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The influence of nest location and the effect of predator removal on Cape Gannet *Morus capensis* egg predation by Kelp Gulls *Larus dominicanus vetula*

Zanri Strydom^{1,2*} , Lauren J Waller^{3,4} , Mark Brown⁵ , Hervé Fritz^{1,2}  and Jan A Venter^{1,2} 

¹ Department of Conservation Management, Faculty of Science, Nelson Mandela University, George, South Africa

² REHABS International Research Laboratory, CNRS-UCBL-NMU, Nelson Mandela University, George, South Africa

³ Department of Biodiversity and Conservation Biology, University of the Western Cape, Bellville, South Africa

⁴ Southern African Foundation for the Conservation of Coastal Birds (SANCCOB), Cape Town, South Africa

⁵ School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa

* Correspondence: zanri.nature@gmail.com

The breeding range of the Cape Gannet *Morus capensis* currently extends to six of the ten islands formerly utilised by this species. The Cape Gannet is classified as an endangered species with a rapidly declining population. Since the mid-1950s, the global population has declined by 51% due to multiple causes, including egg predation by the Kelp Gull *Larus dominicanus vetula*. To assess the effect of this predation, we monitored 100 nests over an 11-week period in 2018 at the Lambert's Bay colony in South Africa. To assess the effect of selective predator removal on the likelihood of predation, data were collected from 2006 and 2018. Our objective was to assess whether nest location and predator removal affected the likelihood of egg predation. The peripheral nests saw a higher level of egg loss (average 1.5 eggs per week) compared with the central nests (average 1 egg per week). Predator control of Kelp Gulls was implemented in 2015, 2017 and 2018. Between years, selective culling decreased the number of Cape Gannet eggs predated. However, within years, except for 2015, the predation rate on Cape Gannet eggs increased post-culling during the same year of implementation. In all three of the implementation years, predation started again (within 48 hours) after the culling commenced. Predation by this indigenous gull species is natural; however, certain human activities might have supported larger populations of Kelp Gulls leading to elevated predation intensity. The most notable being the ever-increasing existence of dumpsites and other sources of food. Predation is affecting the Cape Gannet breeding population; therefore, we suggest that an alternative, long-term, and sustainable solution be planned and implemented to reduce the effects thereof.

L'influence de l'emplacement des nids et de la suppression de prédateurs sur la prédation des œufs du Fou du Cap *Morus capensis* par les Goélands Dominicains *Larus dominicanus vetula*

L'aire de reproduction du fou du Cap *Morus capensis* s'étend actuellement à six des dix îles autrefois utilisées par cette espèce. Le Fou du Cap est classé comme une espèce en danger, dont la population décline rapidement. Depuis le milieu des années 1950, la population globale a diminué de 51% pour de multiples raisons, dont la prédation des œufs par le Goéland Dominicain *Larus dominicanus vetula*. Nous avons suivi 100 nids sur une période de onze semaines en 2018, à la colonie de Lambert's Bay, en Afrique du Sud afin d'évaluer les effets de cette prédation. Des données ont également été collectées entre 2006 et 2018 afin d'estimer les effets de la suppression sélective des prédateurs. Notre objectif était d'estimer si l'emplacement d'un nid et l'élimination de prédateurs affectent la probabilité de prédation sur les œufs. Les nids localisés à la périphérie ont compté un niveau plus élevé de perte d'œufs (en moyenne environ 1.5 œufs par semaine) que les nids situés plus au centre (en moyenne environ 1 œuf par semaine). Le prélèvement de goélands dominicains a été mis en œuvre en 2015, 2017 et 2018. L'abattage sélectif a permis de réduire le nombre d'œufs du Fou du Cap prédatés entre les années. Toutefois, au cours des années, à l'exception de 2015, le taux de prédation des œufs de Fou du Cap a augmenté après l'abattage sélectif, et ce pendant la même année de mise en œuvre. Pour toutes les trois années de mise en place de cette mesure, la prédation a recommencé (en l'espace de 48 heures) après l'abattage. La prédation est naturelle pour cette espèce indigène de goéland, néanmoins, certaines activités humaines ont peut-être favorisé l'augmentation de la population de goélands dominicains et, de ce fait, accru l'intensité de prédation, l'activité la plus notable étant l'existence croissante de décharges et autres sources de nourriture. La prédation affecte la reproduction de la population de Fous du Cap; c'est pourquoi nous suggérons la planification et mise en œuvre d'une solution alternative, à long terme et durable, afin d'en réduire les effets.

Keywords: conservation, endangered species, Lambert's Bay, nest predation, peripheral nest, selective culling

Supplementary material: available online at <https://doi.org/10.2989/00306525.2022.2110535>

Introduction

The Cape Gannet *Morus capensis* is endemic to southern Africa (Crawford et al. 1983). The species is classified as Endangered, with a global population size estimated at 134 775 pairs in 2018/19 (Sherley et al. 2019). In the course of three generations between 1956 and 2015 the global population declined by about 51.5% (BirdLife International 2018a). This decline was caused by several ongoing threats, which include competition with fisheries species over resources (Pichegru et al. 2009), oil spills (Parsons and Underhill 2005), disease (Khomenko et al. 2018), and predation (Green and Pistorius 2013).

Cape Gannets have six extant breeding colonies, three of which are in South African waters and the other three in Namibian waters (Sherley et al. 2019). Formerly, Cape Gannets bred on four additional islands, in both Namibia and South Africa (Sherley et al. 2019); however, they no longer utilise those islands for breeding because of diminishing food resources and historical guano collection (Crawford et al. 1983). Cape Gannet eggs and small chicks are prone to predation by the Kelp Gull *Larus dominicanus vetula* (Rishworth and Pistorius 2015). This predator species is classified as Least Concern and its population trend is increasing globally (BirdLife International 2018b). Anthropogenic activities provide additional resources to Kelp Gulls (generalist feeders) whose population, unlike specialist-feeding seabird species, has not experienced marked decreases (Whittington et al. 2016). Fishing discards from boats further benefit the population growth of many seabird species, including gulls (Furness 2003). Additional factors that promote Kelp Gull population growth include: *Theba pisana* snails on agricultural land (common in the Western Cape and Eastern Cape provinces); scraps scavenged from seal predation, bycatch and poor waste disposal (Whittington et al. 2016); and urban waste sites (Giaccardi and Yorio 2004). Kelp Gull predation rates on seabirds can fluctuate in terms of space and time (e.g. Voorbergen et al. 2012). Within a season, predation may vary in relation to the time of day (e.g. Voorbergen et al. 2012) and weather conditions experienced (Green and Pistorius 2013). One of the benefits of breeding in a colony is protection against predators (Götmark and Andersson 1984), although the predation rate usually varies between peripheral and central nests (Green and Pistorius 2013). Therefore, the choice of nest site in a colony is especially important to species that display site tenacity, such as in the case of Cape Gannets (Klages 1994) whose eggs are vulnerable to predation.

On-land predation by Kelp Gulls specifically is one threat to Cape Gannet offspring (Sherley et al. 2019) and is considered a conservation concern (BirdLife International 2018a). One conservation action to limit mortality of this seabird includes predator control, like culling wherein the numbers of Kelp Gulls are controlled, particularly when there is an increase in predation on seabird populations (e.g. Pichegru 2013). Some southern African seabird species prone to predation by gulls are classified as Endangered, including the African Penguin *Spheniscus demersus* (Pichegru 2013; BirdLife International 2020), Cape Cormorant *Phalacrocorax capensis* (Voorbergen et

al. 2012; BirdLife International 2018c) and Cape Gannet (Rishworth and Pistorius 2015; BirdLife International 2018a). One way to investigate the effect of predation on seabird populations is to determine the proportion of the population lost in relation to the number of breeding pairs in a specific year (Makhado et al. 2006). Estimation of the proportion that is predated could give an indication of the sustainability of the predation and whether predator control should be implemented. Selectively removing the predators through selective culling (Makhado et al. 2006) has helped the recovery of some seabird populations (Sanz-Aguilar et al. 2009), and it is not an uncommon approach (Goodrich and Buskrik 1995). Even so, predator removal can sometimes have unintended consequences, such as increased predator immigration (Lisnizer et al. 2014). Territories freed by the removal of gulls are filled by new gull individuals (Pichegru 2013); hence, to optimise the efficacy of conservation management interventions, an understanding of the predation dynamics on site is required. In this study we aimed to determine the effect of nest location on the predation of Cape Gannet eggs, the temporal aspects of predation, and the effect that the number of Cape Gannet breeding pairs has on predation of their eggs. We also aimed to determine the effect that culling has had on the number of Cape Gannet eggs predated, to assess the efficiency of this approach as a tool to manage the impact of Kelp Gull predation on Cape Gannet eggs.

Materials and methods

Study area

The Cape Gannet colony at Lambert's Bay, South Africa, is situated on Penguin (Bird) Island (32°05'24.43" S, 18°18'9.47" E), a 3-ha (Duffy and La Cock 1985) provincial nature reserve in the Benguela upwelling system on the Atlantic coast (David et al. 2003). The island is protected under the jurisdiction of CapeNature, the provincial conservation agency of the Western Cape. Since the mid-19th century, the island has been connected to the mainland via a manmade causeway (Jarvis and Cram 1971). Kelp Gulls are one of the seabird species that breed on the island. Some Kelp Gulls breed as close as 50 m from the Cape Gannet colony. Furthermore, the island is located 100 m from a factory that produces potato chips; this factory discards small potatoes into an outside skip that allows easy and continued access by Kelp Gulls to the potato discards.

Spatial aspects of nest predation

Throughout the course of 11 weeks (10 October to 18 December) in 2018, 100 nests were monitored weekly for nest contents. Nests were marked by placing a rock (15 × 15 × 15 cm or larger) on the outer rim of each nest to be monitored (Figure 1). The nest marking in its entirety took place in one day under wet conditions. This secured the rock's position once the nest had dried (Figure 1). The rocks were removed from the nests at the end of the breeding season.

Fifty nests were monitored in both section A and section B (Figure 2), and the nests in each section were randomly



Figure 1: A Cape Gannet nest in the Lambert's Bay colony; study nests were marked with a rock placed on the outside of the nest to aid nest identification during the study

selected. Section A is on the eastern side of the colony, with the bird hide 15 m from the colony's edge. Section B is on the northern side of the colony, 20 m from the edge of the island, where natural boulders break the impact of the surf. In each section, we marked and monitored 25 central and 25 peripheral nests. A peripheral nest was defined as one that was not entirely surrounded by other nests in the colony. In contrast, a central nest was defined as one having other nests surrounding it on all sides (e.g. Quintana and Yorio 1998). The relevance to the findings meant that a predator would have to pass at least one peripheral nest to predate on the contents of a central nest (Quintana and Yorio 1998). To minimise disturbances to the birds, we selected nests within 2.5 m from the edge of the colony (Antolos et al. 2006). Monitoring along the edge of the colony was achieved by using a kayak paddle to monitor the nest's content. The status of each of our study nests remained constant throughout the study; that is, central nests did not become peripheral nests when some peripheral nests failed.

Nest monitoring was carried out between 11:00 and 15:00 to improve the visibility of the nests and their contents. Outside of this timeframe the return of mates to the nests increased the density of birds in the colony. Monitored nests were approached slowly by a single observer on

hands and knees. The adult gannet was gently lifted using the scooping surface of the kayak paddle to minimise discomfort to the incubating bird. The duration of the physical contact varied between roughly 3 and 7 seconds per incubating parent, which was sufficient to record the nest contents. In certain cases (depending on weather conditions), incubating parents stood up at their nests, enabling the nest contents to be observed and recorded without the need for physical contact. During each nest check, the nest content was recorded (as empty or with egg or chick). If a previously active study nest was found empty, it was recorded as a nest that failed (lost an egg). We acknowledge that this could result in an overestimation of predation. Eggs could have rolled out of the nest (Evans 1995) and then predated upon subsequently. While this was not observed during the observation periods of the study, it could have possibly taken place when one adult returned from foraging and the adults swapped over, or when conspecifics ran past and accidentally scooped an egg out. If nest failure did take place, the assumption we made is that this did not occur on a frequent basis. No extreme weather events occurred during the 11-week period of nest monitoring, and no monitored Cape Gannet nest was abandoned. Neither during nor after the nest monitoring

was there a gannet that was startled on the nest to the extent that an egg was lost through movement.

Temporal aspects of nest predation

From 2006 to 2018, observations on the predation of Cape Gannets were conducted during the breeding season. However, for this study we focused on egg predation by Kelp Gulls during the Cape Gannet incubation period. From 2006 to 2012, throughout the incubation period, CapeNature staff conducted daily patrols around the outskirts of the island (Figure 2) in search of partially broken eggshells. We refer to incidents of egg predation as the number of eggshells counted. The patrolling staff were mostly in the line of sight of Cape Gannets on the island, but the staff did not approach the gannets. While moving slowly around the island in search of predated eggs, the staff crushed any eggs that had been carried away from the colony periphery by gulls. However, if an egg was found

within 3 m from the colony's edge, a pole was used to drag the egg closer to the staff member to have it crushed. For this reason, it is unlikely that staff caused a gannet to move while it was on its nest to the extent of having an egg roll out or having an egg predated from the nest. Since 2013, unstandardised hourly patrols (rather than daily) took place between 07h00 and 19h00 each day, which allowed for hourly patterns of predation to be investigated (Figure 3). However, for our statistical data analysis, the predation was measured in years (all the predations in a year were totalled to calculate the annual predations). Kelp Gulls typically carry an egg with their bill and then break it open a few meters from the gannet colony (pers. obs.). No other predator species was observed predated on the gannet eggs during the incubation stage in the study period. To prevent recounting of egg predations, partially broken shells were crushed to easily distinguish between the counted and uncounted shells.

During 2015, 2017 and 2018, selective culling of Kelp Gull individuals that were observed predated on eggs in the Cape Gannet study colony was implemented on the island. The culling of 10 Kelp Gulls took place on 27 October 2015, 5 gulls on 22 September 2017, and 8 gulls on 23 October 2018 (a single day each year). To ensure selective culling of predatory gulls, the hunter (CapeNature staff) had to wait for a predation event on the day, before culling the Kelp Gull responsible for the predation. Owing to logistical difficulties, the culling effort or time spent waiting for predations varied each day. Culling took place from land, not from the sea. Valid licenses and permits were obtained prior to the culling procedure.

Our descriptive culling data were explored using a within-year approach (Figure 4; Supplementary Figure S1). To make the data comparable, we report on the daily predation rate as a proportion of the number of eggs available per year (determined from the estimated number of breeding pairs, as obtained by Sherley et al. [2019]) (Table 1).

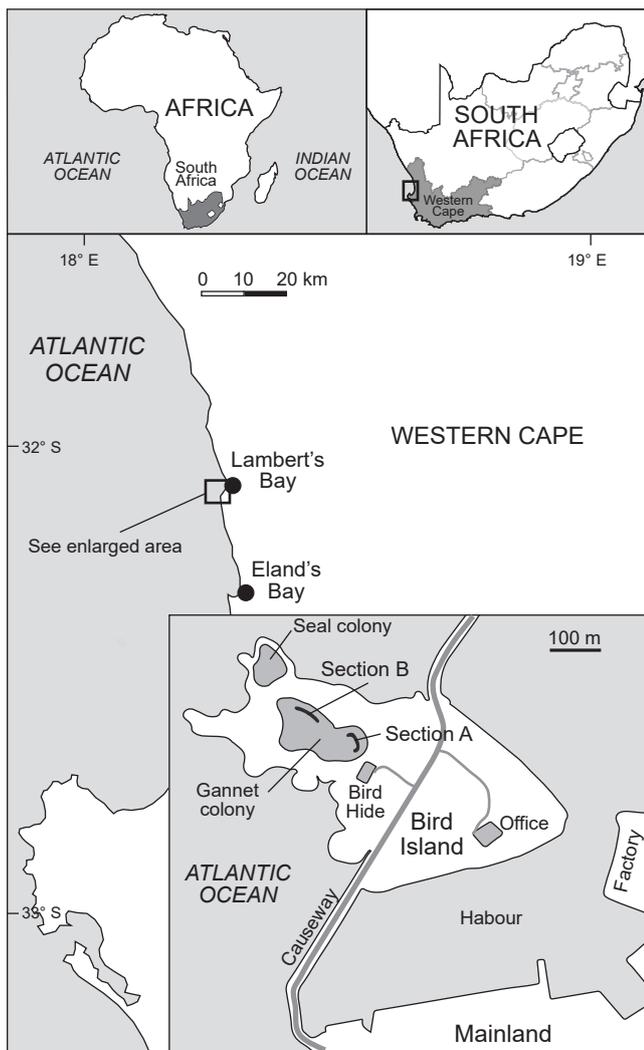


Figure 2: Nest locations designated as section A or B in the Lambert's Bay, South Africa, Cape Gannet colony, where nests were monitored for Kelp Gull predation. A potato-processing factory is located ~100 m from the island

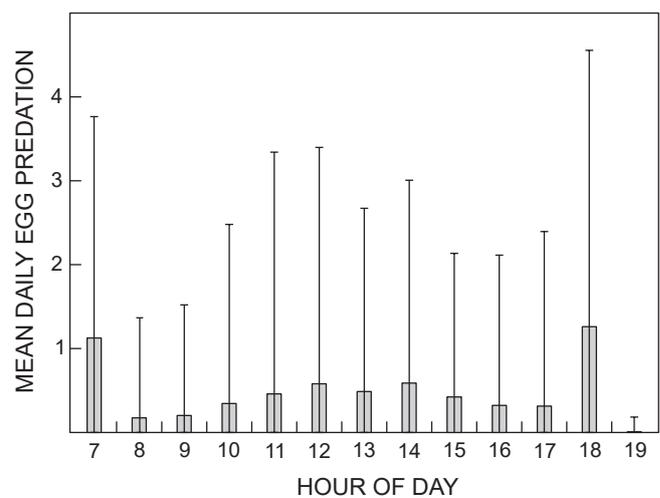


Figure 3: Mean and standard error of Kelp Gull daily predation on Cape Gannet eggs at different times of day during the incubation period, between 2013 and 2018, at the Lambert's Bay, South Africa, Cape Gannet colony

Statistical analysis

A Kruskal–Wallis *H*-test was run to determine whether there was a difference in total predations during different hours of the day.

Two generalised linear models (GLMs) with binomial distributions were run in the package MASS (Venables and Ripley 2002) in R version 3.5.3 (R Core Team 2017). In our analysis of selective culling, we applied the function `cbind` to scale the number of egg predations to the number of eggs available (deduced from the number of Cape Gannet breeding pairs for a specific year). Using data for the period 2006–2018, a GLM (Table 2) was used to

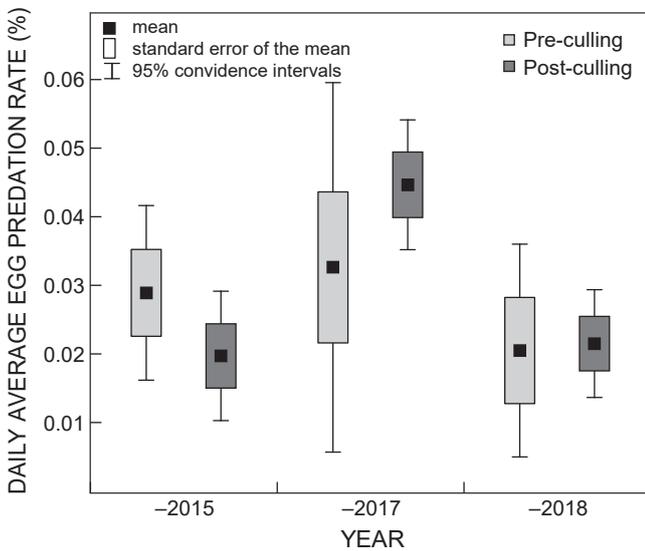


Figure 4: Kelp Gull daily egg predation rate in proportion to the amount of Cape Gannet eggs available during the incubation periods, at the Lambert’s Bay Cape Gannet colony, in 2015, 2017 and 2018. Light grey bars represent the pre-culling period, and dark grey bars represent the post-culling period

determine the effect of the presence/absence of culling and the annual estimated breeding pairs on egg predation. The egg predation total was the response variable, and the explanatory variables were Kelp Gull culling and the annual estimated Cape Gannet breeding pairs during the egg predation period at the Lambert’s Bay gannet colony.

With the data from 2018, a GLM was used to determine effect of nest location and egg availability on egg predation (Table 3). The presence/absence of predation was the response variable, while section, location and egg availability were the explanatory variables. Egg availability refers to the weekly total Cape Gannet eggs recorded for 11 weeks, across the study nests during the breeding season. The section refers to the side of the colony on which the nests were studied (section A or B) (Figure 2). Location in the colony refers to whether the nest was centrally or peripherally located.

Results

From 2006 to 2018, Kelp Gulls were responsible for 7 732 gannet egg predation events, with a maximum of 111 gannet eggs eaten in a single day. On average, 591 eggs were predated annually in a population of an annual average estimate of 7 012 breeding pairs of Cape Gannets (Table 1). The Kruskal–Wallis *H*-test showed that between 2013 and 2018 there was a positive significant difference between the daily predations by Kelp Gulls and different times of the day ($H = 836.81, p < 0.001$). Just under half of the total Kelp Gull predations (48%, $n = 1 536$) between 2013 and 2018 occurred in the early morning or late afternoon (data gathered from 07h00–07h59 and 18h00–18h59 combined) (Figure 3). Over the study period (2006–2018) there was a decrease in the number of Cape Gannet eggs likely predated, with both an increase in the annual estimated Cape Gannet breeding pairs, and during the years when culling was implemented (Tables 1 and 3). Apart from 2015, when comparing predation within the three years when culling was implemented, the daily predation

Table 1: Annual estimated Cape Gannet breeding pairs and the numbers of failed nests that lost an egg at the Lambert’s Bay Gannet colony, Western Cape, South Africa

Year	Annual estimated Gannet breeding pairs**	Total Gannet eggs lost	Proportion (%) of estimated breeding pairs that lost an egg
2006	5 530	105	2
2007	6 870	1 289	19
2008	7 180	814	11
2009	7 030	668	10
2010	7 680	568	7
2011	7 660	450	6
2012	7 210	689	10
2013	5 830	1 521	26
2014	6 720	515	8
2015*	7 340	174	2
2016	7 640	289	4
2017*	7 380	362	5
2018*	7 090	288	4
Annual average	7 012	591	

*A year when selective culling of predatory Kelp Gulls was implemented

**Data obtained from Sherley et al. (2019)

Table 2: Results of the generalised linear model (GLM) with binomial distribution using 2006–2018 data, with the response variable being the likelihood of eggs being predated by Kelp Gulls in proportion to the estimated breeding pairs of Cape Gannets, and the explanatory variables being culling (presence or absence of selective culling of gulls) and the annual estimated number of gannet breeding pairs during the egg predation period at the Lambert's Bay Cape Gannet colony, South Africa

GLM	Estimate	SE	Z-value	p-value
Intercept	-0.008015	0.1209	-0.066	0.947
Culling	-0.8564	0.03833	-22.341	<0.001
Annual estimated gannet breeding pairs	-0.0003317	0.00001752	-18.936	<0.001

rate increased post-culling compared with pre-culling (Figure 4). Within years, predation started again almost immediately (within the first 48 h in 2015, and within 24 h in both 2017 and 2018) after culling was implemented.

Across years, culling reduced the predation as the proportion of gannet pairs that lost an egg to predation is highly reduced since the start of the implementation of culling in 2015 as compared with in previous years (Table 1). The peripheral nests were at a greater loss of eggs (on average 1.5 eggs per week) compared with the central area (on average 1 egg per week) (Table 3). A GLM was run with an interaction between section and location, but that model (AIC value: 37.61) was less fitting than without the interaction (AIC value: 35.61) (Supplementary Table S1).

Discussion

We found that, in all three culling years, predation persisted after culling was implemented. The daily predation rate in 2017 and 2018 post-culling was higher than that in the pre-culling period of the same year. Reasons for predation to have persisted post-culling need to be understood to guide appropriate management responses. After culling was implemented each year, the Kelp Gull population may have experienced increased immigration as a result of lower density and subsequently reduced competition (Lisnizer et al. 2014). An alternate explanation could be that only a few of the predatory individuals were culled, suggesting that after culling occurred, the remaining predatory gulls could continue predated with reduced competition between conspecifics. Kelp Gulls are highly territorial (Quintana and Yorio 1998), and once a culled gull's territory becomes available, new recruits will instantly (Magella and Brousseau 2001) and constantly occupy these territories (Sanz-Aguilar et al. 2009). Therefore, the Kelp Gull population can return to the pre-culling density once culling is discontinued (Magella and Brousseau 2001). For that reason, we suggest that the selective culling effort should not be limited to one day per breeding season but rather conducted multiple days throughout a season.

By monitoring 100 study nests we found that predation was positively related to the increased availability of eggs. This may be because a density-dependent encounter (e.g. Getty and Pulliam 1993) leads to greater success in

Table 3: Results of the generalised linear model (GLM) with binomial distribution using 2018 data, with the response variable being Cape Gannet egg predation (presence or absence of predation by Kelp Gulls), and the explanatory variables being availability of eggs, nest section and nest location at the Lambert's Bay Cape Gannet colony, South Africa. Egg availability refers to the weekly total of gannet eggs recorded throughout the 11 weeks across 100 study nests during the breeding season

GLM	Estimate	SE	Z-value	p-value
Intercept	-1.68296	0.82205	-2.047	<0.001
Egg availability	0.12155	0.05034	2.415	<0.001
Section	1.13441	0.74071	1.532	0.076
Location	-1.95754	0.86662	-2.259	<0.001

predation on the number of Cape Gannet eggs per predation attempt. However, overall predation in the colony was reduced in years with increased Cape Gannet breeding pairs. An increase in breeding pairs limits the Kelp Gulls' ability to predate on the eggs as there are fewer points of entry into the dense gannet colony for the gulls to use as a window of opportunity. This condition therefore increases the likelihood of the predator being attacked by an incubating bird (e.g. Tenaza 1971). We found that there was a greater risk of losing an egg in peripheral nests than in central nests. A similar trend was discovered for Kelp Gull predation in the Cape Gannet colony on Malgas Island (Staveres et al. 2008) and in a colony of Imperial Shags *Phalacrocorax atriceps* at Punta León, Argentina (Quintana and Yorio 1998). This reduced risk of losing an egg in central areas of a colony compared with in peripheral areas could be attributable to the aggressive behaviour displayed by gannets while defending their nests (Nelson 1965), thus peripheral nests are more vulnerable to predation, with limited neighbours deterring the predator. Some Cape Gannet populations are splitting into smaller sub-colonies (Green and Pistorius 2013) within their breeding colonies. This increases the edge effect of a colony (ratio of perimeter to area), putting the colony at greater risk of losing eggs as the peripheral to central area ratio is reduced. Increasing the Cape Gannet population will reduce the gaps between sub-colonies, thereby reducing the edge effect. One way to increase the Cape Gannet population is to ensure that adequate Cape anchovy *Engraulis encrasicolus* and South African sardine *Sardinops sagax* fish stocks are available to them. This will contribute to improving Cape Gannet breeding success (Crawford and Jahncke 1999; Grémillet et al. 2008; Cury et al. 2011) and recruitment, and ultimately increase the breeding population (Lewis et al. 2006; Crawford et al. 2007; Pichegru et al. 2007; Cohen et al. 2014; Crawford et al. 2015), which could reduce the edge effect in the colonies, thereby limiting Kelp Gull predation.

Nest predation in birds is spatiotemporally variable (Banda and Blanco 2017); hence, it is important to ensure that management efforts take this into account for maximum effectiveness. Between 2013 and 2018, the specific time periods in which most of the egg predation at the Lambert's Bay gannet colony took place were 07h00–07h59 and 18h00–18h59. We suggest this may be linked to the gannets' departure and return times during foraging trips

(pers. obs.; Rishworth et al. 2014). Therefore, to be most efficient in terms of time, if culling is to be implemented, it should be implemented either early mornings (07h00–07h59) or later in the afternoon (18h00–18h59), which is when most predation takes place. A study of Kelp Gull predation on the Cape Cormorants of Dyer Island yielded similar results, where gulls primarily depredated cormorant nests between 07h00–10h00 and 16h00–19h00, which correlated with cormorant departure and return times (Voorbergen et al. 2012). This similarity between the active periods of prey and predators is influenced by increased nest activity, when the parents shift from incubation to foraging by departing and returning to the nest (Martin et al. 2000), making access to eggs easier for gulls. Our research suggests that if nest predation is to be minimised, gulls need to be intensively managed beginning at the start of the Cape Gannets' breeding season, with this management effort maintained as the season progresses. Both the local and metapopulations of Kelp Gulls should be carefully monitored post-culling to assess the effect. Other studies have found that culling was not as effective as planned owing to the birds' compensatory behaviour in coping with the culling. The compensatory measures of Kelp Gulls include an earlier age at first reproduction (i.e. birds start to breed at a younger age) and increased immigration from other colonies (Lisnizer et al. 2014). In our study, the impact of culling lasted for an extremely short period as we found that the first predation event each year occurred within 48 hours post-culling. We suggest that a long-term ringing operation for Kelp Gulls of all ages is needed both around the Lambert's Bay gannet colony and at adjacent Kelp Gull breeding areas. This would provide insight into the age of first breeding and the immigration rates of this predator species. Furthermore, we advise that future studies should include long-term data on the effect of weather conditions on Kelp Gull predation rates, population trends, breeding success, and their presence both at the Cape Gannet colony and near the potato factory.

Predation is a biological interaction between predator and prey (Rosenzweig and MacArthur 1963). However, natural predation levels can rise to unsustainable levels (Whittam and Leonard 1999) as a consequence of various factors, including an increase in predator numbers driven by human activities (Giaccardi and Yorio 2004). Because of the Cape Gannets' threatened conservation status, we suggest that a sustainable and long-term method to reduce the activity of Kelp Gulls at the Lambert's Bay colony should be explored. Certain human activities (e.g. the discarding of potatoes into an open container/skip at the factory since 1995) can greatly modify predator–prey dynamics (Sanz-Aguilar et al. 2009). A possible solution may be to cover the skips with a strong, durable net to prevent access to the discards, which are eventually removed as a source of farm animal fodder.

Culling has greatly reduced annual predation totals (when compared with years between 2006 and 2018) since it was implemented in 2015; however, the effect of culling from a pre-culling to a post-culling period within a given year was not significant. Several other methods are available to possibly reduce predation and increase the breeding success of the prey population. Methods for managing predators include reproductive inhibition, direct population reduction, and denied access (Wagner and Seal 1992). A

study on European Herring Gulls *Larus argentatus* and Great Black-backed Gulls *L. marinus* was successful in its reproductive inhibition methods; success was achieved by destroying the gulls' nests and nest contents, and preventing them from constructing additional nests in typical nesting habitats (Olijnyk and Brown 1999). An alternative method aimed at harassing predatory gulls at their nests (Olijnyk and Brown 1999). However, predator control is not the only method that could be used to reduce predation on gannets. A study investigating Cape fur seal *Arctocephalus pusillus pusillus* predation on Cape Gannet fledglings found that in years with an increase in anchovy and sardine biomass, there was a decrease in seal predation on the gannet fledglings (Strydom et al. 2022). Effective management of fish populations may be achieved through the establishment of no-take marine protected areas. Such areas in which fishing is not permitted should be created around Cape Gannet colonies and their foraging hotspots (Pichegru et al. 2009) to increase their effectiveness in space and time. An alternate proposal to improving food security for the gannets includes focusing efforts on developing and implementing an ecosystem approach to fisheries management in which fishing quotas account for the needs of marine predators (Pichegru et al. 2009). We advise that viable long-term methods to increase the Cape Gannet populations must be explored, such as predation prevention and increasing fish stock availability, to achieve sustainable solutions.

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ORCIDiS

Zanri Strydom: <https://orcid.org/0000-0002-3369-0787>

Lauren J Waller: <https://orcid.org/0000-0001-5263-1646>

Mark Brown: <https://orcid.org/0000-0002-0253-9363>

Hervé Fritz: <https://orcid.org/0000-0002-7106-3661>

Jan A Venter: <https://orcid.org/0000-0002-4548-2571>

References

- Antolos M, Roby DD, Lyons DE, Anderson SK, Collis K. 2006. Effects of nest density, location, and timing on breeding success of Caspian Terns. *Waterbirds* 29: 465–472. [https://dx.doi.org/10.1675/1524-4695\(2006\)29\[465:EONDLA\]2.0.CO;2](https://dx.doi.org/10.1675/1524-4695(2006)29[465:EONDLA]2.0.CO;2).

- Banda E, Blanco G. 2017. Does nest placement in buildings influence nest predation in Red-billed Choughs? *Ethology Ecology and Evolution* 29: 436–448. <https://dx.doi.org/10.1080/03949370.2016.1230561>.
- BirdLife International. 2018a. *Morus capensis*. The IUCN Red List of Threatened Species 2018: e.T22696668A132587992. <https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22696668A132587992.en> [accessed 7 October 2021].
- BirdLife International. 2018b. *Larus dominicanus*. The IUCN Red List of Threatened Species 2018: e.T22694329A132542863. <https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22694329A132542863.en> [accessed 7 October 2021].
- BirdLife International. 2018c. *Phalacrocorax capensis*. The IUCN Red List of Threatened Species 2018: e.T22696806A132594943. <https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22696806A132594943.en> [accessed 13 October 2021].
- BirdLife International. 2020. *Spheniscus demersus*. The IUCN Red List of Threatened Species 2020: e.T22697810A157423361. <https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22697810A157423361.en> [accessed 13 October 2021].
- Cohen LA, Pichegru L, Grémillet D, Coetzee J, Upfold L, Ryan PG. 2014. Changes in prey availability impact the foraging behaviour and fitness of Cape Gannets over a decade. *Marine Ecology Progress Series* 505: 281–293. <https://dx.doi.org/10.3354/meps10762>.
- Crawford RJ, Dundee BL, Dyer BM, Klages NT, Mejer MA, Upfold L. 2007. Trends in numbers of Cape gannets (*Morus capensis*), 1956/1957–2005/2006, with a consideration of the influence of food and other factors. *ICES Journal of Marine Science* 64: 169–177. <https://dx.doi.org/10.1093/icesjms/fsl011>.
- Crawford RJM, Jahncke J. 1999. Comparison of trends in abundance of guano-producing seabirds in Peru and southern Africa. *South African Journal of Marine Science* 21: 145–156. <https://doi.org/10.2989/025776199784126006>.
- Crawford RJM, Makhado AB, Whittington PA, Randall RM, Oosthuizen WH, Waller LJ. 2015. A changing distribution of seabirds in South Africa—the possible impact of climate and its consequences. *Frontiers in Ecology and Evolution* 3: article 10, pp 1–11. <https://doi.org/10.3389/fevo.2015.00010>.
- Crawford RJM, Shelton PA, Cooper J, Brooke RK. 1983. Distribution, population size and conservation of the Cape Gannet *Morus capensis*. *South African Journal of Marine Science* 1: 153–174. <https://dx.doi.org/10.2989/025776183784447458>.
- Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T, Crawford RJ, Furness RW, Mills JA, Murphy EJ, Österblom H, Paleczny M, et al. 2011. Global seabird response to forage fish depletion— one-third for the birds. *Science* 334: 1703–1706. <https://dx.doi.org/10.1126/science.1212928>.
- David JHM, Cury P, Crawford RJM, Randall RM, Underhill LG, Meyer MA. 2003. Assessing conservation priorities in the Benguela ecosystem, South Africa: analysing predation by seals on threatened seabirds. *Biological Conservation* 114: 289–292. [https://dx.doi.org/10.1016/S0006-3207\(03\)00018-1](https://dx.doi.org/10.1016/S0006-3207(03)00018-1).
- Duffy D, La Cock G. 1985. Partitioning of nesting space among seabirds of the Benguela upwelling region. *Ostrich* 56: 186–201. <https://dx.doi.org/10.1080/00306525.1985.9639588>.
- Evans RM. 1995. Incubation temperature in the Australasian Gannet *Morus senator*. *Ibis* 137: 340–344. <https://dx.doi.org/10.1111/j.1474-919X.1995.tb08030.x>.
- Furness RW. 2003. Impacts of fisheries on seabird communities. *Scientia Marina* 67: 33–45. <https://dx.doi.org/10.3989/scimar.2003.67s233>.
- Getty T, Pulliam HR. 1993. Search and prey detection by foraging sparrows. *Ecology* 74: 734–742. <https://dx.doi.org/10.2307/1940801>.
- Giaccardi M, Yorio P. 2004. Temporal patterns of abundance and waste use by Kelp Gulls (*Larus dominicanus*) at an urban and fishery waste site in northern coastal Patagonia, Argentina. *Ornitologia Neotropical* 15: 93–102.
- Goodrich JM, Buskirk SW. 1995. Control of abundant native vertebrates for conservation of endangered species. *Conservation Biology* 9: 1357–1353. <https://dx.doi.org/10.1046/j.1523-1739.1995.09061357.x>.
- Götmark F, Andersson M. 1984. Colonial breeding reduces nest predation in the Common Gull (*Larus canus*). *Animal Behaviour* 32: 485–492. [https://dx.doi.org/10.1016/S0003-3472\(84\)80285-7](https://dx.doi.org/10.1016/S0003-3472(84)80285-7).
- Green D, Pistorius P. 2013. Living on the bare edge: fitness consequences for Cape Gannets *Morus capensis* at Bird Island, Algoa Bay. *Ostrich* 84: 123–127. <https://dx.doi.org/10.2989/00306525.2013.830652>.
- Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJ, Ryan PG. 2008. A junk-food hypothesis for gannets feeding on fishery waste. *Proceedings of the Royal Society B: Biological Sciences* 275: 1149–1156. <https://dx.doi.org/10.1098/rspb.2007.1763>.
- Jarvis MJF, Cram DL. 1971. Bird Island, Lamberts Bay, South Africa: an attempt at conservation. *Biological Conservation* 3: 269–272. [https://dx.doi.org/10.1016/0006-3207\(71\)90334-X](https://dx.doi.org/10.1016/0006-3207(71)90334-X).
- Khomenko S, Abolnik C, Roberts L, Waller L, Shaw K, Monne I, et al. 2018. 2016–2018 Spread of H₅N₈ highly pathogenic avian influenza (HPAI) in sub-Saharan Africa: epidemiological and ecological observations. Focus On No. 12. Rome: FAO.
- Klages NTW. 1994. Dispersal and site fidelity of Cape Gannets *Morus capensis*. *Ostrich* 65: 218–224. <https://dx.doi.org/10.1080/00306525.1994.9639685>.
- Lewis S, Grémillet D, Daunt F, Ryan PG, Crawford RJ, Wanless S. 2006. Using behavioural and state variables to identify proximate causes of population change in a seabird. *Oecologia* 147: 606–614. <https://dx.doi.org/10.1007/s00442-005-0321-z>.
- Lisnizer N, García-Borboroglu P, Yorio P. 2014. Demographic and breeding performance of a new Kelp Gull *Larus dominicanus* colony in Patagonia, Argentina. *Ardeola* 61: 3–14. <https://dx.doi.org/10.13157/arla.61.1.2014.3>.
- Magella G, Brousseau P. 2001. Does culling predatory gulls enhance the productivity of breeding common terns? *Journal of Applied Ecology* 38: 1–8. <https://dx.doi.org/10.1046/j.1365-2664.2001.00564.x>.
- Makhado AB, Crawford RJ, Underhill LG. 2006. Impact of predation by Cape fur seals *Arctocephalus pusillus pusillus* on Cape Gannets *Morus capensis* at Malgas Island, Western Cape, South Africa. *African Journal of Marine Science* 28: 681–687. <https://dx.doi.org/10.2989/18142320609504216>.
- Martin TE, Scott J, Menge C. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London B* 267: 2287–2293. <https://dx.doi.org/10.1098/rspb.2000.1281>.
- Nelson JB. 1965. The behaviour of the Gannet. *British Birds* 58: 233–288.
- Olijnyk CG, Brown KM. 1999. Results of a seven-year effort to reduce nesting by Herring and Great Black-backed Gulls. *Waterbirds* 22: 285–289. <https://dx.doi.org/10.2307/1522217>.
- Parsons NJ, Underhill LG. 2005. Oiled and injured African Penguins *Spheniscus demersus* and other seabirds admitted for rehabilitation in the Western Cape, South Africa, 2001 and 2002. *African Journal of Marine Science* 27: 289–296. <https://dx.doi.org/10.2989/18142320509504087>.
- Pichegru L. 2013. Increasing breeding success of an Endangered penguin: artificial nests or culling predatory gulls? *Bird Conservation International* 23: 296–308. <https://dx.doi.org/10.1017/S0959270912000135>.
- Pichegru L, Ryan P, Le Bohec C, Van der Lingen C, Navarro R, Petersen S, et al. 2009. Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: implications for

- marine protected areas. *Marine Ecology Progress Series* 391: 199–208. <https://dx.doi.org/10.3354/meps08283>.
- Pichegru L, Ryan PG, van der Lingen CD, Coetzee J, Ropert-Coudert Y, Grémillet D. 2007. Foraging behaviour and energetics of Cape Gannets *Morus capensis* feeding on live prey and fishery discards in the Benguela upwelling system. *Marine Ecology Progress Series* 350: 127–136. <https://dx.doi.org/10.3354/meps07128>.
- Quintana F, Yorio P. 1998. Kelp Gull *Larus dominicanus* predation on an Imperial Cormorant *Phalacrocorax atriceps* colony in Patagonia. *Marine Ornithology* 26: 84–85.
- R Core Team. 2017. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Rishworth GM, Pistorius PA. 2015. Protection and provisioning: the role of parental behaviour in terms of chick growth and survival in a pelagic seabird. *Marine Ecology Progress Series* 530: 153–162. <https://dx.doi.org/10.3354/meps11317>.
- Rishworth GM, Tremblay Y, Green DB, Connan M, Pistorius PA. 2014. Drivers of time-activity budget variability during breeding in a pelagic seabird. *PLoS ONE* 9: e116544. <https://dx.doi.org/10.1371/journal.pone.0116544>.
- Rosenzweig ML, MacArthur RH. 1963. Graphical representation and stability conditions of predator-prey interactions. *The American Naturalist* 97: 209–223. <https://dx.doi.org/10.1086/282272>.
- Sanz-Aguilar A, Martínez-Abraín A, Tavecchia G, Mínguez E, Oro D. 2009. Evidence-based culling of a facultative predator: efficacy and efficiency components. *Biological Conservation* 142: 424–431. <https://dx.doi.org/10.1016/j.biocon.2008.11.004>.
- Sherley RB, Crawford RJ, Dyer BM, Kemper J, Makhado AB, Masotla M, et al. 2019. The status and conservation of the Cape Gannet *Morus capensis*. *Ostrich* 90: 335–346. <https://dx.doi.org/10.2989/00306525.2019.1684396>.
- Staverees L, Crawford RJM, Underhill LG. 2008. Factors influencing the breeding success of Cape Gannets *Morus capensis* at Malgas Island in 2002/2003. *Ostrich* 79: 67–72. <https://dx.doi.org/10.2989/OSTRICH.2008.79.1.8.364>.
- Strydom Z, Waller L, Brown M, Fritz H, Shaw K, Venter JA. 2022. Factors that influence Cape Fur Seal predation on Cape Gannets at Lambert's Bay, South Africa. *PeerJ* 10: e13416. <https://doi.org/10.7717/peerj.13416>.
- Tenaza R. 1971. Behavior and nesting success relative to nest location in Adelie penguins (*Pygoscelis adeliae*). *The Condor* 73: 81–92. <https://dx.doi.org/10.2307/1366127>.
- Venables WN, Ripley BD. 2002. Modern applied statistics with S (4th edn). New York: Springer. <https://dx.doi.org/10.1007/978-0-387-21706-2>.
- Voorbergen A, De Boer WF, Underhill LG. 2012. Natural and human-induced predation on Cape Cormorants at Dyer Island. *Bird Conservation International* 22: 82–93.
- Wagner FH, Seal US. 1992. Values, problems, and methodologies in managing overabundant wildlife populations: an overview. In: McCullough DR, Barrett RH (eds), *Wildlife 2001: Populations*. Dordrecht: Springer. https://dx.doi.org/10.1007/978-94-011-2868-1_23.
- Whittam RM, Leonard ML. 1999. Predation and breeding success in Roseate Terns (*Sterna dougallii*). *Canadian Journal of Zoology* 77: 851–856. <https://dx.doi.org/10.1139/z99-047>.
- Whittington PA, Crawford RJM, Martin AP, Randall RM, Brown M, Ryan PG, et al. 2016. Recent trends of the Kelp Gull (*Larus dominicanus*) in South Africa. *Waterbirds* 39: 99–114. <https://dx.doi.org/10.1675/063.039.sp102>.