Biological Conservation 286 (2023) 110318

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Penguins in the anthropause: COVID-19 closures drive gentoo penguin movement among breeding colonies

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ARTICLE INFO

Keywords:
Antarctic Peninsula
Anthropause
Gentoo penguin
IAATO
Metapopulation
Tourism

ABSTRACT

The COVID-19 pandemic caused the Port Lockroy post office, a popular Antarctic tourism destination, to close in 2020, creating a natural experiment to test human impacts on the local gentoo penguins. This study examines the abundance of nesting gentoo penguins before, during, and after the COVID-19 anthropause at different spatial scales centered around the post office. We found that the Port Lockroy population increased 83 % (~450 nesting pairs) from 2018 to 2021, with areas of the island open to pedestrians seeing the greatest gains in the number of nests. Jougla Point, a site just 150 m away from Port Lockroy and located within the same harbor, increased 90 % (~900 nesting pairs) during the closure, while two nearby sites outside the harbor decreased by 60 % and 59 % (~1000 nesting pairs total). We conclude that gentoo penguins immigrated from neighboring sites into the Port Lockroy harbor. This apparent redistribution of nesting gentoo penguins immediately reversed itself when the post office re-opened in 2022. These findings, which are particularly striking given the assumed strong site fidelity of gentoo penguins, suggest that human activity can alter gentoo penguins' choice in nesting location, and that the spatial extent of disturbance is perhaps larger than previously appreciated. We suggest testing the impacts of ship and zodiac traffic on breeding behavior, the cumulative effects of tourism on sets of geographically proximate colonies, and the timing of tourism in relation to nest initiation to inform policies focusing on minimizing disturbances to gentoo penguins as Antarctic tourism resumes.

1. Introduction

One of the concerns regarding Antarctic tourism is that the presence of humans may cause stress or other disturbance to Antarctica's wildlife (Coetzee and Chown, 2016), particularly *Pygoscelis* spp. penguins, whose breeding season in the austral summer coincides with the peak of Antarctic tourism (Bender et al., 2016). Studies to investigate the impacts of human activity on *Pygoscelis* penguins have yielded mixed results (Coetzee and Chown, 2016), in part because impacts have been measured in different ways, including population trends, reproductive success, and physiological measures indicating stress or changes in behavior. Early efforts were concerned with the impacts of research activity; for example, Young (1990) found that the number of Adélie penguin (*P. adeliae*) nests in subcolonies next to the active Cape Bird research station declined over a 22 year period while the other subcolonies further from the station in the same population increased. At a larger spatial scale, Woehler et al. (1991) reported that the Adélie penguin population on Shirley Island plateaued after the nearby Casey Station opened, discordant with increases seen at other Adélie penguin populations in the region and at Shirley Island prior to the base opening. More recent efforts have focused primarily on the impacts of tourism, which has been growing steadily on the Antarctic Peninsula (Bender et al., 2016). Cajiao et al. (2022) found that both chinstrap penguins (*P. antarctica*) and gentoo penguins (*P. papua*) showed more vigilant behavior when pedestrians approached nests closely, quickly, and while talking than when they kept their distances, stood still, and were quiet. However, chinstrap penguins showed more vigilant behavior in response to all pedestrian activities than gentoo penguins (Cajiao et al., 2022). Physiological studies found that incubating Adélie penguin heart rates increased when humans came into view (Culik et al., 1990) and

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https://doi.org/10.1016/j.biocon.2023.110318
Received 22 May 2023; Received in revised form 9 September 2023; Accepted 25 September 2023
0006-3207/

chinstrap penguin heart rates increased when humans approached quickly or to within 3 m (Nimon et al., 1995), but gentoo penguin heart rates did not increase in response to pedestrians (Nimon et al., 1996), highlighting the species-specific nature of the response. Complicating this picture is the potential for habituation of penguins. Holmes et al. (2006) reported that incubating gentoo penguins far from human activity showed vigilant behavior for up to five minutes after being approached by pedestrians, but gentoo penguins nesting on an active research base were habituated to humans and showed less vigilant behavior. Corticosterone, a stress induced hormone, has been used as a measure of stress that might be more sensitive than observable changes to behavior or reproductive success, but neither Lynch et al. (2019) nor Marciau et al. (2023) found any significant correlations between corticosterone levels and exposure to tourism in gentoo or Adélie penguins, respectively. Additional studies of gentoo penguins have shown that increased tourism does not increase predation by skuas (*Stercorarius* spp.), the main threat to Antarctic penguins at the colony (Crosbie, 1999), and while Cobley and Shears (1999) and Trathan et al. (2008) did not see impacts of tourism on reproductive success, a more recent study by Dunn et al. (2019) did. It is worth noting that despite different findings regarding the impact of tourism on reproductive success, both Trathan et al. (2008) and Dunn et al. (2019) found evidence to link the decreasing abundance of breeding gentoo penguins to human disturbance.

Goudier Island on the Western Antarctic Peninsula is one of the most visited sites in Antarctica because it contains an operational post office, a gift shop, and a gentoo penguin colony. This site is better known by the name Port Lockroy and we will use the name Port Lockroy here to indicate both the island and the penguin colony situated on the island (Fig. 1a). Tourism on the 3.6 acre island fluctuated between about 13,500 to 18,500 landed passengers per austral summer from the 2006/07 to 2018/19 seasons (Fig. 1b; IAATO, 2022a). The United Kingdom Antarctic Heritage Trust occupies the island for the entirety of the gentoo penguin breeding season to staff the post office and complete surveys of the penguins nesting adjacent to it. Unlike nearly all other gentoo penguin colonies on the Western Antarctic Peninsula, the Port Lockroy colony saw a significant population decline between 1996 and 2016 (Trathan et al., 2008; Dunn et al., 2019). In 1996, the British Antarctic Survey - seeing an opportunity to use the popularity of the island for scientific study - split the 215 m long island into a visited portion containing the landing site and the post office and an unvisited portion that is off-limits to tourists (see Cobley and Shears (1999) for more details on the original study).

Multiple studies have attempted to quantify the impacts of human visitation on the Port Lockroy gentoo penguin colony with mixed results (Cobley and Shears, 1999; Trathan et al., 2008; Dunn et al., 2019). Cobley and Shears (1999) found no difference in breeding success between Port Lockroy subcolonies visited by tourists and subcolonies not visited by tourists, or between Port Lockroy and less visited neighboring populations, thus concluding that tourism was not affecting the gentoo penguins. When looking at changes in abundance, Trathan et al. (2008) showed that unlike the subcolonies unvisited by tourists, some of the visited subcolonies at Port Lockroy had decreasing numbers of nests between 1996 and 2007, though no difference was seen in reproductive success. Notably, they also found that a subcolony not often visited by tourists but frequently monitored by the resident post office staff had a negative trend in the number of nests over the same time period (Trathan et al., 2008). They concluded that both tourism and scientific monitoring may be dissuading gentoo penguins from nesting in certain areas of the island, though such disturbances do not affect reproductive success once a pair has chosen their nest location (Trathan et al., 2008). These findings suggest that gentoo penguins are impacted at the stage of selecting a nesting site, and that penguins choosing to breed despite intense human activity may have traits that would buffer them from the stresses of disturbance, consistent with Lynch et al. (2019)'s finding that corticosterone levels were no higher in gentoo penguins nesting at Port Lockroy than at other, less frequently visited sites. After another decade of monitoring and high tourism rates, Dunn et al. (2019) found that the number of nests and reproductive success declined over time in both visited and unvisited subcolonies on Port Lockroy, and that the number of visitors to the island was a predictor of the colony-wide population size. They also reported a decrease in the number of nesting pairs at the well-visited neighboring site of Jougla Point, but an increase in six other less-visited, nearby gentoo penguin colonies, concluding that tourism was depressing the population sizes of the more popular sites (Dunn et al., 2019).

The International Association of Antarctica Tour Operators (IAATO) restricts the number of passengers landing at each Antarctic site to 100 at a time, mandates a minimum of 1 guide per every 20 landed passengers, and recommends that pedestrians do not approach closer than 5 m from nesting penguins (IAATO, 2022b, 2023a). Despite this guideline, pedestrians at Port Lockroy must regularly approach gentoo penguins to closer than the suggested 5 m on their walks from the landing site to the post office because of the proximity of the colony and penguin trails to the post office. It is also the case that gentoo penguins often approach visitors, being habituated to the presence of humans at the site, reducing the distance to below the 5 m guideline. Though the Antarctic Treaty Consultative Meeting (ATCM) site guidelines report

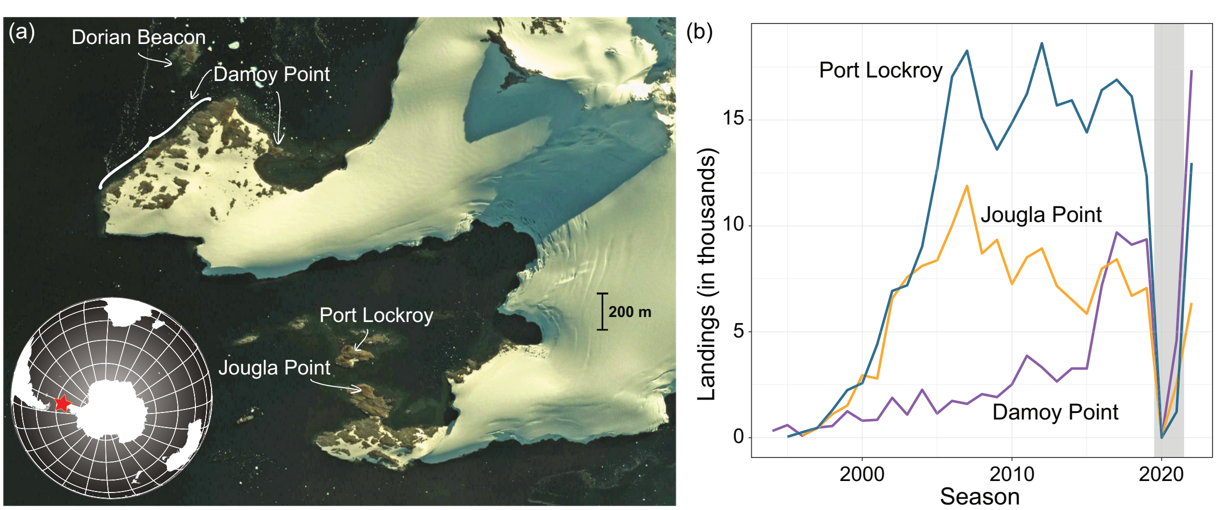

Fig. 1. Study Site Information: (a) An aerial image of the gentoo penguin populations in the Port Lockroy area (Google Earth Pro, 2011), and (b) the number of landed passengers on each site, with the years the Port Lockroy post office was closed highlighted in gray (IAATO, 2023b).

that tourism has no known impact on gentoo penguin breeding at the Port Lockroy colony, and no known impacts at all at the neighboring Jougla Point and Damoy Point colonies (ATCM, 2006a, 2013b), they have enacted additional restrictions that tourships are obligated to follow beyond those enforced by IAATO for the three sites. In 2006, new IAATO regulations required that no more than three vessels may visit Port Lockroy per day, and no more than 60 and 350 visitors may land on the island at a time and per day, respectively (ATCM, 2006a, 2006b). At the neighboring site of Jougla Point, the ATCM enacted restrictions in 2005 and updated them in 2013 to limit daily visitation to three vessels with a total of 1500 passengers (ATCM, 2005, 2013b, 2013c). At Damoy Point, the ATCM enacted restrictions in 2010 and updated them in 2013 to limit daily visitation to three vessels with a total of 900 passengers (ATCM, 2010, 2013a, 2013c).

Quantifying the effects of tourism on *Pygoscelis* penguin populations is difficult for a host of reasons. First, prior research has found that responses are species specific (Coetzee and Chown, 2016; Lee et al., 2017; Cajiao et al., 2022) and may be subject to habituation that is, in its own way, an impact of tourism, but is also a behavioral adaptation that may mute the observed response of penguins to human activity (Culik et al., 1990; Williams, 1995; Holmes et al., 2006). Secondly, penguin population time series are characterized by large inter-annual variability, which can make it difficult to link changes in abundance to potential causal drivers (Che-Castaldo et al., 2017; Humphries et al., 2018; Sen et al., 2023). Third, the impacts of tourism may occur at very short time scales (physiological responses on the order of seconds to minutes; e.g., Culik et al., 1990; Nimon et al., 1995; Nimon et al., 1996; Cajiao et al., 2022), longer time scales (months to years) associated with the selection of a breeding location with concomitant changes in distribution (Trathan et al., 2008), and even longer time scales (years to decades) as penguins concentrated at the least disturbed sites experience density dependence with concomitant impacts on regional abundance. Finally, penguins on the Antarctic Peninsula are also faced with the concurrent stressors of climate change and krill fishing with considerable spatial and temporal overlap that makes the isolation of any one factor difficult (Hinke et al., 2017; Watters et al., 2020). In this context, the unanticipated natural experiment provided by the COVID-19 pandemic 'anthropause' (Rutz et al., 2020) provides a unique opportunity to isolate and study the role of human activity.

The reduced human movement brought about by the COVID-19 pandemic revealed a variety of effects of human removal in different systems; examples include population increases in Atlantic ghost crabs (*Ocypode quadrata*; Costa et al., 2022), dehabituation to noise pollution in bottlenose dolphins (*Tursiops truncatus*; Stevens et al., 2023), and an increase in white-tailed eagle (*Haliaeetus albicilla*) presence causing reduced productivity in common murres (*Uria aalge*; Hentati-Sundberg et al., 2021). In March 2020, the COVID-19 pandemic largely shut down Antarctic tourism (IAATO, 2022c) and the number of cruise ships going to the region did not fully recover until the 2022/23 austral summer. The Port Lockroy post office was not staffed for the 2020/21 or 2021/22 seasons. The most recent 2022/23 season saw pre-pandemic levels of visitation throughout the Peninsula, and staff returned to the Port Lockroy post office and reopened it to tourism. The unique combination of a heavily-visited location already divided into experimental treatments, the near total shut down of human activity during the first two years of COVID-19, and data on abundance at Port Lockroy and neighboring colonies before, during, and after the pandemic provides an unmatched opportunity to test human impacts on gentoo penguins at varying spatial scales. Here we use this unique natural experiment to explore how the removal of humans from Antarctica affected the gentoo penguins around Port Lockroy and, in doing so, hope to inform policies designed to limit future disturbance.

2. Methods

We examined the number of nesting gentoo penguins before, during, and after the pandemic cessation of Antarctic tourism centered around the Port Lockroy post office. We report the number of nests on Port Lockroy, including how those nests were distributed across the "unvisited," "moderately visited," and "highly visited" areas of the island. (Fig. 2a), as well as the number of nests at three neighboring gentoo penguin breeding sites.

We defined the "unvisited" area as the eastern side of the island that has been roped off to pedestrians since 1996 (Cobley and Shears, 1999). We defined the area between the boat landing and the post office and all areas where tourists regularly walk during visits to the island as "highly visited," and the area in between, where tourists may roam but do so less frequently, as "moderately visited." This delineation of treatment areas is informed by the description of subcolonies in Dunn et al. (2019) and by personal experience of researchers familiar with the site. We analyzed data from remotely piloted aircraft system (RPAS) surveys of Port Lockroy collected during the incubation or guard phases of the 2018/19, 2020/21, and 2021/22 breeding seasons (hereafter the 2018, 2020, and 2021 breeding seasons, respectively). There were two RPAS surveys in the 2018 season (December 16th and January 3rd), one survey in the 2020 season (January 3rd), and one survey in the 2021 season (January 10th). We were unable to conduct RPAS surveys in the 2019 and 2022 seasons. We annotated RPAS imagery by placing a point at the center of each incubating or guarding penguin, which allowed us to count the number of penguin nests in each treatment area of the

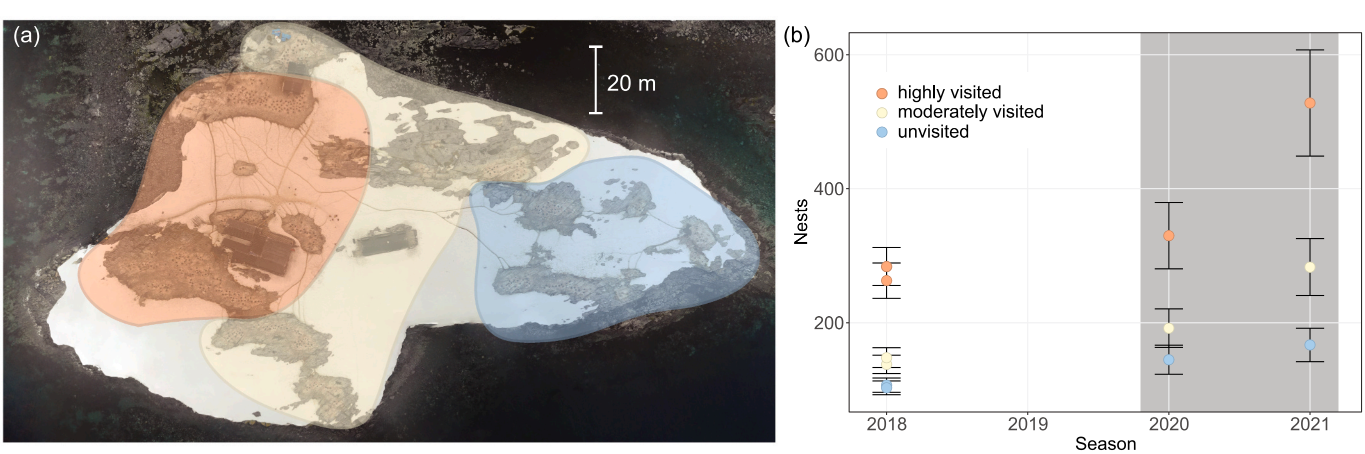

Fig. 2. Port Lockroy Visitation: (a) An RPAS orthomosaic of Port Lockroy, Goudier Island from the 2018 season, with the area highly visited by pedestrians in orange, the moderately visited area in yellow, and the unvisited area in blue, and (b) the number of nests in each treatment area, with the years the post office was closed highlighted in gray. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

island. In order to estimate uncertainty around each census count from RPAS imagery, we annotated a large subcolony three times- once with a conservative threshold for what qualified as a nest (which likely missed nests), once with a liberal threshold for what qualified as a nest (which likely included non-nesting penguins), and once using our best judgement (the same that we used when counting the entire site). We used the spread among these three counts to calculate the percent uncertainty and categorize each census count as being within either ±5 %, ±5–10 %, ±10–15 %, ±25–50 %, or the nearest order of magnitude of the true census count (N1, N2, N3, N4, or N5 respectively, as laid out by Croxall and Kirkwood (1979)). We combined these counts from RPAS images with nest census counts and their associated uncertainty levels available through the Mapping Application for Penguin Populations and Projected Dynamics database (MAPPPD; Che-Castaldo et al., 2023) and from Dunn and Nichol (2023) to create a time series of abundance at Port Lockroy.

There are three other gentoo penguin colonies within a 2 km radius of Port Lockroy– Jougla Point, Dorian Beacon, and Damoy Point (Fig. 1a). We compiled all available nest census counts for these three locations from MAPPPD (Che-Castaldo et al., 2023). We also conducted a complete RPAS survey of Jougla Point in the 2020 season and a survey of most of the Jougla Point colony in the 2021 season. We used the same annotation method described above for Port Lockroy to obtain a 2020 nest census count and uncertainty for Jougla Point. The 2021 image covered 89 % of the nests from the 2020 image, so we counted the number of nests visible in the 2021 image then divided the 'best judgement' count by 0.89 to estimate the total number of nests at the entire Jougla Point colony in 2021, and divided the conservative and liberal counts by 0.89 as well to calculate the uncertainty. Data on the number of tourists landing on each site derive from the number of "Small Boat Landings" reported by IAATO (IAATO, 2023b).

3. Results

The number of nesting gentoo penguin pairs at Port Lockroy increased 83 % (535 to 978 nesting pairs) from 2018 to 2021, then decreased by 46 % (978 to 529) from 2021 to 2022 (Fig. 3a). From the Port Lockroy RPAS images, we designated the uncertainty of both census counts from the 2018 season as ±5–10 % (N2) and the 2020 and 2021 counts as ±10–15 % (N3). We designated both the 2020 and 2021 Jougla Point RPAS images as ±10–15 % (N3). The uncertainty arose from varying levels of image quality and adult attendance, both of which can make distinguishing between adults on or off of a nest difficult, and in the case of the 2021 Jougla Point image, from missing ~ 11 % of nests.

Our annotations of RPAS images of the Port Lockroy gentoo penguin colony from before and during the pandemic closure allow us to understand how the increase in the number of nesting pairs was distributed across the different areas of the island (Fig. 2b). In the highly visited area of the island, the number of nesting pairs increased 87 % (284 to 528) from 2018 to 2021, whereas in the moderately visited area, the increase was 91 % (148 to 283), and in the unvisited area the increase was 62 % (103 to 167). We do not have RPAS imagery from the period after the reopening of the post office to determine how the 449 pairs lost from 2021 to 2022, the reopening year, were distributed across the island.

Jougla Point, the gentoo penguin colony 150 m south of Port Lockroy, increased 90 % (1002 to 1905 pairs) from 2019 to 2021, then decreased by 57 % (1905 to 812) from 2021 to 2022, when the post office reopened (Fig. 3b). The two sites located just outside of the Port Lockroy harbor, Dorian Beacon and Damoy Point, showed the opposite patterns from Port Lockroy and Jougla Point during the pandemic. The number of nesting pairs at Damoy Point declined 60 % (1519 to 615 pairs) from 2018 to 2021, then increased by 117 % (615 to 1333) from 2021 to 2022 (Fig. 3c). The much smaller Dorian Beacon colony decreased by 59 % (164 to 67 pairs) from 2018 to 2021, then increased by 51 % (67 to 101) from 2021 to 2022 (Fig. 3d).

In aggregate, the two sites inside the harbor (Port Lockroy and Jougla Point) increased by 1346 nesting pairs during the pandemic, while the two sites just outside the harbor (Damoy Point and Dorian Beacon) collectively decreased by 1001 nesting pairs. In a reversal of these changes following the post office's re-opening, Port Lockroy and Jougla Point decreased by 1542 nesting pairs, while Damoy Point and Dorian Beacon increased by 752 nesting pairs.

From 2005 to 2019, Port Lockroy consistently experienced over 5000 more landed passengers every season than Jougla Point or Damoy Point, with a high of 18,623 passengers landing in the 2012 season (Fig. 1b, IAATO, 2023b). IAATO has not reported any tourism numbers for Dorian Beacon, likely because it is so small (~2 acres) that it cannot accommodate passengers landing from most IAATO vessels. It is also possible that any occasional visits to this small island are reported as

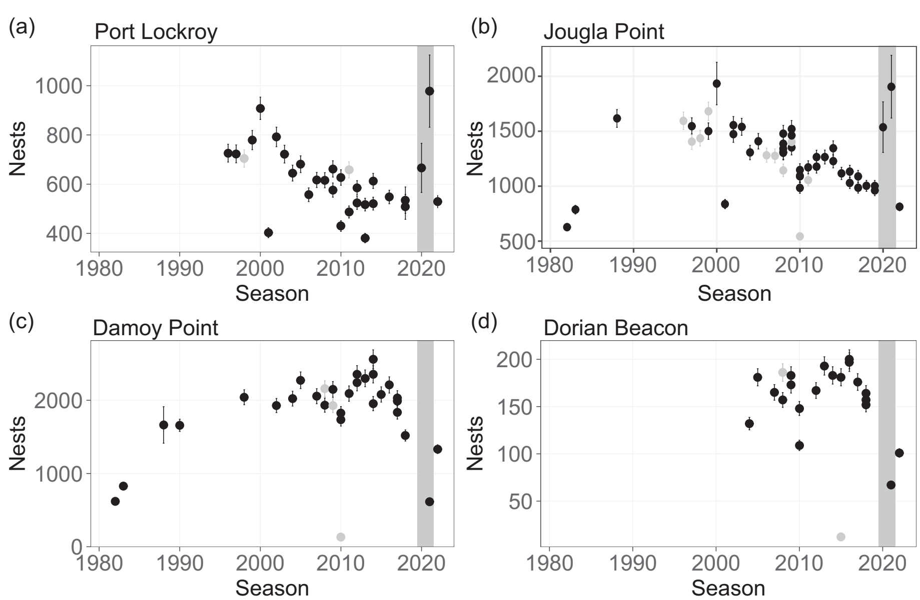

Fig. 3. Study Site Time Series: The number of gentoo penguin nests at (a) Port Lockroy, (b) Jougla Point, (c) Damoy Point, and (d) Dorian Beacon. The points in light gray represent census counts completed in November as they may not represent the total number of nests depending on the phenology of that site and season, and the black points are from counts completed in December onward. The error bars represent reported observer error, and the years the post office was closed are highlighted in dark gray.

visits to the much larger adjacent Damoy Point site. IAATO did not report any tourism numbers for the 2020 season because there were only two expeditions to the entire continent (IAATO, 2022a). Tourism resumed in 2021 at reduced levels, with Damoy Point receiving more visitors than Port Lockroy or Jougla Point. When the post office reopened in 2022, Port Lockroy had 12,974 landed passengers, and Jougla Point had 6364 (IAATO, 2023b). Damoy Point experienced the most landings of the region with 17,352 passengers landing, 79 % more than its previously most visited season (IAATO, 2023b). When combined, the three sites experienced 36,690 passengers landing, which is over 1500 more passengers than the three sites ever received prior to the pandemic (IAATO, 2023b).

4. Discussion

When the Port Lockroy post office closed to visitors and staff in the 2020 and 2021 seasons, the Port Lockroy penguin population nearly doubled. The post office's reopening in 2022 then immediately brought about a reversal to a near pre-pandemic population size. Importantly, the number of nesting gentoo penguins increased in all areas of Port Lockroy during the pandemic, though most extremely in the moderately and highly visited areas. In addition, the other colony in the Port Lockroy harbor, Jougla Point, showed the same pattern as Port Lockroy even though it experienced 52 % fewer landed passengers in the decade before the pandemic. Because only nesting penguins are included in census counts and gentoo penguins do not breed until they are at least two years of age, a shift in reproductive success would not be observed in the census size of the breeding population for at least two years. Therefore, these rapid increases in the Port Lockroy and Jougla Point population sizes cannot be a result of increased reproductive success during the two years of the pandemic closure. Both the shift towards breeding in the Port Lockroy harbor and its reversal must be driven by immigration and changes in breeding propensity. Approximately 1000 nesting pairs that would have plausibly nested at Damoy Point or Dorian Beacon in pre-pandemic conditions instead chose to nest at Port Lockroy or Jougla Point, and an additional ~ 350 pairs that would have bred at further sites or skipped breeding in pre-pandemic conditions also nested in the Port Lockroy harbor during the shutdown. This represents a total of about 1350 nesting pairs, or 2700 individuals in this metapopulation whose breeding behavior was altered by the pandemic shutdown. These findings suggest a middle ground between Trathan et al. (2008), who found that tourism and scientific monitoring only impacted the number of nests in most highly visited subcolonies, and Dunn et al. (2019), who found impacts on the entire island. In other words, both scenarios seem to be true – impacts can occur at scales larger than the 5 m minimum approach distance, and the greatest impacts are seen in the most intensively disturbed areas.

There are several mechanisms by which disturbance might occur even for portions of the colony that appear distant from human activity. One is that, as was noted in Dunn et al. (2019) and can be seen in the RPAS image of Port Lockroy in Fig. 2a, penguin trails cross the entire island and so gentoo penguins nesting in the moderately or unvisited areas may still be exposed to pedestrians while commuting to and from their nests. Secondly, the UK Antarctic Heritage Trust staff live on the island and enter the unvisited side of the island three times per breeding season to conduct surveys (Dunn et al., 2019), which adds an additional source of human activity wholly separate from the visitation by tourists. Finally, the number of ships sitting offshore throughout the season and the zodiac traffic involved in ferrying passengers ashore may create a zone of disturbance in the water that requires penguins to divert from the shortest path back to the colony when foraging, or even disturb the penguins' foraging areas. The physical re-direction combined with any noise pollution may dissuade penguins from nesting near areas of intense marine traffic even if such areas are unvisited by pedestrians. Supporting this hypothesis is the observation that visitation at Jougla Point has been lower than at Damoy Point since 2017 and yet the changes observed at Jougla Point during the pandemic mirror those of Port Lockroy, suggesting a shared driver for the sites within the relatively closed harbor in which they are both situated.

In this light, it is important to note that Dorian Beacon and Damoy Point showed the opposite trends as Port Lockroy and Jougla Point during the pandemic closure, despite being located less than 2 km from the Port Lockroy harbor, and Damoy Point experiencing more tourism than Jougla Point in the three years prior to and in the two years after the 2020 shutdown. The Damoy Point population began declining around 2017, when tourism to Damoy Point doubled. Surprisingly, it further declined in 2021 even though there was little tourism. We attribute this to the greater loss of tourism in the Port Lockroy harbor than at Damoy Point in 2020 and 2021; the removal of tourism increased the habitat quality of Port Lockroy and Jougla Point more than it did the habitat quality of Damoy Point and Dorian Beacon. There was likely more unoccupied, suitable nesting habitat in the Port Lockroy harbor before the pandemic closure than at the sites outside of the harbor because of the difference in tourism levels. When the tourism pressure lessened, gentoo penguins moved into the open habitat in the harbor, equilibrating the density of nests among colonies. It is also worth noting that gentoo penguins are commonly observed nesting around human structures, likely because they provide protection from wind and snow, and it is possible that the buildings at Port Lockroy are particularly attractive for nesting penguins in the absence of the associated human activity. While the population sizes at Port Lockroy and Jougla Point fell to pre-pandemic levels in 2022, the populations of Damoy Point and Dorian Beacon were somewhat reduced compared to their 2018 sizes (−12 % and −39 %, respectively). Heavy snowfall during the 2022 breeding season had widespread impacts along the Antarctic Peninsula and many gentoo penguin pairs were delayed in nest building or suffered nest failure. This could have contributed to the decrease in the number of nesting pairs at Port Lockroy and Jougla Point in 2022. However, our findings that the Damoy Point and Dorian Beacon population sizes increased from 2021 to 2022 are even more surprising considering the unusually heavy snowfall in 2022. The 2022 Damoy Point and Dorian Beacon census counts may represent an underestimate of the total number of pairs that will ultimately return to these two colonies, though considering the previously decreasing trend and annual variation of Damoy Point, the population there may have fully recovered.

These data are among the most extreme levels of gentoo penguin immigration recorded, and suggest weaker levels of site fidelity than has been previously reported (Williams and Rodwell, 1992; Williams, 1995). Until recently, gentoo penguin colonies were treated as closed populations with negligible movement among colonies (e.g., Hinke et al., 2007; El-Laham et al., 2022), bolstered by genetic findings that gene flow on the Western Antarctic Peninsula has been limited and likely occurred in discrete bouts (Levy et al., 2016; Vianna et al., 2017; Clucas et al., 2018; Korczak-Abshire et al., 2021). However, recent studies of gentoo penguin population growth and range expansion have concluded that high levels of gentoo penguin immigration must be occurring on a regular basis (Herman et al., 2020; Herman and Lynch, 2022), which long-range winter dispersal by gentoo penguins from northern colonies in Antarctica may be facilitating (Baylis et al., 2021; Korczak-Abshire et al., 2021). While the limitations imposed by flipper banding make it difficult to directly measure gentoo penguin immigration, a model by Herman and Lynch (2022) reported an average of 344 first-time breeding female gentoo penguins immigrated to Biscoe Point annually over 19 years. However, the sheer magnitude of fluctuations between Damoy Point/Dorian Beacon and Port Lockroy/Jougla Point, and the immediate return to near prepandemic numbers at each site in 2022, implies that experienced breeders, not just first time breeders nesting away from their philopatric sites, also immigrated between colonies. This level of movement suggests that these four sites form a metapopulation with at least sporadic movement of individuals among the sites. However, without mark-recapture data for any of these penguins, it is difficult to know how much movement regularly occurs between these colonies. Recent genetic evidence finds that while the Damoy Point gentoo penguin colony has lower genetic diversity than the Jougla Point colony and some genetic drift between the two has occurred, the two colonies are not genetically distinct populations and likely exchange alleles (Herman et al., in review).

This study adds to a growing body of work on the population structure and spatial dynamics of *Pygoscelis* penguins. Other studies highlighting periods of population mobility include Dugger et al. (2010) who documented Adélie penguin immigration rates of up to 3.5 % in the southwestern Ross Sea in seasons with extremely high sea ice, Dunn et al. (2016) who detailed Adélie and chinstrap population fluctuations at Signy Island consistent with pairs immigrating between breeding colonies on the island, and Southwell et al. (2021) reporting Adélie penguins colonizing a new site at the Windmill Islands. Port Lockroy, Jougla Point, Damoy Point, and Dorian Beacon should be closely monitored in the coming years to assess the lasting impacts of redistribution. If all first time breeders return to their natal sites, we would expect to see a sharp uptick in nesting pairs at Port Lockroy and Jougla Point when the 'anthropause' generation reaches maturity and returns to breed starting around 2023. However, it is possible that philopatry is so weak within this tightly coupled metapopulation that first-time breeders will establish themselves at one of the less visited colonies outside of the harbor. This follows from conclusions by Trathan et al. (2008) that breeders may be selecting less disturbed sites within Port Lockroy; our findings suggest this same dynamic may also be occurring at a larger spatial scale as well.

This study provides conclusive evidence that humans are affecting gentoo penguin population dynamics. IAATO and the ATCM's current restrictions, in conjunction with activity levels surrounding an active base, are not sufficient to avoid disturbance levels that change population sizes. While the British Antarctic Survey closure of the eastern side of Port Lockroy lessened the human impacts on nesting gentoo penguins compared to the rest of the island, the number of nests on the unvisited side still increased during the COVID-19 anthropause. Zodiac traffic around Port Lockroy may also have contributed to the changes observed, and both the direct and noise related impacts of zodiac traffic on nesting penguin populations should be evaluated. Operators should also consider limiting the number of zodiac cruises permitted in and around popular penguin colonies, particularly if further pedestrian limits are imposed, or sites close to landings due to avian flu, which could result in increases in the number of zodiac cruises. Because tourism may have impacts that extend beyond the visited colony, this study also raises the question as to whether tourism management at the scale of individual sites is sufficient to minimize excessive cumulative disturbance at geographically proximate colonies.

Finally, we would like to raise one final issue relating to tourism impacts, which relates to the timing of tourism activities relative to the breeding phenology of gentoo penguins. Gentoo penguins may be less likely to abandon their nests despite stressful human disturbance if they have established nests before tourism activities begin, whereas they may decide to breed elsewhere if passenger landings precede nest establishment. As the number of visitors to Antarctica grows, landings have advanced in time (Bender et al., 2016). Over the last decade, gentoo penguin phenology on the Antarctic Peninsula has also advanced (I. Juárez, unpublished data). For example, in 2012, Port Lockroy gentoo penguins began settling on nests on November 17th (I. Juárez, unpublished data) and the first landed passenger vessels arrived on November 16th (Bender et al., 2016). Because the timing of these two events are so closely matched at these colonies, even small changes in the start of passenger landings may drive large changes in response. While there is no straightforward way to balance the risks of human-driven movement vs. stress on nesting penguins, the timing of tourism at these gentoo penguin colonies - rather than just its magnitude - may need further discussion.

This local-scale movement of gentoo penguins towards more suitable, less disturbed habitats is a behavioral adaptation that may increase this species' resilience to human impacts. The impacts observed in this study were ameliorated at the larger scale of the four colonies by the surprisingly plastic response of gentoo penguins to anthropogenic disturbance. This could explain why Lynch et al. (2019) did not find elevated levels of corticosterone in Port Lockroy gentoo penguins - the individuals that were prone to stress from the presence of humans emigrated away, or potentially became habituated. While these results provide promising evidence that gentoo penguins may be able to adapt to human disturbances through re-distribution to less visited locations, we do not know whether Adélie and chinstrap penguins are similarly capable and what we do know suggests that recovery from disturbance may be slow and require human assistance (Kim et al., 2023). The COVID-19 anthropause has provided a critical, once-in-a-lifetime opportunity to study human impacts in the Antarctic, with lessons worthy of serious consideration in our ongoing efforts to minimize the human footprint in Antarctica.

CRediT authorship contribution statement

C.M.F: conceptualization, methodology, formal analysis, investigation, data curation, writing- original draft preparation, writing- reviewing and editing, visualization; **T.H:** conceptualization, investigation, resources, writing- reviewing and editing, supervision, project administration, funding acquisition; **G.V.C:** investigation, resources, data curation, writing- reviewing and editing, supervision, project administration; **H.J.L:** conceptualization, methodology, formal analysis, data curation, writing- original draft preparation, writing- reviewing and editing, visualization, supervision, project administration, funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank everyone who contributed to the collection of the data used in this paper, especially Jane Younger who organized and led the 2021 expedition to Port Lockroy and Jougla Point. C.M.F. also gratefully acknowledges her committee members Resit Akçakaya and Lesley Thorne for providing guidance and feedback on this project, and her labmates Katherine Gallagher, Emma Talis, Rachael Herman, Michael Wethington, Caitlin Blackwell, Carole Hall, and Madeline Hallet for their feedback on the writing in this manuscript. C.M.F. acknowledges funding from the NASA biodiversity program (Award 80NSSC21K1027), and T.H. from Quark Expeditions, Cheeseman's Ecology Safaris, and Save Our Seas Foundation, who also provided logistical support for the 2020 expedition.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110318.

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