African penguin *Spheniscus demersus* foraging on juvenile fish in jellyfish tentacles

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Abstract

Technological advances have enabled the observation of foraging behaviour in wild marine animals. We can observe where they go, how deep they dive, how much energy they expend, and with the use of animal-borne cameras we can capture specific foraging behaviours. Here we describe a newly observed foraging behaviour in African Penguins *Spheniscus demersus* in which they target fish located in jellyfish tentacles. As animal-borne cameras have only been deployed on African Penguins since 2015 it is unclear whether this behaviour is novel or previously unobserved. The behaviour appears to be opportunistic and beneficial to the African Penguins as it enables them to catch stationary prey. As the availability of the African Penguin's traditional schooling fish prey changes in the southern Benguela Current ecosystem due to climate change and overfishing, opportunistic foraging strategies like this could enable African Penguins to supplement foraging success at a low energetic cost.

Introduction

African Penguins *Spheniscus demersus* are endemic to southern Africa where they breed in South Africa and Namibia. Their numbers have declined by >80% since the first comprehensive census in the 1970s (Sherley *et al.* 2020). As a consequence, the species was listed as 'Endangered' on the IUCN Red List in 2010 (Sherley *et al.* 2020) and may soon meet the criteria for being listed as 'Critically Endangered' (Sherley *et al.* 2024). The common prey species of the African Penguin, determined through stomach flushing on breeding adults, have traditionally been Southern African Anchovy *Engraulis capensis* (hereafter 'Anchovy') and Sardine *Sardinops sagax* (Crawford *et al.* 2011). However, following the collapse of Sardine stocks in the northern Benguela in the 1960s and 1970s, the Namibian population of African Penguins switched to feeding almost exclusively on Bearded Goby *Sufflogobius bibarbatus* (Ludynia *et al.* 2010). In the southern Benguela Current, the Sardine stock has been in a poor state for the last c. 15 years following a combination of climate change and fishing pressure (Coetzee *et al.* 2008, Coetzee *et al.* 2022), and although Anchovy remains abundant, its availability to seabirds may have changed following an eastward displacement of spawning habitat (Crawford *et al.* 2019; Mhlongo *et al.* 2015).

The change in forage fish distributions and abundances in the Benguela ecosystem, alongside declining African Penguin populations, has led to substantial research interest in how the availability of prey resources to African Penguins may be changing (e.g. Crawford *et al.* 2006, 2011; Campbell *et al.* 2019). The colony on Robben Island, South Africa, is the focus of one of the longest running monitoring projects on African Penguins (Crawford *et al.* 2006, Leith *et al.* 2022). In addition to monitoring metrics like breeding success and chick condition on land (e.g., Campbell *et al.* 2019; Sherley *et al.* 2013), we have deployed GPS dive loggers on breeding African Penguins since 2008, providing important information for management, especially where they are foraging and how this varies through time (e.g., Campbell *et al.* 2019). However, at this time, dive data allows only for inference on when African Penguins are foraging, but not details about what they are eating.

Many diet analysis techniques for use on seabirds are necessarily highly invasive, e.g. stomach flushing (Wilson, 1984). It can be difficult to justify these invasive techniques from a contemporary viewpoint, particularly when working with endangered species, like the African Penguin. Fortunately, less invasive methods are increasingly available. The use of camera technology to study seabird diet is becoming widespread (e.g., Gaglio *et al.* 2018b, Mattern *et al.* 2018), with animal-borne video cameras providing valuable information on prey species, when the resolution of footage is high enough (McInnes *et al.* 2017, Watanabe &Takahasi, 2013, Ponganis *et al.* 2000). Furthermore, video cameras have the added benefit of documenting foraging behaviour and success (e.g., Sutton *et al.* 2020, Sutton *et al.* 2021, Watanabe & Takahasi, 2013).

This paper reports observations from camera footage collected on African Penguins from Robben Island foraging at sea across four years: 2018, 2019, 2022, and 2023. In particular, we report a behaviour that we do not believe to have been reported in this species before, where individual African Penguins target fish located amongst jellyfish tentacles.

Methods

Adult African Penguins in the guard stage of breeding (with chicks between c. 6–15 days old; Seddon & Van Heezik, 1993) were equipped with animal-borne video cameras (2018–19: Replay XD 1080 Mini, total dimensions: 94 x 28 x 23 mm, 65 g, resolution 1920 x 1080 px; 2022–23: TechnoSmArt, Rome, Italy, total dimensions: 70 x 23 x max. 24 mm, 32 g, resolution 1280 x 690 px) for one foraging trip from Robben Island (33° 48'S, 18° 22'E) during 2018, 2019, 2022 and 2023. Birds were captured by hand at their nest. On Robben Island there are very few predators, and the African Penguin nests are predominantly under vegetation. Chicks were therefore protected while the adult was being handled. Cameras and time-depth-accelerometer loggers (TechnoSmArt, Rome, Italy; L x W x H = 15 x 9 x 2 x mm, mass = 0.7 g) were then attached to the midline of the bird's mid- and caudal portion (respectively) on the back using overlapping layers of waterproof tape (Tesa tape #4651, Beiersdorf AG, Hamburg, Germany; Wilson *et al.* 1997). The tape was then secured with cyanoacrylate adhesive (Loctite 401, USA) to prevent the bird from preening the tape off. Combined mass of the loggers did not exceed 4% of the total mass of the African Penguin. Handling time from capturing the bird to release after attaching devices was maximum 17 minutes (mean: 10.5 minutes, n = 21). Cameras were deployed for one foraging trip (usually c. 13 hours), and nests were checked daily to ensure the African Penguins went to sea and that the other adult of the pair had resumed brooding. The birds went to sea for one day and the cameras were retrieved the following morning at the nest. If the bird had not gone to sea on the second day after deployment, the device was removed. On retrieval, cameras and any other devices were removed, then head length, bill length, bill depth (mm) and bird mass (g) were measured and used to gauge the sex of the bird (Campbell *et al.* 2016).

To ensure the footage captured foraging behaviour and to maximise useful battery life, the cameras were set up to turn on approximately one hour after sunrise (when the African Penguins are typically already at sea; Ryan *et al.* 2007). The 2018 and 2019 cameras were limited in their battery life and so were set up to run for 20 minutes, then switch off for an hour before switching back on. This resulted in around 1 hour of footage. The cameras used in 2022 and 2023 had better battery life so would run continuously (with c. 5 second gaps in between c. 10 minute videos) until the battery died which resulted in around 6 hours of footage per trip. We labelled and analysed the footage using the software BORIS (an event logging software for video data; Friard *et al.* 2016). For the purpose of this study, prey encounters and prey capture attempts were recorded as point events (time-stamped to the moment that the prey became visible in the footage, or the moment the individual attempted to catch prey, respectively). Prey capture events were defined as successful, unsuccessful, or unknown. Prey encounters were categorised as ‘individual fish’ (with no shoal in sight), ‘shoal’, ‘squid’, or ‘other’. It was not possible to measure the exact size of prey, because camera position varied slightly between individuals, but fish seen in videos recorded by one individual could comparatively be categorised as ‘large’ or ‘small’.

Results

Over the four years, we collected foraging footage from 15 African Penguins (a further nine deployments resulted in no video data due to African Penguins not initiating a foraging trip or device failure). The most common prey type was fish, typically small forage fish. Of known prey encounters (n = 280), 258 were fish with 73.6% of these fish occurring as an individual fish rather than part of a visible shoal. Other notable prey items include a squid (Figure 1d) and a crustacean (Figure 1c). These are probably Cape Hope (or Chokka) Squid *Loligo reynaudii* and Cape Mantis Shrimp *Pterygosquilla capensis* respectively, as these species have previously been recorded in the diet of penguins and other seabirds off South Africa (e.g. Sherley *et al.* 2013, Gaglio *et al.* 2018a, Connan *et al.* 2016). We also recorded one African Penguin interacting with a small piece of orange rope (Figure 1f). Free-swimming gelatinous zooplankton (hereafter 'jellyfish') were often encountered but were never seen being targeted directly by the African Penguins. The number of jellyfish encountered differed between deployments with many videos not containing a single jellyfish during the period cameras were recording.

Two African Penguins were observed targeting jellyfish that had small fish either entangled or taking refuge within their tentacles. This behaviour typically started with the African Penguin approaching the jellyfish from their underside and plucking the fish out from the tentacles (Figure 2 and 3). In most cases low image quality, and sometimes water visibility, prevented the identification of the gelatinous zooplankton species with which fish were associated. Although in a few cases we could identify to genus or family level, such as Hydrozoa jellyfish (e.g. *Aequorea* spp.) and other zooplankton taxa including ctenophores or salps. In a few instances, the fish appeared to be surrounded by gelatinous material which we believe to be either a ctenophore or a salp (Figure 2d). This behaviour, targeting fish associated with jellyfish, or in some cases other gelatinous zooplankton, was seen in one individual in 2019 (from n = 2 individuals tracked) and one in 2023 (n = 6 individuals). Foraging on fish in association with jellyfish was not observed in 2018 (n = 3 individuals) or 2022 (n = 4 individuals). The 2019 African Penguin was observed inspecting jellyfish 11 times, and on three those occasions we were able to confirm that the jellyfish had small fish within its tentacles. In 2023, the individual was observed encountering jellyfish 60 times and on 16 of those we could confirm fish within the jellyfish tentacles (Table 1). In most cases, jellyfish only contained one individual small fish, typically forage fish like Anchovy, or pipefish *Syngnathus* sp. (Figure 2c and d, and Figure 3), in which case the African Penguin would catch the fish then continue its dive (duration spent interacting with a single jellyfish = c. 1 – 2 seconds), typically continuing search behaviour or continue their ascent to the surface. Interactions with jellyfish seemed to occur while ascending from search dives rather than the African Penguins diving to target them specifically. Often jellyfish would be clustered meaning the African Penguin could interact with more than one jellyfish within a dive. Less commonly, the African Penguin encountered a large jellyfish (Figure 2a and b) with multiple fish inside. During these encounters the African Penguin spent up to c. 10 seconds taking the fish out of the tentacles.

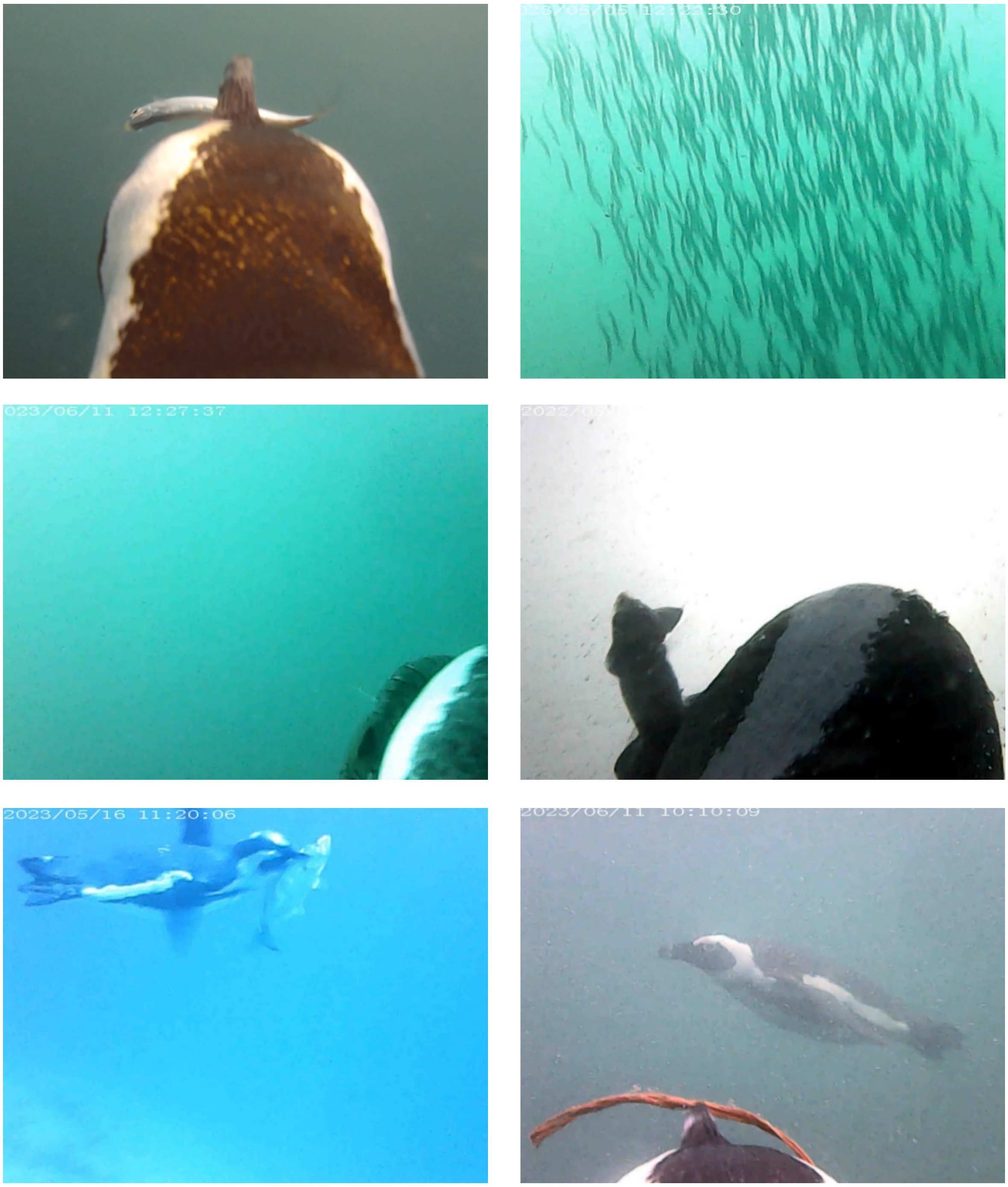

Figure 1. Images of prey items encountered by African Penguins (*Spheniscus demersus*). a) individual forage fish. b) school of forage fish. Cc) crustacean, likely Cape Mantis Shrimp *Pterygosquilla capensis*. d) Squid, *Loligo* sp. e) unidentified large fish. f) rope fragment.

Figure 2. African Penguins (*Spheniscus demersus*) foraging on jellyfish-fish aggregations. a) African Penguin approaching a jellyfish with many small fish amongst tentacles. b) African Penguin closer to jellyfish with fish (circled) amongst tentacles. c) African Penguin catching a pipefish (*Syngnathus* sp.) from the tentacles of a jellyfish. d) African Penguin catching fish in the body of a gelatinous zooplankton.

Figure 3. Image sequence of prey capture involving a jellyfish (*Aequorea* sp.) and fish (pipefish, *Syngnathus* sp.) aggregation. See S1 for full video.

Table 1. Summary of gelatinous zooplankton (jellyfish) encountered on a single foraging trip by two African Penguins (*Spheniscus demursus).* *No morphological measurements were taken to identify sex in this individual.

Individual ID	Year	Sex	Number of jellyfish encountered but not interacted with	Number of jellyfish interacted with	Number of prey capture events involving a jellyfish
25_2019R	2019	Unsexed*	2	11	33
30_2023R	2023	Female	324	60	51

Discussion

Here we report a newly described foraging behaviour in the African Penguin whereby they target small fish associating with jellyfish. This behaviour was observed in two different individual African Penguins (out of 15 on which video cameras were deployed) during different years, which implies that it could be used by multiple individuals. The small fish are likely juvenile forage fish, such as Anchovy, due to the timing of the camera footage corresponding with southward juvenile fish movements (Hutchings *et al.* 2002). Juvenile Anchovy or 'recruits', have been commonly identified as the main prey source of the African Penguin in this region (Campbell *et al.* 2019, Crawford *et al.* 2011). Fish within the tentacles could either be jellyfish prey or associated as commensals. Either way, the jellyfish appear to act as natural fish aggregating devices. Large jellyfish are therefore particularly beneficial for African Penguins to investigate as they may contain several, easier to catch prey which require very little energetic expense since there is limited amount of chasing. African Penguins appeared to travel at slower swimming speeds when capturing prey associated with jellyfish compared to normal prey capture attempts and so we hypothesise they will expend less energy (Wilson *et al.* 2010). African Penguins typically interacted with jellyfish while on their ascent from a search dive – meaning the main energetic cost of diving has already been incurred (Wilson *et al.* 2010). This upward angle of approach is consistent with other studies, which showed that Little Penguins *Eudyptula minor* and Brünnich's Guillemot *Uria lomvia* approached jellyfish from the underside when ascending from deeper dives (Sutton *et al.* 2015, Sato *et al.* 2015). Jellyfish were once considered energetic 'dead ends' (Arai, 2005, Sommer *et al.* 2002) but have since been documented as crucial prey species for some marine megafauna such as Leatherback Turtles *Dermochelys coriacea* (Houghton *et al.* 2006), as well as supplementary prey for some penguin species (Thiebot *et al.* 2017, Sutton *et al.* 2015), and are increasingly understood to facilitate prey capture in others (Sato *et al.* 2015). Here, we highlight for the first time that foraging on fish in association with jellyfish has been witnessed in the African Penguin; however, it has previously been documented in other penguins, suggesting that multiple species take advantage of jellyfish-fish aggregations. Indeed, jellyfish-fish aggregations have been targeted by Yellow-eyed Penguin *Megadyptes antipodes* (Mattern, 2020), Humbolt Penguin *Sphensicus humboldti* (Ursula Ellenberg pers. comm), Brünnich's Guillemot (Sato *et al.* 2015), and in some fish species (Bonaldo *et al.* 2004, Masuda *et al.* 2008).

The fish observed in these jellyfish-fish aggregations tended to be small, typically smaller than the average size of fish being caught by the African Penguins (as seen in the camera footage), either individually or as part of a shoal (Figure 2 compared to Figure 1a). There have been many examples of juvenile fish aggregating within the tentacles of jellyfish as a protection strategy (e.g., Griffin *et al.* 2019, Richardson *et al.* 2009) – albeit unsuccessfully in this African Penguin example. Juvenile fish tend to be of lower energetic content than adults because fish weight is related to fish length by a non-linear power function (Froese 2006). In the European Anchovy (*Engraulis Encrasicolus),* a close relative of the Southern African Anchovy (*Engraulis capensis*) which is the main prey for African Penguins, energy density is proportional to body length and body mass (Dubreuil & Petitgas, 2009). Therefore, we can hypothesise that the fish caught by the African Penguins from the tentacles of jellyfish are of low energetic content.

Foraging on fish in association with jellyfish does not only seem to necessarily be linked with low prey availability as in the footage of the individual in 2023, many schools and individual fish were recorded and indeed successfully preyed upon. Rather, this appears to be an opportunistic foraging behaviour which has, at least, been used by a few individuals. We also observed pipefish (*Syngnathus* sp.) being fed on (Figure 3), which typically only occur in African Penguin diet when prey availability is low, suggesting they are also low energy prey (Sherley *et al.* 2013). However, pipefish were only confirmed to be predated upon in 2023 (when we also observed forage fish schools) when they were associated with jellyfish. Greater Crested Terns *Thalasseus bergii* breeding at Robben Island have also been observed predating on pipefish (Gaglio *et al.* 2018a) and while Greater Crested Terns dive less that 1 m under the surface (Gaglio *et al.* 2018a), pipefish are predominantly found deeper than 1 m in the water column, and so it is possible the terns are also taking advantage of pipefish using jellyfish for refuge.

Both fishes (Anchovy and pipefish) identified associating with jellyfish are known African Penguin prey species (Ludynia *et al.* 2010). The majority of other individual prey species (not associated with jellyfish) identified from the animal-borne camera footage generally matches with the results of diet analysis studies, with forage fish species being the most common prey (Connan *et al.* 2016, Ludynia *et al.* 2010).

While some studies on *Spheniscus* penguins have found cnidaria jellyfish (including *Chrysaora* and *Aequorea* sp.) in their diets (e.g., Thiebot *et al.* 2017), we did not directly observe foraging on jellyfish, only the targeted foraging on fish within their tentacles. In most cases where only jellyfish were seen, there was no attempt to investigate by the African Penguin, but in cases where fish were in association with the jellyfish, African Penguins swam directly to the jellyfish. For example, the African Penguin in 2023 encountered 324 jellyfish which they did not approach (Table 1). No fish were seen in association with these unapproached jellyfish.

We also documented one observation of an African Penguin investigating a piece of rope, highlighting the potential for ingestion of plastic materials. There has been evidence of plastic ingestion in multiple penguin species including the African Penguin (Brandao *et al.* 2011, Vanstreels *et al.* 2019, Caruso *et al.* 2022). While it was not possible to see from the footage whether the African Penguin in question ingested this piece of rope, it showed that the bird caught the rope in its bill in the same way it would have with a fish.

Camera footage enables detailed diet information to be obtained without using invasive methods, while concurrently collecting data on foraging success, conspecific interactions, and specific foraging behaviours (e.g., McInnes *et al.* 2017, Sutton *et al.* 2020). In this study, animal-borne video camera technology has enabled us to document a newly described opportunistic foraging behaviour in the African Penguin whereby individuals are taking advantage of stationary prey that was either captured or taking refuge within jellyfish tentacles. Although the fish found within the jellyfish tentacles seemed to be small, and potentially have a lower energetic value compared to other available prey, the energy expenditure in catching them is likely low due to the African Penguins not having to chase them. Foraging on fish associating with jellyfish does not seem to only occur as a backup strategy during poor conditions, as plenty of shoals were observed in the footage in 2023, but we recognise that it could become more common during years of low Anchovy (preferred prey source) biomass. We hypothesise that these prey captures are only supplementary to other typical African Penguin foraging behaviour.

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