 2016)

Behaviours	Description
Backward movement	Individual backward lifting from a standing or sitting position and/or shifting away from its nest backward
Alertness	Head up and watchful of environment and conspecifics; stand with neck fully retracted, head held horizontal or slightly above horizontal with eyes half-closed or blinked and rotated slightly from side to side; single event was scored as horizontal head turn to left or right when the bird was in watchful position
Threat	<i>Head turn</i> : alternate stare (neck fully retracted or extended to varying degree while the head is rotated from side to side alternately and irregularly, sometimes held briefly on one side); single event was scored as vertical head turn from 0 to 180° from a forward-facing position
Attack	<i>Non-reaching attack</i> : basic threat in which the targeted bird points directly towards the object of aggression while the head is fully extended to a greater or lesser degree; <i>attack</i> : reaching or pecking recipient within reach (wooden stick)

In 2016, as no video footage was recorded, nest defence was only assessed from the number of backward movements and of attacks, respectively, representative of “flight and fight” behaviours (Eilam, 2005). Comparisons between years were made using two categories: the median number of all attacks exhibited by individual birds was four; therefore, a category of shy individuals was defined as ≤4 attack events or at least a backward movement, while bold nest defender displayed >4 attacks but no backward movement (only one bird made one backward movement and displayed >4 attacks simultaneously).

2.4 | Repeatability

Behaviours are defined as part of personality if they are repeatable (Réale et al., 2007; Sih et al., 2004). To assess the stability of the different behaviours constituting boldness and mobility in nest defence over time, we repeated the approach twice during the 2015 breeding season on a subsample of 19 individuals, after a time lapse of 5 days before each trial (i.e., three assessments in total within 10 days). One additional individual was only tested twice as it was inadvertently approached between the second and third trial. Penguins on which repeatability was tested were selected from the first assessment to represent the full range of personality types present in the colony. During this period, penguins involved in the repeatability trial were not disturbed by any human approach to avoid potential habituation (Ellenberg, Mattern, & Seddon, 2009; Patrick & Weimerskirch, 2014). In 2016, 13 birds tested in 2015 were re-sighted rearing chicks and personality tests were conducted again on eight of them. The five other birds tested were not at comparable breeding stages, which may have influenced their response (Pichegru et al., 2016). Due to a small sample size in 2016 and a difference of methods of data collection between years, the repeatability across years was not statistically analysed.

2.5 | Adult sexing and reproductive output

Adults were sexed from their morphometric measurements (bill length and depth, flipper length and mass) using the Discriminant Function

Analysis (DFA) described in Pichegru et al. (2013). Morphometric measurements were assessed for a total of 82 nests in 2015 (82 females and 81 males) and 97 nests in 2016 (97 females and 89 males). Penguins were gently caught from their nest and carried away to be measured. Once measurements were taken, the birds were placed back on their nests (within 5 min), ensuring they do not desert their brood. This protocol is standard for African penguins and provides minimum disturbance. Both partners within pairs were measured and when results of the DFA gave two individuals of the same sex within a pair, the individual with at least three morphometric measures larger than its partner was assigned to be a male (Cooper, 1972; Pichegru et al., 2013).

We recorded the number of chicks in a nest (dead or alive) at the beginning of the field season to estimate the initial clutch size (163 nests in total). All nests chosen had similar chick age (ca 1 week). We then estimated an index of chick survival (for 245 chicks) at the end of the 3–5 weeks of our study period: (0) the chick died, (1) the chick survived.

We also determined chick growth rates by weighing chicks every 5/6 days. Growth increments (GI, in g/day) were calculated using mass changes between two consecutive measurements:

$$GI = (M2 - M1)/(T2 - T1)$$

with M1 and M2 the chick mass at T1 and T2, the respective dates in day at which they were measured. Individual chick growth rate was obtained by averaging all individual growth increments. Because clutch size did not affect chick growth during both 2015 and 2016 seasons (LMM: $t = -0.75$, $df = 92$, $p > .05$), we used the grand mean of growth rates per nest. Average growth rates were estimated for 164 nests (74 in 2015 and 90 in 2016), 145 of which we also assessed parental nest defence behaviour.

2.6 | Statistical analyses

All statistical analyses were performed using R (R × 64 3.2.2 version). Boldness (i.e., number of threats, attacks, backward movements and alertness) and mobility indices as counted in 2015 were

analysed separately from the 2015/2016 nest defence categories. From the 2015 count data, we assessed repeatability for all behaviours separately and for mobility. In addition, we investigated differences in behaviour between sexes and explored patterns of pair assortment. The 2015/2016 categories were then used to estimate the influence of individual behaviour and of pair assortment on breeding success during the 2 years of contrasting environmental conditions.

The repeatability indices (R , $R = 1$ highly consistent, $R = 0$ non-consistent) of boldness and mobility were estimated using generalized linear mixed-effect models (GLMM, using rptR package, following Nakagawa & Schielzeth, 2010) with the behaviour as dependant variable and the bird's ID as random effect using Poisson's distributions. Mobility index and the different behaviour constituting boldness were then averaged for every bird which was approached several times.

A correlation matrix was used to assess the level of correlation between the different behaviours extracted from the human approach protocol using Spearman's method. A multivariate model (count data, MCMCglmm package) and a generalized linear model (GLM, mobility index) were performed to assess whether sex influenced individual behaviour in 2015 with the behaviour as dependent variables and sex as fixed effect. GLMs were used to assess pair assortment in each behaviour, with male's behaviour as dependent variable and female's behaviour as fixed effect.

The influence of nest defence on reproductive success was assessed using GLMs with initial clutch size or chick growth rates as dependant variables using Binomial and Gaussian distribution, respectively, and using a GLMM for chick survival. The interaction between female and male nest defence behaviour and the year were set as fixed effect in the full models (see Appendix 2). For chick survival, nest was set as random effect and clutch size was nested in this last parameter to control for the brood size (see Appendix 2). To avoid any information loss (Burnham, Anderson, & Huyvaert, 2011), all models were averaged performing a multi-model inference technic (package MuMIn). The final output was generated using model probabilities (i.e., model weight, see Burnham et al., 2011; Appendix 2).

3 | RESULTS

From all the birds approached (163 penguins in 2015 and 186 in 2016), only one individual temporarily deserted its nest during the marking which followed the behavioural test. Several days later, we noticed the absence of its partner, which may have explained this individual's extreme response to the experiment. We ceased the nest monitoring for this bird and removed the data from the analyses.

3.1 | Indices of personality, sex and pair assortment in 2015

Consistency trials conducted in 2015 for 20 individuals revealed a high individual repeatability (R) in boldness degree (attacks: $R = 0.68$, $p < .001$; threats: $R = 0.84$, $p < .001$; alertness: $R = 0.69$, $p < .001$; backward movements: $R = 0.58$, $p = .002$) and mobility index ($R = 0.64$ and $p < .001$). The different estimates of boldness and mobility were, therefore, averaged per penguin when the human approach protocol was repeated.

Mobility was strongly correlated with the number of threats ($r = .83$, $p < .001$) and weakly to the number of attacks ($r = .15$, $p = .05$), while the number of attacks was significantly correlated with all other movements (all $p < .001$, Table 2). Alertness and backward movements were also correlated to each other ($r = .21$, $p = .01$).

In 2015, nest defence behaviour was assessed for 82 females and 81 males from a total of 82 nests. Sex did influence boldness degree (post-mean = -0.02 , $p = .04$) and mobility ($z = 3.19$, $p = .001$) in African penguin. Indeed, female generally exhibited less movements than males ($Mob_{female} = 16.35 \pm 7.11$, $Mob_{male} = 18.44 \pm 6.74$) and tended to be shyer on average when defending their nest (Figure 1), that is doing more backward movements (Figure 1a) and performing less threats (Figure 1c). Nevertheless, the number of alertness (Figure 1b) and of attacks (Figure 1d) was similar between sexes (Figure 1a and 1c).

Female mobility was positively associated with male mobility ($z = 3.29$, $df = 78$ and 79 , $p = .001$), which seemed to suggest

Parameters	Mobility	Attack	Threat	Alertness	Backward movement
Correlation coefficient					
Mobility	X	X	X	X	X
Attack	.15	X	X	X	X
Threat	.83	-.28	X	X	X
Alertness	-.01	-.44	-.14	X	X
Backward movement	-.05	-.31	-.02	-.021	X
p-Value associated					
Mobility	X	X	X	X	X
Attack	.05	X	X	X	X
Threat	<.001	<.001	X	X	X
Alertness	.86	<.001	.07	X	X
Backward movement	.49	<.001	.76	.01	X

TABLE 2 Correlation matrix between all the nest defence behaviours exhibited by African penguin rearing chicks during a standard pedestrian approach, on Bird Island, Algoa Bay, South Africa in 2015

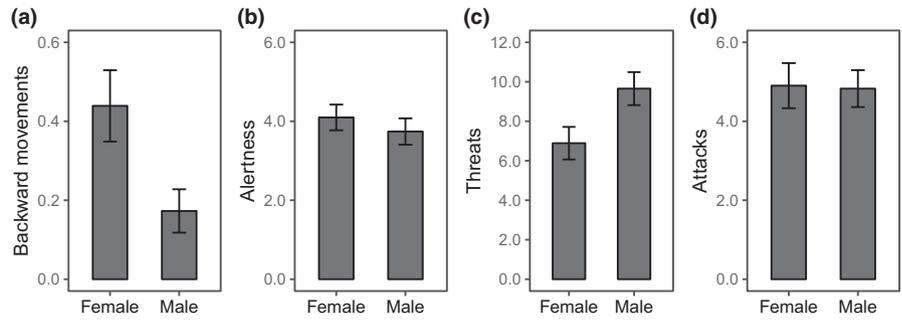


FIGURE 1 Average (± SE) number of (a) backward movements, (b) alertness, (c) threat and (d) attack exhibited by females and males African penguins in response to a human approach experiment during the chick-rearing period on Bird Island, Algoa Bay (South Africa)

assortment by mobility within pairs during our study, although the correlation was weak (Figure 2a). Parents were also positively assorted by the number of threats displayed ($F = 10.21, df = 1, p = .002$, Figure 2b).

3.2 | Nest defence, reproductive success and environmental conditions

Most clutches were constituted of two chicks (70.29% both years combined) and clutch size did not differ between years ($z = 0.90, p = .36$), nor with female ($z = 0.43, p = .67$) or male nest defence behaviour categories ($z = 0.56, p = .57$). Similarly, clutch size was not affected by the interaction between both adult nest defence ($z = 0.96, p = .33$).

Average chick growth rates per nest was significantly higher in 2015 (48.33 ± 9.62 g/day) than in 2016 (32.81 ± 11.64 g/day) ($N = 145, z = 8.71, p < .001$). In both years, chicks from bolder females ($z = 2.17, p = .03$) and bolder males ($z = 1.93, p = .05$) had slower growth rates (Figure 3). These results were accentuated in 2016 (female: $\text{diff}_{\text{mean 2015}} = 2.85, \text{diff}_{\text{mean 2016}} = 7.32$; male: $\text{diff}_{\text{mean 2015}} = 2.79, \text{diff}_{\text{mean 2016}} = 6.57$; Figure 3). Contrarily, the interaction between male and female boldness degree did not influenced the growth rates of their chicks ($z = 0.33, p = .74$).

Overall, there were a large proportion of nests which did not lose any chick throughout the field season (2015: 75.5% and 2016: 60.2%). However, chick survival was lower in 2016 compared to 2015 on Bird Island ($z = 2.61, p = .01$). Survival was slightly lower when chicks were raised by a bold male (20.90% of chicks raised by a bold male died against 14.81% for a shy one) but not significantly so ($z = 1.06, p = .28$). At the opposite, neither female boldness degree ($z = 0.15, p = .88$) nor the interaction between male and female behaviour ($z = 0.24, p = .81$) did influence chick survival.

4 | DISCUSSION

Our findings reveal that boldness degree and mobility in nest defence in African penguins are repeatable and potentially related to personality in that species. We show here for the first time that African penguin risk-taking behaviour in nest defence is associated with their reproductive output, with pairs containing at least one risk-prone parent being disadvantaged, especially during years in which food availability may be low.

Repeatability of both boldness and mobility of African penguins rearing chicks was high in our study. The stability of these traits indicates that these behaviours might be associated to personality in African penguin, even if our sample size was small ($N = 20$). This observed high repeatability might be a result of our small sample size but also possibly the short period of time we repeated our tests in (i.e., over 10 days). Nevertheless, the individuals re-sighted and re-tested in 2017 ($N = 22$) had similar nest defence behaviour ($R = 0.46, p = .01$, Trainsel G. & Pichegru L., unpubl. data), thereby supporting our hypothesis that this behaviour may be related to personality in African penguins.

In accordance with our hypothesis, male African penguins were more risk-prone compared to females, as they generally are the ones claiming a territory and attracting a mate (Hockey et al., 2005). They might be particularly risk-prone on Bird Island as a skewed adult sex ratio in favour of males on Bird Island has been recently hypothesized, as a possible consequence of (i) a biased brood sex ratio in favour of males (Spelt & Pichegru, 2017) and (ii) a higher mortality of juvenile and adult females (Pichegru & Parson 2014). Skewed adult sex ratio may increase the competition between males to access females (Donald, 2007), therefore favouring males displaying a higher level of risk to keep a territory (Sundström et al., 2004) ensuring their chance to reproduce especially when competition for mate is high.

In the wild, mate choice relies on a complex mechanism in which environmental conditions must be considered as pair assortment may vary from a year to another depending on the benefit of being assorted or dis-assorted (Fargevieille et al., 2017; Schuett et al., 2010). For example, exhibiting an energetically expensive level of nest defence might be an advantage to secure a nest site and/or a mate, but be mal-adaptive when food is scarce (Careau et al., 2008). Therefore, risk-prone individuals could choose a risk-averse mate to reduce the costs of their behaviour (Rosvall, 2009). Previous studies have documented signs on both dis-assorted (great tits, Dingemanse et al., 2004) and assorted mating (zebra finches, Schuett, Dall, et al., 2011; dumpling squid *Euprymna tasmanica*, Sinn, Apiolaza, & Moltschaniwskij, 2006) in risk-taking behaviour (i.e., exploration behaviour and boldness). However, other studies on mate assortment, whether related to behaviour or other individual characteristics (e.g., plumage colour), indicated either clear pair assortment (Grist et al., 2017) or a fluctuation in pair assortment between years (Fargevieille et al., 2017). Adult African penguins tended to assort positively by behaviour with their partner (i.e., similar index of mobility and similar number of threats), but the relations were

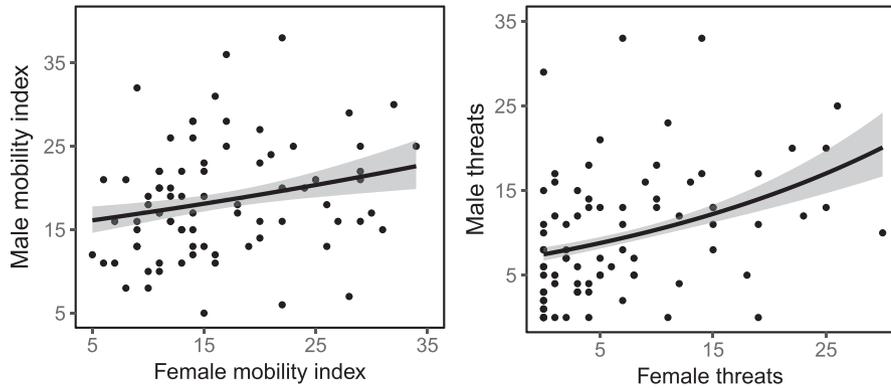


FIGURE 2 Within pair relation of female and male (a) mobility index and (b) number of threats when responding to a human approach during the chick rearing period on Bird Island, Algoa Bay (South Africa)

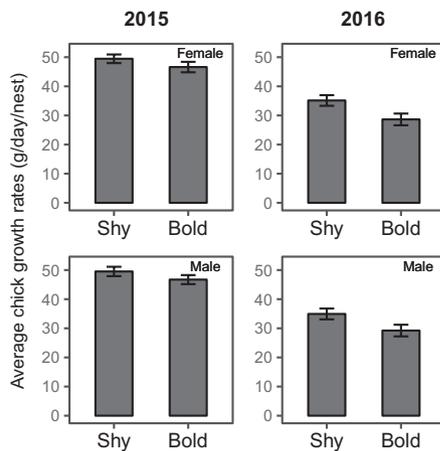


FIGURE 3 Average (\pm SE) growth rates of chicks raised by shy and bold adult females (top panel) and males (bottom panel) African penguins in 2015 (left panel) and 2016 (right panel) on Bird Island, Algoa Bay (South Africa)

weak, which suggests an overall diversity of pair assortment. This diversity may be maintained throughout years, due to varying advantages of one behaviour type or another according to environmental conditions.

Risk-prone and risk-averse individuals exhibit a differential investment in parental duties (Hollander et al., 2008) which may affect their success. Risk-prone individuals usually invest more energy in their reproductive effort (Careau et al., 2008; Hollander et al., 2008) by acquiring and defending good territories, outcompeting risk-averse individuals (Sundström et al., 2004). This high rate of energy expenditure may become too costly when food availability is limited (Biro & Stamps, 2008; Careau et al., 2008). In African penguins, a reduced energy allocation in foraging effort from bold parents could have resulted in the observed lower offspring's growth rates, especially in 2016, when high foraging effort suggested low food availability (Appendix 1). Post-fledging survival is lower in chicks with longer rearing periods, that is which grew more slowly (Sherley et al., 2013), probably due to reduced fat reserves. Therefore, even though survival of chicks from bold adults was similar to that of shy ones, overall fitness of bold parents is probably lower due to a possible higher post-fledging mortality of their offspring. In contrast, shy African penguins (i.e., risk-averse

birds) might have balanced their energy allocation when the resources were limited (Biro & Stamps, 2008; Careau et al., 2008), resulting in higher breeding success (e.g., Barnett, Thompson, & Sakaluk, 2012). Given the overall lower reproductive success (chick growth) of bold parents, we hypothesize that risk-prone defenders may decrease the overall success of the nest, regardless of the type of assortment. A high level of boldness in nest defence could be mal-adaptive on Bird Island since 2010 when the only predator at the nest (i.e., kelp gulls *Larus dominicanus*) started to be regularly culled (Pichegru, 2013). However, and at this stage of the study, it is difficult to favour one hypothesis or another. Altogether, our results suggest that individual risk-taking behaviour may influence population dynamics of this endangered species, by leading to inter-individual differences in breeding success according to behavioural types in a fluctuating environment. Overall, risk-prone birds did not exhibit any advantage; however, the time scale of the study may not have been long enough to allow observation when these birds may also be at advantages.

This work highlights the importance of behavioural studies in understanding some mechanisms behind population dynamics, particularly in African penguins where population decline urges a better understanding of all factors influencing population trends. It also underlies the importance of considering parental assortment in behaviour when looking at their reproductive success. Across years, the fluctuating selection occurring on the behaviour at the nest may allow penguins to maintain the behavioural diversity and therefore the genetic diversity observed in the colony (Dingemanse et al., 2004). However, as a direct impact of climate change and anthropogenic activities (Coetzee, Van Der Lingen, Hutchings, & Fairweather, 2008; Mhlongo et al., 2015), the abundance of small pelagic fish (i.e., sardines, *Sardinops sagax* and anchovies, *Engraulis encrasicolus*), the main prey of breeding African penguins (Pichegru et al., 2012), has declined locally (Coetzee et al., 2008). This decline of the small pelagic stocks might act as a directional selection by decreasing the fitness of risk-taking birds, thus reducing the behavioural diversity in the penguin population of Bird Island. Further work involving the use of Individual-Based Models (IBM) could reveal which mechanisms may underlie some of these inter-individual variations in breeding success, notably by investigating individual differences in parental care and/or foraging effort in relation to behavioural consistency across years.

ACKNOWLEDGEMENT

A great thanks to L. Edwards and Raggy charters, R. Hickcox, M. Nyahamba, J. Raath, P. V. Rukini, A. Spelt, G. Sutton and rangers from the South African National Parks (SANParks) for their help collecting data. Thanks to V. Goodall for her input on the statistical analyses and T. Clemen, the editor of *Ethology* and two anonymous referees for constructive comments on previous versions of the manuscript. Financial and logistical supports were provided by DST-NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology, the Institute for Coastal and Marine Research and Department of Zoology at the Nelson Mandela Metropolitan University. Finally, we would like to thank the SANParks, the Department of Environmental Affairs and Nelson Mandela Metropolitan University for providing all appropriate permits and ethic clearance.

ORCID

Gwendoline Trainel  <http://orcid.org/0000-0003-2868-2878>

REFERENCES

- Barnard, P. L., Hoover, D., David, M., Hubbard, D. M., Snyder, A., Ludka, B. C., ... Serafin, K. A. (2017). Extreme oceanographic forcing and coastal response due to the 2015–2016 El Niño. *Nature Communications*, 8, 14365. <https://doi.org/10.1038/ncomms14365>
- Barnett, C. A., Thompson, C. F., & Sakaluk, S. K. (2012). Aggressiveness, boldness and parental food provisioning in male house wrens (*Troglodytes aedon*). *Ethology*, 118(10), 984–993. <https://doi.org/10.1111/j.1439-0310.2012.02092.x>
- Benhamou, S. (2004). How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology*, 229(2), 209–220. <https://doi.org/10.1016/j.jtbi.2004.03.016>
- Betini, G. S., & Norris, D. R. (2012). The relationship between personality and plasticity in tree swallow aggression and the consequences for reproductive success. *Animal Behaviour*, 83(1), 137–143. <https://doi.org/10.1016/j.anbehav.2011.10.018>
- Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23(7), 361–368. <https://doi.org/10.1016/j.tree.2008.04.003>
- Both, C., Dingemanse, N. J., Drent, P. J., & Tinbergen, J. M. (2005). Pairs of extreme avian personalities have highest reproductive success. *Journal of Animal Ecology*, 74(4), 667–674. <https://doi.org/10.1111/j.1365-2656.2005.00962.x>
- Brommer, J. E., Karell, P., Ahola, K., & Karstinen, T. (2014). Residual correlations, and not individual properties, determine a nest defense boldness syndrome. *Behavioral Ecology*, 25(4), 802–812. <https://doi.org/10.1093/beheco/aru057>
- Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65(1), 23–35. <https://doi.org/10.1007/s00265-010-0102-9>
- Burtka, J. L., & Grindstaff, J. L. (2013). Repeatable nest defense behavior in a wild population of Eastern bluebirds (*Sialia sialis*) as evidence of personality. *Acta Ethologica*, 16(3), 135–146. <https://doi.org/10.1007/s10211-013-0143-7>
- Careau, V., Thomas, D., Humphries, M. M., & Réale, D. (2008). Energy metabolism and animal personality. *Oikos*, 117(5), 641–653. <https://doi.org/10.1111/j.2008.0030-1299.16513.x>
- Caro, T. M. (2005). *Antipredator defense in birds and mammals*. Chicago, IL: University of Chicago Press.
- Carrillo, J. & Aparicio, J. M. 2001: Nest defence behaviour of the Eurasian kestrel (*Falco tinnunculus*) against human predators. *Ethology*, 107(10), 865–875.
- Coetzee, J. C., Van Der Lingen, C. D., Hutchings, L., & Fairweather, T. P. (2008). Has the fishery contributed to a major shift in the distribution of South African sardine? *ICES Journal of Marine Science*, 65(9), 1676–1688. <https://doi.org/10.1093/icesjms/fsn184>
- Cooper, J. (1972). Sexing the jackass penguin. *Safring News*, 1, 23–25.
- Crawford, R. J. M., Barham, P. J., Underhill, L. G., Shannon, L. J., Coetzee, J. C., Dyer, B. M., ... Upfold, L. (2006). The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biological Conservation*, 132(1), 119–125. <https://doi.org/10.1016/j.biocon.2006.03.019>
- Crawford, R. J., Makhado, A. B., Whittington, P. A., Randall, R. M., Oosthuizen, W. H., & Waller, L. J. (2016). A changing distribution of seabirds in South Africa—the possible impact of climate and its consequences. *Climate Change and Marine Top Predators*, 43, <https://doi.org/10.3389/fevo.2015.00010>
- Culina, A., Radersma, R., & Sheldon, B. C. (2015). Trading up: the fitness consequences of divorce in monogamous birds. *Biological Reviews*, 90(4), 1015–1034. <https://doi.org/10.1111/brv.12143>
- Davies, N. B., Krebs, J. R. & West, S. A. (2012). *An introduction to behavioural ecology*. Hoboken, NY: John Wiley & Sons.
- Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 271(1541), 847–852. <https://doi.org/10.1098/rspb.2004.2680>
- Dingemanse, N. J., Kazem, A. J., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25(2), 81–89. <https://doi.org/10.1016/j.tree.2009.07.013>
- Donald, P. F. (2007). Adult sex ratios in wild bird populations. *Ibis*, 149(4), 671–692. <https://doi.org/10.1111/j.1474-919X.2007.00724.x>
- Eilam, D. (2005). Die hard: a blend of freezing and fleeing as a dynamic defense-implications for the control of defensive behavior. *Neuroscience & Biobehavioral Reviews*, 29(8), 1181–1191. <https://doi.org/10.1016/j.neubiorev.2005.03.027>
- Ellenberg, U., Mattern, T., & Seddon, P. J. (2009). Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. *Animal Behaviour*, 77(2), 289–296. <https://doi.org/10.1016/j.anbehav.2008.09.021>
- Fargevielle, A., Grégoire, A., Charmantier, A., Rey Granado, M., & Doutrelant, C. (2017). Assortative mating by colored ornaments in blue tits: space and time matter. *Ecology and Evolution*, 7(7), 2069–2078. <https://doi.org/10.1002/ece3.2822>
- Garamszegi, L. Z., Markó, G., & Herczeg, G. (2012). A meta-analysis of correlated behaviours with implications for behavioural syndromes: Mean effect size, publication bias, phylogenetic effects and the role of mediator variables. *Evolutionary Ecology*, 26(5), 1213–1235. <https://doi.org/10.1007/s10682-012-9589-8>
- Grist, H., Daunt, F., Wanless, S., Burthe, S. J., Newell, M. A., Harris, M. P., & Reid, J. M. (2017). Reproductive performance of resident and migrant males, females and pairs in a partially migratory bird. *Journal of Animal Ecology*, <https://doi.org/10.1111/1365-2656.12691>
- Hockey, P. A. R., Dean, W. R. J. & Ryan, P. G. (2005). *Roberts birds of Southern Africa*, 7th ed. Cape Town: The Trustees of the John Voelcker Bird Book Fund. In PubMed, Abstract OpenURL.
- Hollander, F. A., Van Overveld, T., Tokka, I., & Matthyssen, E. (2008). Personality and nest defence in the great tit (*Parus major*). *Ethology*, 114(4), 405–412. <https://doi.org/10.1111/j.1439-0310.2008.01488.x>
- Knight, R. L., & Temple, S. A. (1988). Nest defense behavior in the red-winged blackbird. *Condor*, 90, 193–200.
- Kontianen, P., Pietiäinen, H., Huttunen, K., Karell, P., Kolunen, H. & Brommer, J. E. 2009: Aggressive Ural owl mothers recruit more

- offspring. *Behavioral Ecology*, 20, 789–796. [arp062](https://doi.org/10.1093/beheco/arp062). <https://doi.org/10.1093/beheco/arp062>
- Krama, T., Bērziņš, A., Rytikönen, S., Rantala, M. J., Wheatcroft, D., & Krams, I. (2012). Linking anti-predator behaviour and habitat quality: group effect in nest defence of a passerine bird. *Acta Ethologica*, 15(1), 127–134. <https://doi.org/10.1007/s10211-011-0117-6>
- Mhlongo, N., Yemane, D., Hendricks, M., & van der Lingen, C. D. (2015). Have the spawning habitat preferences of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) in the southern Benguela changed in recent years? *Fisheries Oceanography*, 24(S1), 1–14. <https://doi.org/10.1111/fog.12061>
- Monaghan, P., Walton, P., Wanless, S., Uttley, J. D., & Bljrn, M. D. (1994). Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge*. *Ibis*, 136(2), 214–222. <https://doi.org/10.1111/j.1474-919X.1994.tb01087.x>
- Montgomerie, R. D., & Weatherhead, P. J. (1988). Risks and rewards of nest defence by parent birds. *The Quarterly Review of Biology*, 63(2), 167.
- Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, 85(4), 935–956. <https://doi.org/10.1111/j.1469-185X.2010.00141.x>
- Orr, H. A. (2009). Fitness and its role in evolutionary genetics. *Nature Reviews Genetics*, 10(8), 531–539. <https://doi.org/10.1038/nrg2603>
- Patrick, S. C., & Weimerskirch, H. (2014). Personality, foraging and fitness consequences in a long-lived seabird. *PLoS One*, 9(2), e87269. <https://doi.org/10.1371/journal.pone.0087269>
- Payne, A. I., Crawford, R. J. & Van Dalsen, A. P. (1989). *Oceans of life off Southern Africa*. Cape Town, South Africa: Vlaeberg Publishers.
- Piatt, J. F., Harding, A. M., Shultz, M., Speckman, S. G., Van Pelt, T. I., Drew, G. S., & Kettle, A. B. (2007). Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series*, 352, 221–234. <https://doi.org/10.3354/meps07078>
- Pichegru, L. (2013). Increasing breeding success of an Endangered penguin: artificial nests or culling predatory gulls. *Bird Conservation International*, 23(3), 296–308. <https://doi.org/10.1017/S0959270912000135>
- Pichegru, L., Cook, T., Handley, J., Voogt, N., Watermeyer, J., Nupen, L., & McQuaid, C. D. (2013). Sex-specific foraging behaviour and a field sexing technique for endangered African penguins. *Endangered Species Research*, 19(3), 255–264. <https://doi.org/10.3354/esr00477>
- Pichegru, L., Edwards, T. B., Dille, B. J., Flower, T. P., & Ryan, P. G. (2016). African Penguin tolerance to humans depends on historical exposure at colony level. *Bird Conservation International*, 26, 307–322. <https://doi.org/10.1017/S0959270915000313>
- Pichegru, L., Grémillet, D., Crawford, R. J. M., & Ryan, P. G. (2010). Marine no-take zone rapidly benefits endangered penguin. *Biology Letters*, 6, 498–501. <https://doi.org/10.1098/rsbl.2009.0913>
- Pichegru, L., & Parsons, N. J. (2014). Female-biased mortality in African penguins. *African Journal of Marine Science*, 36(2), 279–282. <https://doi.org/10.2989/1814232X.2014.920728>
- Pichegru, L., Ryan, P. G., Van Eeden, R., Reid, T., Grémillet, D., & Wanless, R. (2012). Industrial fishing, no-take zones and endangered penguins. *Biological Conservation*, 156, 117–125. <https://doi.org/10.1016/j.biocon.2011.12.013>
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemans, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>
- Redmond, L. J., Murphy, M. T., Dolan, A. C., & Sexton, K. (2009). Parental investment theory and nest defense by Eastern Kingbirds. *The Wilson Journal of Ornithology*, 121(1), 1–11. <https://doi.org/10.1676/07-166.1>
- Redondo, T. (1989). Avian nest defence: theoretical models and evidence. *Behaviour*, 111(1), 161–195.
- Rosvall, K. A. (2009). Do males offset the cost of female aggression? An experimental test in a biparental songbird. *Behavioral Ecology*, 21(1), 161–168. <https://doi.org/10.1093/beheco/arp167>
- Schuett, W., & Dall, S. R. (2009). Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, 77(5), 1041–1050. <https://doi.org/10.1016/j.anbehav.2008.12.024>
- Schuett, W., Dall, S. R. X., & Royle, N. J. (2011). Pairs of zebra finches with similar “personalities” make better parents. *Animal Behaviour*, 81(3), 609–618. <https://doi.org/10.1016/j.anbehav.2010.12.006>
- Schuett, W., Godin, J. G. J., & Dall, S. R. X. (2011). Do female zebra finches, *Taeniopygia guttata*, choose their mates based on their “personality”? *Ethology*, 117(10), 908–917. <https://doi.org/10.1111/j.1439-0310.2011.01945.x>
- Schuett, W., Tregenza, T., & Dall, S. R. (2010). Sexual selection and animal personality. *Biological Reviews*, 85(2), 217–246. <https://doi.org/10.1111/j.1469-185X.2009.00101.x>
- Sherley, R. B., Underhill, L. G., Barham, B. J., Barham, P. J., Coetzee, J. C., Crawford, R. J. M., ... Upfold, L. (2013). Influence of local and regional prey availability on breeding performance of african penguins *Spheniscus demersus*. *Marine Ecology Progress Series*, 473, 291–301. <https://doi.org/10.3354/meps10070>
- Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: an integrative overview. *The Quarterly Review of Biology*, 79(3), 241–277.
- Sinn, D. L., Apiolaza, L. A., & Moltschanivskyj, N. A. (2006). Heritability and fitness-related consequences of squid personality traits. *Journal of Evolutionary Biology*, 19(5), 1437–1447. <https://doi.org/10.1111/j.1420-9101.2006.01136.x>
- Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, 19(2), 448–455. <https://doi.org/10.1093/beheco/arm144>
- Spelt, A., & Pichegru, L. (2017). Sex allocation and sex-specific parental investment in an endangered seabird. *Ibis*, 159(2), 272–284. <https://doi.org/10.1111/ibi.12457>
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, 3(3), 259–268.
- Sundström, L. F., Petersson, E., Höjesjö, J., Johnsson, J. I., & Järvi, T. (2004). Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): implications for dominance. *Behavioral Ecology*, 15(2), 192–198. <https://doi.org/10.1093/beheco/arg089>
- Trivers, R. L. (1972). Parental investment and sexual selection. *Sexual Selection and the Descent of Man, 1871–1971*(August), 136–179.
- Verbeek, M. E. M., Boon, A., & Drent, P. J. (1996). Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour*, 133, 945–963.
- Weatherhead, P. J. (1990). Nest defence as shareable paternal care in red-winged blackbirds. *Animal Behaviour*, 39(6), 1173–1178.
- Whitman, D. W. & Agrawal, A. A. (2009). What is phenotypic plasticity and why is it important. In Taylor & Francis group (Eds), *Phenotypic plasticity of insects: Mechanisms and consequences* (pp. 1–63). USA: Science Publishers. <https://doi.org/10.1201/b10201-2>
- Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447(7144), 581–584. <https://doi.org/10.1038/nature05835>
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8), 452–461. <https://doi.org/10.1016/j.tree.2012.05.001>

How to cite this article: Trainsel G, Pichegru L. Does it always pay to defend one's nest? A case study in African penguin. *Ethology*. 2018;124:74–83. <https://doi.org/10.1111/eth.12704>

APPENDIX 1

Additional methods and results describing contrasting food conditions between 2015 and 2016 breeding season around Bird Island, Algoa Bay (South Africa).

Between March and June 2015 and 2016, we deployed 69 Cat Tracks GPS loggers (43 × 28 mm, ~30 g, Perhold Engineering LLC) during single or consecutive foraging trips on adult African penguins during the rearing period (chicks 1–3 weeks old). Parameters were set to record geographic positions (latitude and longitude) every minute. Maximum distance travelled (MD, km), bearing (from the colony to the maximum distance, degree), trip duration (h), path length (total distance travelled, km) and straightness index (SI, scored between 0 and 1, straightness increases with the score, Benhamou, 2004) were estimated for each trip to assess penguins' foraging effort.

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

Analyses were performed using R software version 3.3.2, "lme4" and "circular" package. Generalized linear mixed-effect models were undertaken with the foraging parameter as dependant variable, year as fixed effect and bird ID as random effect. Maximum distance, trip duration and SI were log-transformed to fulfil normality requirements. Bearing was analysed using a circular ANOVA with the foraging parameter as dependant variable and year as fixed effect.

A total of 144 trips were recorded between 2015 and 2016, and the results are summarized in Table 1A. In overall, penguins spent more time at sea in 2016 than in 2015 ($t = 2.03, p = .04$) and their path was more sinuous ($t = -4.19, p < .001$). In seabird species, foraging parameters and prey availability are tightly related (e.g., Monaghan, Walton, Wanless, Uttley, & Bljrns, 1994). An increase in trip duration is often correlated to decreased prey availability (e.g., Piatt et al., 2007) and increased energy expenditure (Pichegru, Grémillet, Crawford, & Ryan, 2010). Moreover, straightness index is a good indicator of search adjustment to prey availability (Benhamou, 2004). In 2016, the increase in trip duration and the lower SI indicate a reduced prey availability during the rearing period.

APPENDIX 2

Additional methods and results describing the models and their characteristics (AIC and weight) when assessing behavioural impact on breeding success in African penguins rearing chicks in 2015 and 2016 on Bird Island, Algoa Bay (South Africa)

Fixed effects	AIC	Weight
Full model: Chick growth rates ~ Female nest defence × Male nest defence + Year		
n = 145		
Female nest defence + Male nest defence + Year	1,101.50	0.56
Female nest defence × Male nest defence + Year	1,103.56	0.20
Female nest defence + Year	1,104.18	0.15
Male nest defence + Year	1,105.38	0.08
Year	1,108.98	0.01
Null model	1,163.10	0.00
Female nest defence	1,164.13	0.00
Male nest defence	1,166.14	0.00
Female nest defence + Male nest defence	1,167.20	0.00
Female nest defence × Male nest defence	1,171.28	0.00
Full model: Clutch size ~ Female nest defence × Male nest defence + Year		
n = 163		
Null model	199.62	0.30
Year	200.89	0.16
Male nest defence	201.15	0.14
Female nest defence	201.30	0.13
Male nest defence + Year	202.35	0.08
Female nest defence + Year	202.52	0.07
Female nest defence + Male nest defence	202.92	0.06
Female nest defence + Male nest defence + Year	204.07	0.03
Female nest defence × Male nest defence	204.08	0.03
Female nest defence × Male nest defence + Year	205.24	0.02
Full model: Chick survival ~ Female nest defence × Male nest defence + Year + (1 Nest:Clutch size)		
n = 245		
Year	225.87	0.41
Male nest defence + Year	226.80	0.26
Female nest defence + Year	227.92	0.15
Female nest defence + Male nest defence + Year	228.80	0.09
Female nest defence × Male nest defence + Year	230.84	0.03
Null model	231.51	0.02
Male nest defence	232.05	0.02
Female nest defence	233.56	0.01
Female nest defence + Male nest defence	234.10	0.01
Female nest defence × Male nest defence	236.19	0.00