POSSIBLE DRIVERS OF NEST USURPATION IN AFRICAN PENGUINS *SPHENISCUS DEMERSUS*

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, Nelson Mandela University, Port Elizabeth, South Africa (traisnel.gwendoline@gmail.com)

Received 10 January 2018, accepted 27 February 2018

ABSTRACT

TRAISNEL, G. & PICHEGRU, L. 2018. Possible drivers of nest usurpation in African Penguins *Spheniscus demersus*. *Marine Ornithology* 46: 85–88.

Nest usurpation is a relatively common phenomenon in birds but remains poorly documented in penguins. This behaviour may advantage bolder and aggressive individuals and influence population dynamics by affecting breeding success. African Penguins *Spheniscus demersus* are aggressive towards conspecifics during the breeding season when competing for territory. However, nest usurpation is rarely observed in this species. We describe three records of nest usurpation in African Penguins from Bird Island, Algoa Bay (South Africa) in 2017. After a climate-related massive breeding failure, late breeders in search of a territory attacked occupants of earlier-breeding nests, sometimes leading to the death of their brood. These observations may be the consequence of an extreme weather event, which created a marked asynchrony in breeding stages in this specific year, with many birds tending chicks, while others were just beginning to look for territories. This mismatch provided the opportunity for particularly aggressive individuals to decrease the breeding output of less aggressive birds, thereby possibly influencing the species' population dynamics.

Key words: African Penguin, nest displacement, nest stealing, asynchrony

INTRODUCTION

Nest usurpation, when an intruder displaces another individual from its nest, has been previously described in birds, especially in terrestrial species. By usurping a nest, the intruder, which can be either heterospecific (Sumasgutner *et al.* 2016) or conspecific (Leffelaar & Robertson 1985, Pérez-Granados & Lopez-Iborra 2015), may optimize its breeding success (Leffelaar & Robertson 1985). The occupant of the nest may aggressively defend its territory and its brood, resulting in aggressive interactions that induce additional energy costs, and may involve injury and reduced breeding success (Leffelaar & Robertson 1985, Pérez-Granados & Lopez-Iborra 2015). Intensity of nest defence varies among individuals (Montgomerie & Weatherhead 1988), and the chance of losing the nest and brood is particularly higher for passive nest defenders (Moreno *et al.* 1995).

Most seabirds breed colonially and generally defend territories/nests aggressively against conspecifics or heterospecifics (Schreiber & Burger 2002), but the level of aggressiveness generally varies with the breeding stage of the birds, decreasing as the season progresses (Côté 2000). It can also differ among individuals, possibly reflecting different personalities (Grace & Anderson 2014) or differences in hormone levels (Williams 1992). Aggression toward heterospecifics (e.g., McInnes *et al.* 2014) and conspecifics, especially chicks, have been recorded in African Penguins *Spheniscus demersus*, which partially explains the formation of chick crèches, as a protection against aggression from adults (Seddon & van Heezik 1993).

African Penguins generally initiate the first breeding peak of the year synchronously (Randall & Randall 1981). They are vulnerable to high temperatures when incubating in surface nests (Lei *et al.* 2014), and heat waves early in the breeding season during austral summer may result in nest desertion (Frost *et al.* 1976a). Although theft of nest material has been observed in this species (Eggleton & Siegfried 1979), nest usurpation remains undocumented, to our knowledge. During March 2017, on Bird Island, Algoa Bay (South Africa), currently the second largest African Penguin colony globally, there was a massive incubation failure following high temperatures (South African National Parks, unpubl. data). Some adults were successfully rearing chicks in April, especially those sheltered from the sun, while others were just settling down again to re-lay a replacement clutch. This asynchrony resulted in a simultaneous, wide-ranging array of breeding stages in the colony: territory search, pair bonding, incubation, and chick rearing. Between March and July 2017, Bird Island became the scene of daily assaults by penguins on nest occupants (adults with eggs and/or chicks), sometimes resulting in injury or death to some of the occupants. This level of aggressive behaviour had not previously been observed, to our knowledge. In this note, we record only three events, which may be related to individual personality of the penguins involved, but many more were observed during the same year either by researchers or rangers from South African National Parks, who are permanently based on the island.

METHODS

Bird Island is the easternmost colony of the endangered African Penguin and has hosted 2 800 breeding pairs on average since 2011 (Department of Environmental Affairs, unpubl. data). In 2017, as part of a long-term (10-year) monitoring programme taking place during the peak of the breeding season (March–June) on Bird Island, three observations of nest usurpation attempts were recorded, either directly or by a camera. The programme has been investigating African Penguins' responses to environmental variability, including fishing pressure (e.g., Pichegru *et al.* 2012,

McInnes *et al.* 2017). Foraging behaviour of chick-rearing adults is tracked, adult morphometric measures are taken, and, since 2015, their individual personality assessed, while chick growth rates are estimated as a proxy for breeding success (Traisnel & Pichegru 2018). During the breeding season, adult gender is determined using morphometric measurements, with males being larger on average but also systematically larger than their female mates within the pair (Campbell *et al.* 2016). Personality is estimated from boldness in nest defence when attending their offspring in response to a human-approach protocol (details in Traisnel & Pichegru 2018). Overall, bold penguins performed more attacks and threats than shy birds. Two of the three nests involved in the observations were actively monitored.

RESULTS

On 10 April 2017, an incubating female (classified as a "bold" nest defender) was attacked by a large individual, presumably a male. The female fought back and managed to protect her nest against the aggressor. After a few minutes, her mate returned from a foraging trip and joined in protecting their nest, finally deterring the intruder. After hatching, the chicks were monitored throughout their growth and were last seen as fledglings in good condition, with multiple incidents of parental provisioning having been observed.

During the same month, another monitored female (classified as "shy") was chased off her nest by a conspecific after spending three days attending her chicks. Her partner was found dead in the colony the day before the intruder's attack. The smallest of the two chicks in the brood escaped into a neighbour's nest 2 m away, while the first hatched chick was strongly pecked by the aggressor. We intervened and rescued the chick to rehabilitate it, but the injuries were too severe, and it died a few hours later. The surviving chick was handed to the South African Foundation for the Conservation of Coastal Birds (SANCCOB), a centre specialised in hand-rearing chicks.

On 1 April 2017, an adult penguin raising two chicks, one to two weeks of age and in good condition, was attacked by a conspecific. The assault was quick, and the nest occupant immediately escaped, abandoning the chicks, who then followed the parent soon after. The following morning, the nest usurpation was complete, with the aggressor and its mate as new occupants. Six weeks later, the former nest occupant was observed with one of its offspring, which by this stage was near to fledging. Only one of the two chicks from the original brood was still in sight (Fig. 1), although raising just one chick is fairly common in African Penguins (Seddon & van Heezik 1991). The new nest occupant was still occupying the nest and was now brooding two chicks. Both chicks were subsequently spotted in good conditions at a P3 stage (losing down feathers).

DISCUSSION

Most of the nest usurpations observed during the breeding season involved a single aggressor. These unusual events may have been a consequence of (1) a possible reduction of nest material availability owing to unusually dry conditions; and/or (2) a mismatch in the adult physiological state due to asynchronous breeding.

The topography of the island (flat with few shelters) and its history (guano harvest in the 19th and early 20th century; Frost *et al.* 1976b) considerably reduced the availability of suitable nests (i.e., providing shade or shelter). The drought and high temperatures during 2017 may have reduced the availability of plant material, which is extensively used by penguins on this colony to build their nests (Eggleton & Siegfried 1979). In Chinstrap Penguins *Pygoscelis antarctica,* attempts to steal stones from other nests are commonly reported (Moreno *et al.* 1995, Carrascal *et al.* 1995, Fargallo *et al.* 2001), with active nest defence sometimes resulting in injury or death (Moreno *et al.* 1995). The low availability of nest material has been shown to increase theft attempts in this species (Carrascal *et al.* 1995). Theft of nest material is assumed to reduce the energetic costs linked to nest building (Mainwaring & Hartley 2013). While common in African Penguins (Eggleton & Siegfried 1979), nest usurpation has not been documented, to our knowledge. To reduce the cost of building a new nest, penguins may choose to usurp a nest site already occupied by an incubating or rearing bird, possibly because the usurpers had held the territory in a previous year. The contest may advantage the usurper, as incubating or rearing individuals may have depleted energetic resources due to the energetic requirements of nest building, incubation, and chick rearing (Mainwaring & Hartley 2013).

During the first peak of the breeding season, breeding stages are fairly synchronised in Algoa Bay (Randall & Randall 1981), but the massive failure during the incubation phase of 2017, due to prolonged high temperatures, promoted higher levels of asynchronous breeding (South African National Parks, unpubl. data), which may have increased the opportunities for such events. Breeding stages varied widely from one adult to another, resulting in a possible mismatch in the adults' physiological states. A previous study conducted on Bird Island in 2013 revealed the consequence of a similar mismatch, when Cape Gannets *Morus capensis* bred later in the year, and African Penguins initiated an early breeding season (McInnes *et al.* 2014). The simultaneous occurrence of fledgling gannets and aggressive territory-seeking penguins resulted in frequent attacks by adult penguins on gannets, often resulting in the mortality of young gannets (McInnes *et al.* 2014). In early breeding stages, i.e., at the arrival to the colony and during copulation, when agonistic interactions are intense (Williams 1992), penguins exhibit high levels of steroids (e.g., Cherel *et al.* 1994). Therefore, when breeding stages are asynchronous in the colony, African

Fig. 1. Nest usurpation between unrelated African Penguin individuals on Bird Island, Algoa Bay (South Africa). The rectangle highlights a nest, previously usurped, occupied by the new resident, while the circle identifies the previous resident with one of its two remaining chicks in the background.

Penguins seeking breeding territories may be more likely to initiate aggressive interactions toward conspecifics, as observed in this study, due to higher levels of steroid hormones.

Usurpation behaviour may also depend on penguin personality traits, particularly their level of aggressiveness or boldness, which may increase or decrease the initiation of such events. While establishing a nesting territory, bolder and more aggressive birds may successfully usurp the nest of others, but also defend their nest better when assaulted in later breeding stages (i.e., avoiding offspring death), thereby improving their fitness. However, these observations are worrying, as boldness in African Penguins has been shown to be associated with lower breeding success during poorer environmental conditions (Traisnel & Pichegru 2018). Similarly, aggressive male Adélie Penguins *Pygoscelis adeliae* at Cape Crozier, Ross Island (Antarctica) were more likely to be non-breeders, although they held a territory (Ainley 1978). The frequency and intensity of extreme weather events are predicted to increase in the current context of climate change (Parmesan *et al.* 2000). As a result, events like the drought of 2017, which decreased availability of nest material and led to asynchronous breeding, due to nest abandonment following heat waves, may become more frequent, thereby increasing usurpation events. Ultimately, this could reduce the overall breeding success of the colony, first, because aggressors actively kill viable chicks and, second, because bold birds (more likely to assault a nest) have lower breeding success compared to shyer individuals (Traisnel & Pichegru 2018). Should droughts become more frequent, providing adequate numbers of artificial nests suitable for the penguins (e.g., Sherley *et al.* 2012, Lei *et al.* 2014) may limit this indirect negative consequence of climate change on the endangered African Penguin population, a population currently undergoing a rapid decrease.

ACKNOWLEDGEMENTS

Many thanks to H.J. Visser from the South African National Parks (SANParks) for his help collecting data, to R. Vanstreels for his valuable comments on a previous version of the manuscript, and to C. McGeorge for sharing information from Stony Point colony. Financial and logistical support was provided by the DST-NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology, the Institute for Coastal and Marine Research, Raggy Charters, and the Department of Zoology at Nelson Mandela University. We would like to thank the SANParks, the Department of Environmental Affairs, and Nelson Mandela University for providing all appropriate permits and research ethics clearance. Finally, many thanks to D. Ainley and two anonymous referees for constructive comments on the manuscript.

REFERENCES

AINLEY, D.G. 1978. Activity patterns and social behavior of non-breeding Adélie penguins. *Condor* 80 (2): 138-146. doi: 10.2307/1367913.

Campbell, K.J., Farah, D., Collins, S. & Parsons, N.J. 2016. Sex determination of African Penguins *Spheniscus demersus* using bill measurements: method comparisons and implications for use. *Ostrich* 87 (1): 47-55. doi: 10.2989/00306525.2015.1108371.

CARRASCAL, L.M., MORENO, J. & AMAT, J.A. 1995. Nest maintenance and stone theft in the Chinstrap penguin (*Pygoscelis antarctica*). *Polar Biology* 15(8): 541-545. doi: 10.1007/BF00239645.

CHEREL, Y., MAUGET, R., LACROIX, A. & GILLES, J. 1994. Seasonal and fasting-related changes in circulating gonadal steroids and prolactin in king penguins, *Aptenodytes patagonicus*. *Physiological Zoology* 67 (5): 1154-1173. doi: 10.1086/physzool.67.5.30163887.

CÔTÉ, S.D. 2000. Aggressiveness in king penguins in relation to reproductive status and territory location. *Animal Behaviour* 59 (4): 813-821. doi: 10.1006/anbe.1999.1384.

CRAWFORD, R.J., SHANNON, L.J. & WHITTINGTON, P.A. 1999. Population dynamics of the African Penguin *Spheniscus demersus* at Robben Island, South Africa. *Marine Ornithology* 27: 139-147.

Eggleton, P. & Siegfried, W.R. 1979. Displays of the jackass penguin. *Ostrich* 50(3): 139-167. doi: 10.1080/00306525.1979.9634105.

FARGALLO, J.A., DE LEÓN, A. & POTTI, J. 2001. Nest-maintenance effort and health status in chinstrap penguins, *Pygoscelis antarctica*: the functional significance of stone-provisioning behaviour. *Behavioral Ecology and Sociobiology* 50 (2): 141-150. doi: 10.1007/s002650100341.

FROST, P.G.H., SIEGFRIED, W.R. & BURGER, A.E. 1976a. Behavioural adaptations of the Jackass Penguin, *Spheniscus demersus* to a hot, arid environment. *Journal of Zoology* 179 (2): 165-187. doi: 10.1111/j.1469-7998.1976.tb02289.x.

FROST, P.G.H., SIEGFRIED, W.R. & COOPER, J. 1976b. Conservation of the jackass penguin (*Spheniscus demersus* (L.)). *Biological Conservation* 9 (2): 79–99. doi: 10.1016/0006-3207(76)90042-2.

GRACE, J.K. & ANDERSON, D.J. 2014. Personality correlates with contextual plasticity in a free-living, long-lived seabird. *Behaviour* 151 (9): 1281-1311. doi: 10.1163/1568539X-00003185.

LEFFELAAR, D. & ROBERTSON, R.J. 1985. Nest usurpation and female competition for breeding opportunities by tree swallows. *Wilson Bulletin* 97 (2): 221-224.

LEI, B.R., GREEN, J.A. & PICHEGRU, L. 2014. Extreme microclimate conditions in artificial nests for endangered African Penguins. *Bird Conservation International* 24(2): 201-213. doi: 10.1017/S0959270913000671.

MAINWARING, M.C. & HARTLEY, I.R. 2013. The energetic costs of nest building in birds. *Avian Biology Research* 6 (1): 12-17. doi: 10.3184/175815512X13528994072997.

McINNES, A.M., SUAREZ, N., RISHWORTH, G.M., GREEN, D.B., PISTORIUS, P.A. & PICHEGRU, L. 2014. Lumbering the gauntlet: Cape Gannet fledglings killed by African Penguins. *Ostrich* 85 (2): 193-196. doi: 10.2989/00306525.2014.955143.

McINNES, A.M., RYAN, P.G., LACERDA, M., DESHAYES, J., GOSCHEN, W.S. & PICHEGRU, L. 2017. Small pelagic fish responses to fine-scale oceanographic conditions: implications for the endangered African penguin. *Marine Ecology Progress Series* 569: 187-203. doi: 10.3354/meps12089.

MONTGOMERIE, R.D. & WEATHERHEAD, P.J. 1988. Risks and rewards of nest defence by parent birds. *Quarterly Review of Biology* 63(2): 167. doi: 10.1086/415838.

MORENO, J., BUSTAMANTE, J. & VIÑUELA, J. 1995. Nest maintenance and stone theft in the chinstrap penguin (*Pygoscelis antarctica*). *Polar Biology* 15 (8): 533-540. doi: 10.1007/BF00239644.

PARMESAN, C., ROOT, T.L. & WILLIG, M.R. 2000. Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society* 81 (3): 443-450. doi: 10.1175/1520-0477(2000)081<0443:IOEWAC>2.3.CO;2.

PÉREZ-GRANADOS, C. & LÓPEZ-IBORRA, G.M. 2015. Nest failure owing to intraspecific agonistic behaviour in Dupont's Lark *Chersophilus duponti*. *Ornithological Science* 14(2): 117-121. doi: 10.2326/osj.14.117.

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. doi: 10.1016/j.biocon.2011.12.013.

RANDALL, R.M. & RANDALL, B.M. 1981. The annual cycle of the jackass penguin *Spheniscus demersus* at St Croix Island, South Africa. *Proceedings of the Symposium on Birds of the Sea and Shore*. Cape Town. pp. 427-450.

SCHREIBER, E.A. & BURGER, J. 2002. Seabirds in the marine environment. In: SCHREIBER, E.A. & BURGER, J. (Eds.) *Biology of Marine Birds*. Marine Biology Series Boca Raton LA: CRC Press. pp. 1-15.

SEDDON, P.J. & VAN HEEZIK, Y. 1991. Effects of hatching order, sibling asymmetries, and nest site on survival analysis of Jackass Penguin chicks. *Auk* 108 (3): 548-555. doi: 10.2307/4088094.

SEDDON, P.J. & VAN HEEZIK, Y. 1993. Chick creching and intraspecific aggression in the jackass penguin (Conglomerado de pichones y agresión intraespecífica en *Spheniscus demersus*). *Journal of Field Ornithology* 64: 90-95.

SHERLEY, R.B., BARHAM, B.J., BARHAM, P.J., LESHORO, T.M. & UNDERHILL, L.G. 2012. Artificial nests enhance the breeding productivity of African Penguins (*Spheniscus demersus*) on Robben Island, South Africa. *Emu* 112 (2): 97-106. doi: 10.1071/MU11055.

SUMASGUTNER, P., MILLÁN, J., CURTIS, O., KOELSAG, A. & AMAR, A. (2016). Is multiple nest building an adequate strategy to cope with inter-species nest usurpation? *BMC Evolutionary Biology* 16 (1): 97. doi: 10.1186/s12862-016-0671-7.

TRAISNEL, G. & PICHEGRU, L. 2018. Does it always pay to defend one's nest? A case study in African penguin. *Ethology* 124 (1): 74-83. doi: 10.1111/eth.12704.

WILLIAMS, T.D. 1992. Reproductive endocrinology of macaroni (*Eudyptes chrysolophus*) and gentoo (*Pygoscelis papua*) penguins: I. Seasonal changes in plasma levels of gonadal steroids and LH in breeding adults. *General and Comparative Endocrinology* 85(2): 230-240. doi: 10.1016/0016-6480(92)90006-6.