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Front cover picture: Black-legged Kittiwake *Rissa tridactyla* at the Shoup Bay colony in Prince William Sound, Alaska, USA, June 2007. (Photo: Greg Peterson)



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MARINE ORNITHOLOGY

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General queries relating to *Marine Ornithology* should be directed to:

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NESTING BEHAVIOR OF MARBLED MURRELETS *BRACHYRAMPHUS MARMORATUS* IN WASHINGTON AND BRITISH COLUMBIA

TERESA J. LORENZ, MARTIN G. RAPHAEL* & THOMAS D. BLOXTON

United States Department of Agriculture, Forest Service, Pacific Northwest Research Station,
3625 93rd Avenue SW, Olympia, Washington 98512, USA *(martin.rafael@usda.gov)

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ABSTRACT

LORENZ, T.J., RAPHAEL, M.G. & BLOXTON, T.D. 2019. Nesting behavior of Marbled Murrelets *Brachyramphus marmoratus* in Washington and British Columbia. *Marine Ornithology* 47: 157–166.

Marbled Murrelets are threatened seabirds that nest predominantly in old-growth forests in the southern part of their western North America range. Little is known about causes of nest failure, timing of parental visits, and nest reuse because it is difficult to locate and monitor nests of this cryptic species. We used radio telemetry to locate murrelet nests from 2004 to 2008 in northwestern Washington and southeastern British Columbia. We monitored four nests with video cameras to document causes of nest failure, and we visited 15 nests after the nesting season to infer nest fate. We also monitored six active nests with telemetry data loggers to determine the timing of parental visits, and eight previous-year nests to determine nest reuse. Among 20 nests, four successfully fledged and 16 failed. Among failed nests, 10 failed from unknown causes and the remaining six failed from non-predatory causes. Parental visits during the incubation period occurred exclusively before dawn (100 % of 32 visits), whereas visits during the nestling period ($n = 73$) occurred during the morning (70 %), afternoon (1 %), and evening (29 %). Among eight nests monitored for reuse, we observed two cases of nest reuse and two cases in which nests were briefly visited by murrelets in later years but were not reused for nesting.

Key words: *Brachyramphus marmoratus*, video surveillance, radio telemetry, nest predator, nest provisioning, nest success

INTRODUCTION

Marbled Murrelets *Brachyramphus marmoratus* are seabirds that are unique in the family Alcidae for nesting in coastal, old-growth forests in western North America. Populations from British Columbia to California are federally threatened, with consistent population decreases reported in British Columbia and Washington (Bertram *et al.* 2015, Falxa *et al.* 2016). Poor recruitment from low nest success is considered a major threat to populations (USFWS 1997). However, there is little definitive information on causes of nest failure because nests are difficult to locate and monitor. Marbled Murrelets nest solitarily, high in old-growth trees throughout their range, and on cliffs or in glaciated, mountainous terrain in the northern part of their range (Hamer & Nelson 1995, Bradley & Cooke 2001, Barbaree *et al.* 2014). Adults are secretive and crepuscular in their nesting behavior, and eggs and nestlings are extremely well-camouflaged. Adults typically visit nests once daily during the incubation period and 1–8 times daily during the nestling period (Naslund 1993, Nelson & Peck 1995, Nelson 1997, Manley 1999, Nelson & Wilson 2002).

All together, we found < 50 accounts of Marbled Murrelet nest failure in which the cause of failure was known with certainty (Appendix 1, available on the website). Corvid depredation appears to be an important issue in Oregon and California, accounting for 50 % of failed nests in these states (Singer *et al.* 1991, Peery *et al.* 2004, Hebert & Golightly 2007, Golightly & Schneider 2011; Appendix 1). Corvids have been identified as nest predators in many other studies where the act of nest predation was not observed directly or was not described explicitly by the study authors (Ford & Brown 1995, Naslund *et al.* 1995, Nelson & Hamer 1995,

Nelson & Peck 1995, Manley 1999). Other causes of nest failure include egg abandonment, death of a parent, and nestlings dying from health-related problems (Appendix 1). For Washington and British Columbia, where the most pronounced murrelet population decreases have been reported (Bertram *et al.* 2015, Falxa *et al.* 2016), we found only two studies where causes of nest failure were observed or described. In one case, Hamer and Cummins (1991) retrieved a downy murrelet chick from beneath a nest, indicating that the chick fell off the nest platform. In Silvergieter (2009), three eggs failed to hatch (one egg was infertile) and one chick was found dead in the nest. In other studies, from Washington and British Columbia, the cause of nest failure was not known with certainty (e.g., Manley 1999). Overall, larger sample sizes of nests are needed to determine the predominant causes of nest failure in this population.

To address this information gap, we used radio telemetry to study Marbled Murrelet nesting behavior in Washington and British Columbia. Our primary goal was to determine causes of nest failure, but over the course of our study we also obtained data on the timing of parental nest visits and nest reuse. This information is useful for informing inland survey protocols for Marbled Murrelets, which in turn are used to guide land management decisions. The objective of this paper is to present causes of nest failure, the timing of nest visits by parents, and observations of nest reuse for Marbled Murrelet nests monitored in Washington and British Columbia.

STUDY AREA

We conducted this study in northwestern Washington and southwestern British Columbia. We captured murrelets in US

waters of the Pacific Ocean, as well as the Strait of Juan de Fuca, Puget Sound, and in Hood Canal, Washington. We searched for nesting murrelets on the Olympic Peninsula and in the Cascade Range of Washington, and on Vancouver Island, British Columbia (see Methods, Locating nest sites). This area has a maritime oceanic and temperate climate with mild, rainy weather year-round, except for a dry period in late summer. Forests used for nesting by murrelets in this region are generally temperate coastal rainforests dominated by western hemlock *Tsuga heterophylla*, Douglas-fir *Pseudotsuga menziesii*, Sitka spruce *Picea sitchensis*, and western red cedar *Thuja plicata*.

METHODS

Locating nest sites

The most efficient method of locating Marbled Murrelet nests involves radio-tagging murrelets at sea and searching for radio signals of tagged breeders at inland nest sites by aircraft. From 2004 to 2008, we radio-tagged Marbled Murrelets in coastal waters of Washington State to locate nest sites. For additional details on radio-tagging methods, see Lorenz *et al.* (2017). We obtained a small sample of blood from each bird for determining sex.

We located radio-tagged murrelets primarily by aerial tracking from fixed-wing aircraft. We used ground-based telemetry for pinpointing the exact location of nest sites and for monitoring nests. We initiated aerial tracking searches within three days after the first murrelet was tagged in each year. We ended searches after the last identified nest had fledged or failed and when significant numbers of transmitters were no longer detectable within our study area, indicating post-breeding dispersal or transmitter battery failure.

Weather permitting, we conducted tracking flights daily. Tracking flights lasted up to 5 h, until all birds had been located or the aircraft needed refueling. Aerial searches included marine foraging areas and terrestrial nesting areas. If we did not locate an individual murrelet at sea or on an inland nest for 2–3 consecutive days, we expanded our search area to find the missing bird, focusing on areas beyond the location that the missing murrelet was last detected. When pilots detected a murrelet's radio signal, they circled over the source and used a global positioning system (GPS) unit to mark the location from which they heard the loudest signal.

Because we were interested in marine locations for studies of breeding season space use, we typically first detected breeding activity when radio-tagged murrelets exhibited the characteristic on-off pattern at sea, in which adults alternate 24-h incubation shifts (Bradley *et al.* 2004). When the on-off pattern was observed for a murrelet, we flew over suitable nesting habitat until the tagged bird was detected. We then visited the area on foot and located the nest by homing to the murrelet's radio signal. It often took multiple visits on foot to locate murrelet nest sites.

Nest fate

We determined nest fate using one of three techniques: (1) we set a remotely powered video camera (Sentinel MAGNUM and Sentinel for daytime footage, and ELF fixed lenses and Starlight Color Zoom Lenses for recording at night; Sandpiper Technologies, Inc., Manteca, CA) at accessible nests to monitor nest activity directly; (2) we climbed nest trees after the nesting season to view

nest contents; and (3) we counted the number of days murrelets exhibited incubation behavior (Bradley *et al.* 2004) or nestling visits from telemetry monitoring at sea. When we visited nests after the breeding season, some contained eggs or chick remains, which we submitted for necropsy to the Washington Animal Disease Diagnostic Lab.

We chose nests to video monitor based on ease-of-access and distance to roads; video-monitored nests also had to be viewable from a nearby tree. Most nests were located in rugged, mountainous terrain and were difficult to access. Therefore, only four of 20 nests were monitored with video: Boulder Creek, Sombrio, Hemmingsen Creek, and Rica Canyon (Appendix 2, available on the website). For these nests, we set video cameras in trees within 30–50 m of the nests. We did not climb trees with active nests. Once we located a limb on a nearby tree where the murrelet's nest could be viewed, we affixed a camera with a zoom lens to the tree limb (Fig. 1). We extended a 50-m cable from the lens to the ground and set batteries for powering the camera on the ground. Cameras were powered with marine deep-cycle batteries and video files were stored on media storage devices that we changed weekly. When we visited monitored nests, we were able to replace batteries and media storage devices without climbing the camera tree. To minimize disturbance to nesting murrelets, we took basic precautions to minimize attracting potential nest predators and affecting murrelet behavior. We also stationed one crew member on the ground to observe nesting murrelets. No murrelets flushed from nests during camera set-up. Cameras ran continuously both day and night, although night footage (from approximately 22h30 to 04h30) was not viewable due to the distance lenses were placed from nests. We reviewed all footage from video-monitored nests to note the time of day for parental visits, chick behavior, and visits by other species.

We visited all nests after the nesting season to view nest contents. For nests that were not video monitored, we considered nests



Fig. 1. Photo showing placement of a zoom lens relative to the Hemmingsen Creek Marbled Murrelet nest in 2006 (nest is indicated with arrow), on Vancouver Island, British Columbia. Zoom lenses were typically placed in nearby trees on limbs 30–50 m from the nest. A ~50-m cable extended from the lens to the ground. Deep-cycle batteries (for powering the camera) and a digital video recorder (for recording and storing video files) were placed on the ground below the camera tree. Thus, when we visited the nest to replace batteries we did not have to climb the camera tree. Inset photo in upper right shows the Hemmingsen Creek Marbled Murrelet incubating an egg on the nest. Photos by N.R. Hatch.

successful if the length of time a radio-tagged adult visited a nest indicated nest attendance for ~ 30-d incubation and 30-d nestling periods, or if we found a large fecal ring during our post-breeding nest visits (Nelson 1997, and references therein). We classified nests as unsuccessful if the timing of adult visits was too short for successful nesting based on known dates of nest initiation (< ~ 60 d; Nelson & Hamer 1995, McFarlane Tranquilla *et al.* 2005), if there was an under-developed fecal ring at the nest site, or if we found an egg or dead chick (Nelson & Hamer 1995, Nelson 1997).

Parental visits

We determined the time of parental visits using one of two techniques: (1) we noted the time of visits from video recordings (for video monitored nests); or (2) we monitored visits by radio-tagged parents using telemetry dataloggers (for nests with dataloggers) ($n = 5$ nests; Appendix 2) (R4500SD Receiver-Datalogger, Advanced Telemetry Systems, Isanti, MN). We set dataloggers on the ground along flight paths of murrelets, 1–15 km from nest sites. Dataloggers recorded continuously. Dataloggers recorded times that radio signals were detected but provided no direct information on the activities of radio-tagged murrelets. For estimating nest visitation times, we included one additional nest that was found incidentally (without radio telemetry) in 2006 in the Heart o' Hills Campground in Olympic National Park, Washington. When found, birds in this nest were in the nestling phase. We climbed the nest tree following the 2006 breeding season and found a thick fecal ring, indicative of nest success. We set a camera in a nearby tree to monitor this nest in 2007.

There are several potential biases that are unaccounted for in our analysis of nest visitation rates. First, if transmitters affected nest visitation rates, radio-tagged murrelets recorded on the dataloggers may not be a representative sample of the population of murrelets in our study. Second, visits detected by dataloggers may reflect

murrelets circling over nests rather than visiting nests. Last, for video-monitored nests, murrelets may have visited nests in full dark. Our cameras were unable to detect nest activities between approximately 22h30 and 04h30 hrs.

Nest reuse among years

We monitored a total of eight nests for reuse in later years. Seven nests were located by radio-tracking murrelets and one nest was found incidentally (Heart o' Hills nest, described above). Nests were monitored for 1–3 y after their discovery. Six of these previous-year nests were video monitored. For these nests, we set up video cameras in a nearby tree or in the nest tree, 1 m above nest platforms. We recorded video opportunistically during the breeding season (May to July), when personnel and equipment could be spared from the main objective of the study, which was monitoring outcomes at active nests. For two additional nests previously reported by Burger *et al.* (2009), we visited the nest once or twice during the nesting period to look for evidence of nesting activity. One of these nests was not visible from the ground, so we also climbed the tree after the nesting period to look for evidence of nesting activity at the nest platform. We acknowledge that we likely missed nest visits and possibly nesting attempts due to our sporadic monitoring.

RESULTS

We radio-tagged 157 murrelets from 2004 to 2008. Most murrelets were captured in the Strait of Juan de Fuca ($n = 113$), followed by Hood Canal ($n = 28$) and the Pacific Ocean ($n = 16$). Twenty murrelets attempted nesting (14 males, six females). Nests were 4–58 km from the nearest shoreline (median distance 18 km; Fig. 2) (Wilk *et al.* 2016). One nest fledged and one nest failed before we pinpointed the nest tree. Nineteen nests were in trees and one nest was on a cliff face (North Fork Sol Duc Cliff; Fig. 2). For additional

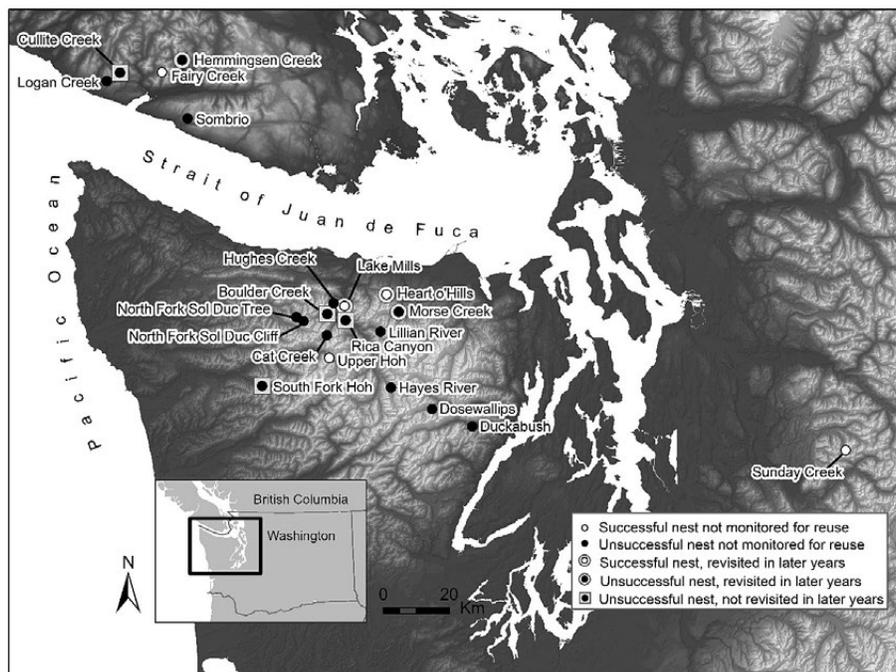


Fig 2. Study area in northwestern Washington and southwestern British Columbia from 2004 to 2008 with locations of 21 Marbled Murrelet nests. The Heart o' Hills nest was not found using radio telemetry and was excluded from our analysis of nest fate.

details on nest characteristics and locations see Wilk *et al.* (2016) and Lorenz *et al.* (2017).

Nest fate

Among 20 nests of radio-tagged murrelets, we concluded that four successfully fledged young and 16 failed (Fig. 2, Appendix 2). Among failed nests, we have information on the cause of nest failure for four nests (Table 1). Two video-monitored nests failed when the eggs did not hatch within a 35-d (Boulder Creek) or 40-d (Sombrio; Appendix 2) period, and were then abandoned. At a third video-monitored nest, the chick fell out of the nest while being fed by the adult (Hemmingsen Creek). One additional nest was abandoned during incubation based on signs left at the nest (Duckabush). At this nest, which was not video-monitored, we found an intact egg in the nest depression. Necropsy revealed that the egg contained a well-developed embryo (Appendix 2).

For three additional nests (Rica Canyon, South Fork Hoh, and North Fork Sol Duc cliff), nest predation did not appear to be the cause of failure, although the ultimate cause of chick death was not known with certainty. At the Rica Canyon nest, the chick was slow to accept fish from parents approximately 6 d post-hatching, and we observed flies (Diptera) on the chick 18 and 19 d post-hatching (05 and 06 July 2005). At 19 d post-hatching (06 July) the chick became nearly motionless. At 20 d post-hatching (07 July) the adult male visited the nest without a fish in the morning. When the adult female visited with a fish in evening of the same day, the chick did not respond and was presumed dead (Appendix 2). Necropsy was performed on the decayed remains of the chick, but soft tissues had

decomposed and we could not determine cause of death. Necropsy showed no damage or fractures to the major long bones.

At the second nest (South Fork Hoh), we found a dead chick in the nest depression when we climbed the nest tree after the nesting season (Appendix 3, available on the website). The chick had a fish in its bill that apparently filled its esophagus, and a second fish was lying in the nest depression. Necropsy was conducted on the desiccated remains, but it revealed no significant gross findings, no bone fractures, no histological inflammation, and no evidence of bacterial infection (Appendix 2). The cause of death is unknown, but it is unlikely that it was from predation because the chick was intact and had no obvious signs of trauma or hemorrhage.

At the third nest (North Fork Sol Duc Cliff), evidence points to the nestling dying after being grounded while fledging. The remains of a chick in juvenile plumage were found at the base of the nest cliff after the nesting season (Appendix 3). Because murrelet nestlings retain down until 8–48 h before fledging (reviewed in Nelson 1997), this indicates that the chick died near the time of fledging.

We did not directly observe nest predation in this study. However, three video-monitored nests were visited by putative predators after they were abandoned by parents but still contained an egg or chick (Appendix 2). One nest (Rica Canyon) was visited by a Steller's Jay *Cyanocitta stelleri* around the time that the nestling murrelet died. We suspect that the chick was dead during the jay's visit, but we cannot not be certain of this. Regardless, the chick was unresponsive and the jay did not touch the chick. A Steller's Jay visited this nest again eight days later, when it pecked at the pile

TABLE 1

Causes of nest failure for 16 unsuccessful Marbled Murrelet nests monitored in Washington and British Columbia from 2004 to 2008^a

| Year | Sex of tagged bird | Site | Cause of nest failure |
|---|--------------------|--------------------------|---|
| Nests that failed during incubation: | | | |
| 2004 | Female | Boulder Creek | Egg failed to hatch (reason unknown) |
| 2007 | Male | Sombrio | Egg failed to hatch (reason unknown) |
| 2005 | Male | Duckabush | Egg was abandoned (reason unknown) |
| 2005 | Male | Dosewallips | Unknown |
| 2005 | Female | Hayes River | Unknown |
| 2005 | Female | Logan Creek | Unknown |
| 2007 | Male | Cat Creek | Unknown |
| 2007 | Male | Hughes Creek | Unknown |
| 2007 | Male | Lillian River | Unknown |
| Nests that failed during nestling phase: | | | |
| 2006 | Male | Hemmingsen Creek | Chick fell out of nest while being fed by adult |
| 2005 | Male | Rica Canyon | Chick died of non-predatory factors |
| 2005 | Female | South Fork Hoh | Chick died of non-predatory factors |
| 2004 | Male | Morse Creek | Unknown |
| 2005 | Female | Cullite Creek | Unknown |
| 2007 | Male | North Fork Sol Duc Cliff | Unknown (suspect grounded while fledging) |
| 2008 | Male | North Fork Sol Duc Tree | Unknown |

^a Details on the determination of nest fate are in Appendix 2 and photos of nests are in Appendix 3.

of feathers but did not visibly consume anything (Appendix 2). A second nest (Sombrio) was also visited by a Steller's Jay. The jay visited approximately 17 d after the egg failed to hatch (assuming an incubation period of ~ 30 d) and seven days after the parents ceased incubation. The jay did not touch the egg. The third nest visited by a putative predator was the Boulder Creek nest. Boulder Creek was visited by a Douglas squirrel *Tamiasciurus douglasii* nine days after adults stopped incubation. The squirrel rolled the egg off the limb with its head (Appendix 2). When we returned to remove the camera we found fragments of eggshell on the ground below the nest.

Parental visits

We noted the time of 105 nest visits by 10 parents (five males, five females) to six active nests. This included 39 visits by females and 38 visits by males (28 visits by birds of unknown sex). We did not formally test for differences in visitation rates by sex due to the small sample size.

During the incubation phase, all visits occurred before official sunrise ($n = 32$ visits between 18 June and 18 July; Fig. 3). Most visits (91 %) occurred during morning civil twilight (Table 2). During the nestling phase (06 June to 11 August), 70 % of 73 parental visits occurred in the morning (within 84 min of sunrise) and 29 % occurred in the evening (within 48 min of sunset), with one unusual mid-day visit that occurred at 13h57 PDT (Fig. 3). On average, morning visits during the nestling phase occurred within 44 min of sunrise (median = 37 min, range 61 min before to 197 min after sunrise). Evening visits occurred within 21 min of

sunset on average (median = 17 min, range 36 min before to 48 min after sunset). The two latest evening visits were to the Sunday Creek nest in the Cascade Range and occurred on clear, moonlit nights.

Nest reuse among years

We monitored eight nests for reuse. Two of these eight nests (25 %) were reused for nesting and two were revisited but not reused (25 %). Seven of the eight nests were initially located with radio-tagged murrelets and were then monitored by video ($n = 5$) or by revisiting ($n = 2$) in later years. The eighth nest (Heart o' Hills) was initially located incidentally and without radio telemetry.

Among five video-monitored nests, we observed nest visits at two of these nests in later years. The first nest (Lake Mills) was successful in its original attempt in 2004. It was visited once on 18 May 2005 by a radio-tagged murrelet (transmitter battery was presumably dead, but a transmitter was visible on the bird's back) near dawn for approximately 5 min. It is likely that this was the same bird that nested at this site in 2004, although this was impossible to verify. The visiting murrelet appeared to look upward at the camera several times, suggesting that the presence of the camera may have disturbed the bird. We also documented one visit by a murrelet to the Morse Creek nest. This nest was unsuccessful in its original attempt in 2004 and was monitored opportunistically during 2005–2007. A murrelet revisited this nest on 10 June 2006; similar to the Lake Mills site, the visiting murrelet was wearing a radio tag.

For two nests that we revisited (but did not video monitor), one had a fresh, partial fecal ring indicating that it was used by murrelets

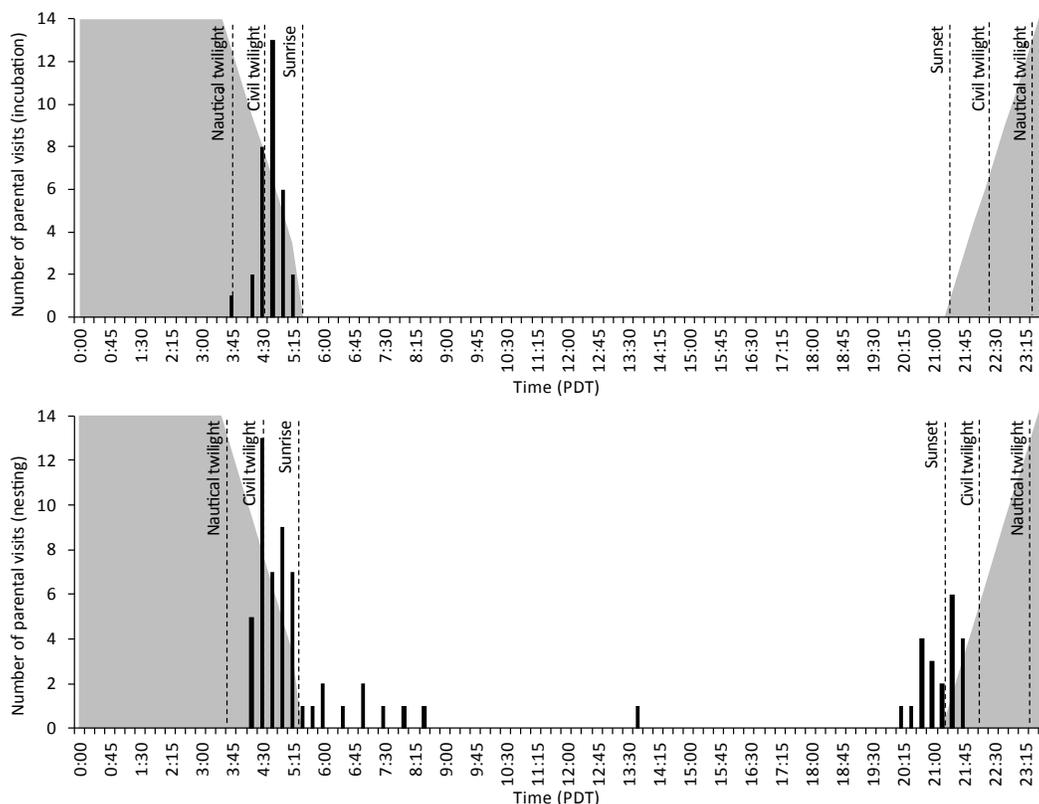


Fig. 3. Number of parental visits to active Marbled Murrelet nests during the incubation phase (top) and nestling phase (bottom) recorded with telemetry data loggers and video cameras for six nests in Washington and British Columbia, from 2004 to 2008 (black bars). Gray shading indicates darkness. Median time of nautical twilight, civil twilight, and sunrise/sunset is indicated with dotted lines.

for two years in a row (but failed in both years). One did not show signs of re-nesting from a ground viewing location. Finally, the eighth monitored nest (Heart o' Hills) was found incidentally in 2006 and monitored with a video camera in 2007. The nest was used successfully in both 2006 and 2007. We observed fledging of the murrelet chick on 22 June 2007 between 21h46 (29 min after official sunset and 13 min before the end of civil twilight) and 24h54, and 3 h 9 min after the last two visits by parents with food.

DISCUSSION

In our study, among Marbled Murrelet nests with a known cause of failure, we observed no cases of nest predation. This was unexpected because nest predation, particularly by ravens *Corvus corax* and jays, was a leading cause of murrelet nest failure in past studies (Singer *et al.* 1991, Peery *et al.* 2004, Hebert & Golightly 2007; Golightly & Schneider 2011). It is especially surprising because corvids are common in our study area. Artificial nest studies with hundreds of monitored nests in Washington and British Columbia have shown that ~ 33 % to 48 % of artificial murrelet nests are visited or depredated by corvids (Luginbuhl *et al.* 2001, Marzluff & Neatherlin 2006, Malt & Lank 2007, 2009). While artificial nest studies have many biases (e.g., Faaborg 2004, Thompson & Burhans 2004), these studies demonstrate that corvids are common in murrelet nesting habitat in our study area. We also found it remarkable that two of four video-monitored murrelet nests in our study were visited by corvids after nest failure. In these cases, corvids visited inactive nests but did not appear to forage on the dead murrelets or otherwise scavenge them. Additional studies with larger sample sizes of monitored nests are needed to determine if our observations are representative of this region.

Instead of corvid nest predation, known causes of nest failure in our study included one observation of a chick falling from the nest platform and three cases of egg abandonment or failure of the egg to hatch. We suspect that one additional nest failed when the chick became grounded while fledging, and we documented two additional cases of nestlings dying from non-predatory factors. Chicks falling from platforms has previously been documented for

Marbled Murrelets (Carter & Sealy 1987, Hamer & Cummins 1991), and nest abandonment is well documented for other alcids when food availability is low and parents cannot obtain enough food to sustain their breeding efforts (e.g., Bertram *et al.* 2001, Sydeman *et al.* 2006). Our study is different from these other alcid studies, however, because in two cases of egg abandonment, parents incubated eggs for sufficiently long incubation periods, thus indicating that lack of food did not directly contribute to nest abandonment. Parent murrelets only abandoned the nest when the egg failed to hatch, indicating problems with the viability of the egg.

Insights may be gained from research on the closely related Kittlitz's Murrelet *Brachyramphus brevirostris* in Alaska. Nest fate is known for > 200 Kittlitz's Murrelet nests monitored during the last 10 years. The Kittlitz's Murrelet has many similar life history traits to the Marbled Murrelet, except that Kittlitz's Murrelets nest exclusively on the ground and do not occur south of Alaska. Among 176 failed Kittlitz's Murrelet nests, nest failure from non-predator factors is common, accounting for 51 % of nest failures that we found in the literature (Appendix 1). During incubation, egg abandonment was the most common non-predatory cause of nest failure. Eggs were abandoned due to problems with egg viability, depredation of a parent, or disturbance to the nest site (see references in Appendix 1). For nestling Kittlitz's Murrelets, major causes of death were exposure, starvation, and saxitoxin poisoning (Appendix 1). One case in our study was strikingly similar to saxitoxin poisoning described for Kittlitz's Murrelets. Our South Fork Hoh nestling was found dead in the nest with one fish on the nest platform and a second fish within the nestling's bill. In Kittlitz's Murrelets, nestlings that tested positive for saxitoxin died within hours of consuming fish (Shearn-Bochsler *et al.* 2014) and were sometimes found with dead fish still in the chick's bill (Knudson *et al.* 2015). Unfortunately, we were not able to test for saxitoxin poisoning in our study because too much time had elapsed between nestling death and necropsy. We are not aware of studies that have tested for saxitoxin in nestling seabirds in this region, although harmful algal blooms (HABs) and dinoflagellum that cause HABs are common in marine areas in Washington (Cox *et al.* 2008, Moore *et al.* 2009, Horner *et al.* 2011) and have caused die-

Table 2
Timing of parental visits to six active Marbled Murrelet nests during the incubation and nestling phase, recorded with telemetry data loggers and video cameras in northwest Washington and southwest British Columbia from 2004 to 2008^a

| | Percent (n) of parental visits | Timing of parental arrival ^a |
|---|--------------------------------|--|
| Incubation phase (n = 32 visits) | | |
| Nautical twilight (morning) | 9 % (3) | Average (range) minutes before sunrise that parent arrived: 58 (44–84) |
| Civil twilight (morning) | 91 % (29) | Average (range) minutes before sunrise that parent arrived: 29 (12–40) |
| Nestling phase (n = 73 visits) | | |
| Nautical twilight (morning) | 12 % (9) | Average (range) minutes before sunrise that parent arrived: 52 (42–61) |
| Civil twilight (morning) | 41 % (30) | Average (range) minutes before sunrise that parent arrived: 30 (7–46) |
| Morning after sunrise | 16 % (12) | Average (range) minutes after sunrise that parent arrived: 72 (1–197) |
| Afternoon | 1 % (1) | |
| Evening before sunset | 8 % (6) | Average (range) minutes before sunset that parent arrived: 15 (3–36) |
| Nautical twilight (evening) | 18 % (13) | Average (range) minutes after sunset that parent arrived: 19 (3–38) |
| Civil twilight (evening) | 3 % (2) | Average (range) minutes after sunset that parent arrived: 48 (47–48) |

^a We did not determine the timing of parents' departure from nests or the duration of their visits.

offs in adult seabirds in Washington and British Columbia (Jones *et al.* 2017). In future studies of Marbled Murrelets, researchers should consider testing for these toxins whenever possible.

Nest monitoring of Kittlitz's Murrelets has also documented cases of nest or egg abandonment in which the nest contents were scavenged (Lawonn *et al.* 2011; Knudson *et al.* 2015, 2016; Kissling & Lewis 2016), resulting in an empty nest cup when researchers visited the site. Without cameras, these nests may have mistakenly been classified as depredated. With this in mind, we encourage the use of video cameras, direct observations, necropsies, and other unequivocal methods in studies of Marbled Murrelets that wish to assign nest fate. Additional studies are needed to determine the major threats to murrelet nests. If corvids are less of a threat in our region than toxins (HABs), prey availability, egg viability, parental depredation, or other factors, managers will need to consider different strategies than those that have been implemented in California to address corvid depredation (Peery & Henry 2010, Bensen 2013). At this time, we do not have enough information to confirm causes of nest failure in Marbled Murrelets, but our study indicates that non-predatory factors may be important determinants of nest outcomes in Washington and British Columbia.

It is important to note possible biases caused by radio-tagging murrelets in this study. As discussed by many other authors (e.g., McFarlane Tranquilla 2001, Kissling *et al.* 2015), the radio tags we used may have affected the ability of murrelets to lay viable eggs, or to properly incubate eggs and provision nestlings, and this may have contributed to unusual nest fates. Many studies have looked at the effects of tags on alcids, including several studies that have reported that tags negatively impact nest success and provisioning rates (Kidawa *et al.* 2001, Paredes *et al.* 2005, Whidden *et al.* 2007, Robinson & Jones 2014, Schacter & Jones 2017). For Marbled Murrelets specifically, Peery *et al.* (2006) reported that radio tags affected murrelet survival, and Barbaree *et al.* (2014) suspected lower breeding propensity for radio-tagged female murrelets (compared to untagged females). Northrup *et al.* (2018) reported that larger 5-g satellite transmitters negatively affected Marbled Murrelets, potentially contributing to death. The size of transmitters, as well as the length and angle of transmitter antennae, are known to impact diving birds (Wilson *et al.* 2004, Ropert-Coudert *et al.* 2007). The 1.2-cm³ tags we used may have contributed to drag underwater, negatively impacting the ability of murrelets to sustain themselves and their young.

It is also important to consider that our activities at nests may have influenced nest fate by disturbing murrelets or affecting predator behavior, although this should not differ from past studies that have used similar nest monitoring methods. Another shortcoming of our study is that we do not know the causes of nest failure for 10 nests in this study. These nests may have been depredated. Thus, although we did not document nest predation, the conclusions derived from this study should be reassessed as new research is conducted and larger numbers of nests are monitored.

One interesting finding from our monitoring of nest reuse was the observation that radio-tagged murrelets visited nests one to two years after being tagged. While it was impossible to verify the identity of these murrelets, it is likely that they were the original breeders at these sites. If so, radio tags attached with the subcutaneous anchor method can be retained on murrelets for up to two years. This conclusion is supported by anecdotal evidence

from recaptured murrelets. There were two occasions on which we recaptured a murrelet that had been radio-tagged in a prior year; one of those individuals had shed its transmitter and one had retained its transmitter. Kittlitz's Murrelets have also been captured wearing previous-year transmitters (two of five recaptured murrelets; M. Kissling unpubl. data). Previously, it was assumed that radio tags attached with a subcutaneous anchor fall off within months of deployment. For example, Newman *et al.* (1999) determined that with prong and suture methods, transmitters were retained on Marbled Murrelets for a maximum of 78 d. The presumed short duration of tag attachment has precluded year-round studies of *Brachyramphus murrelet* space use. We encourage researchers to use longer-lasting batteries or programmable transmitters that last for at least one year to track marbled murrelets. Transmitters in the 1–2 g range are currently available that last one year, some of which contain programmable chips that turn transmitters off at user-defined times, allowing use of a lightweight battery that permits an increased study duration. Among a sample of murrelets tagged with the subcutaneous anchor method, some are likely to retain their transmitter for at least one year. Tracking these murrelets for one or two years could shed light on many important information gaps, such as space use among years, breeding site fidelity, and fall and winter space use.

Information on the timing of murrelet nest visits is important for informing inland survey protocols for Marbled Murrelets. In turn, these survey protocols are used to guide land management decisions. This information is also important for wind power risk models, disturbance restrictions, assessing the potential for collisions with power lines, and more. For the six nests we monitored for parental visitation, incubation visits occurred exclusively before dawn, whereas nestling visits were concentrated in the morning around sunrise but also occurred in the evening. These observations align with past studies (Naslund 1993, Nelson & Peck 1995, Manley 1999, Nelson & Wilson 2002). For example, Nelson & Peck (1995) reported that incubation visits at nine nests in Oregon occurred 8–30 min before sunrise. Nestling feeding visits were concentrated in the morning but also occurred within 90 min of sunrise, but rarely occurred during the day. In California, Naslund (1993) found that most incubation visits occurred before dawn, whereas nestling visits occurred around sunrise and sunset, with two mid-day visits. Manley (1999) noted similar behavior in British Columbia; incubation visits occurred 25–28 min before dawn, whereas nestling feeding visits occurred in the evening and morning but were most common at dawn, with one unusual mid-day visit. Other studies using audio-visual surveys, radar, and telemetry have also reported peaks of activity near sunrise and sunset, although these studies cannot distinguish between breeders and non-breeders, or breeders at different stages of the nesting cycle (Burger 2001, Bradley *et al.* 2002, Cooper & Blaha 2002, Hebert & Golightly 2007).

We documented one case of successful nest reuse, one case of unsuccessful reuse, and two cases in which previous-year nests were briefly visited by murrelets. Because of small sample sizes, it is difficult to confidently compare the rates of nest reuse between our study and past studies (Hebert & Golightly 2007, Burger *et al.* 2009, Golightly & Schneider 2011). Hebert & Golightly (2007) reported that 30 % of 10 nests were reused in subsequent years in California. Golightly & Schneider (2011) monitored one nest cup for 10 y with video and found that it was used in 7 of 10 y. Burger *et al.* (2009) consolidated information on nest reuse for British Columbia. Rates of reuse for nest trees ranged from 11 % to 18 % for different

studies, and rates of reuse for nest cups averaged 6 % (two of 35 nest cups monitored; Manley 1999). Our rates of nest-cup reuse were higher, at 25 % (two of eight limbs monitored). Burger *et al.* (2009) hypothesized that nest reuse may be higher in areas where suitable habitat has been reduced or fragmented. While we lack sufficient data to test this hypothesis, it is noteworthy that three nests that were revisited or reused in our study occurred in the northern Olympic Peninsula and within 20 km of the city of Port Angeles, Washington, which has substantial agricultural and suburban development. Overall, our results add to the literature that murrelets show fidelity to individual nest sites. They also indicate that rates of nest reuse in Washington may be higher than reported elsewhere.

CONCLUSION

Despite our small sample sizes of monitored nests, our study provides some of the only definitive information on causes of Marbled Murrelet nest failure in Washington and British Columbia. Our findings suggest that nest failure resulted from problems with chick vigor and health (potentially caused by lack of food or disease), parental attentiveness (possibly due to adult mortality, overly long commutes, or poor foraging conditions), egg viability and fertility, and nest platform size. For some of these problems—such as poor egg viability and fertility—we do not have sufficient information about the events that led to nest failure to make management recommendations. Overall, however, we suggest that providing large, contiguous tracks of high-quality, suitable nesting habitat close to sea would almost certainly benefit this species. In our study area, suitable nesting habitat for Marbled Murrelets is often located far inland compared to historic times. While murrelets are capable of successfully nesting as much as 58 km from sea in this region (Lorenz *et al.* 2017), long commutes are more energetically costly than short commutes and could reduce nest success in many ways. To mitigate problems with chicks falling from platforms, we encourage managers to retain trees with the largest platforms. The limb occupied by one fallen chick in our study was 18 cm diameter, with a tree diameter at breast height (DBH) of 128 cm, compared to a mean limb size of 31 cm and a tree DBH of 136 cm for other nests (Appendix 2). Providing large trees with limbs, and platforms larger than 18–21 cm, should be a focus of conservation efforts. Last, we call for additional research studies that monitor larger numbers of Marbled Murrelet nests. Studies are needed that use video-monitoring, necropsy, and similar unambiguous methods to determine causes of Marbled Murrelet nest failure within their threatened range. Currently, managers are forced to make land management decisions based on extremely small sample sizes, which may not be representative of murrelet nest success in this region.

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VETERINARY CARE AND WHOLE BLOOD COUNT OF A JUVENILE BLACK-BROWED ALBATROSS *THALASSARCHE MELANOPHRIS* BEACHED ON THE COAST OF BRAZIL

ADRIANA MASTRANGELLI¹, PAULA BALDASSIN³, HASSAN JERDY² & MAX R. WERNECK³

¹ *Serviços em Meio Ambiente, CTA, Rua Saturnino Rangel Mauro 283, Pontal de Camburi, Vitória, ES 29062-030, Brazil (dri.mastrangelli@hotmail.com)*

² *Universidade Estadual do Norte Fluminense Darcy Ribeiro – UENF, Campos dos Goytacazes, RJ 28013-602, Brazil*

³ *BW Veterinary Consulting, Rua Professora Sueli Brasil Flores 88, Praia Seca, Araruama, RJ 28970-000, Brazil*

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ABSTRACT

MASTRANGELLI, A., BALDASSIN, P., JERDY, H. & WERNECK, M.R. 2019. Veterinary care and whole blood count of a juvenile Black-browed Albatross *Thalassarche melanophris* beached on the coast of Brazil. *Marine Ornithology* 47: 167–168.

We conducted an erythrocyte and leukocyte analysis for a juvenile Black-browed Albatross *Thalassarche melanophris* that was found beached at Maricá, Rio de Janeiro state, Brazil. The absence of data on this species was problematic in our unsuccessful rehabilitation. We present our findings here to assist future rehabilitations of other individuals of this species.

Key words: Black-browed Albatross, Brazil, hematology, rehabilitation, *Thalassarche melanophris*

The Black-browed Albatross *Thalassarche melanophris* has a circumpolar distribution, ranging from subtropical to polar waters in both the northern and southern hemispheres (ACAP 2009). Brazilian offshore waters are significant to many albatrosses and petrels of the South Atlantic Ocean (Vooren & Brusque 1999), but no hematological data have been published on this particular species. This provides a challenge to veterinarians faced with the rehabilitation of beached individuals. Therefore, we describe the hematological analysis of a Black-browed Albatross that was found beached on the coast of Rio de Janeiro state, Brazil.

In July 2017, a juvenile Black-browed Albatross was found by the Santos Basin beach monitoring team at Itaipuaçu-Jaconé Beach (22°56'0.02"S, 42°30'28.48"W), Maricá, in the state of Rio de Janeiro, Brazil.

Clinical examination revealed its feathers to be soaked and impregnated with sand; cloacal temperature was 37 °C, respiratory rate was 18 breaths/min, and heart rate was 240 beats/min. The bird had a debilitated appearance, having viscous oral mucus, dull eyes, pale oral and cloacal mucosa, as well as watery blackish-green diarrhea. The bird was given water and electrolyte replacement (0.9 % NaCl solution), along with oral administration of 25 % glucose and an intramuscular injection of the quinolone antibiotic enrofloxacin (10 %, 20 mg/kg/d). Blood was collected at the start of treatment. Whole blood samples were placed in tubes containing an anticoagulant solution of sodium heparin. The erythrocyte, leukocyte, and differential cell counts were performed using the method described by Weiser (2012). No blood parasites were found in either of the two samples collected.

The clinical progression was noteworthy. Dehydration was reversed and force-feeding was initiated via oral administration of mashed fish, saline solution, and vitamin supplementation. The bird demonstrated progress and began to nibble on fish on the fourth day; diarrhea ceased on the fifth day. However, the bird's general condition then worsened: it became less active and its cloacal temperature dropped to that registered upon admission. A second blood collection was performed on the fifth day of care (Table 1). The bird died at the end of the fifth day.

Necropsy revealed congestion and caseous plaques distributed throughout the lungs. Parasites were found in the esophagus and stomach (*Contracaecum pelagicum* and *Seuratia shipleyi*), as well as in the small and large intestines (*Tetrabothrius* spp.). Tissue samples submitted for histological analysis revealed bacterial colonies immersed in cell debris and enveloped by multinucleated

TABLE 1
Results of hematological analyses for a juvenile Black-browed Albatross found beached in Brazil

| | 1st Sample | 2nd Sample |
|--|------------|------------|
| Erythrogram | | |
| Erythrocytes (10 ⁶ /mm ³) | 1.8 | 3.83 |
| Hemoglobin | 12.7 | 11.7 |
| PCV ^a (%) | 38 | 35 |
| MVC ^b (µm ³) | 211 | 91 |
| MCHC ^c (g/dL) | 33 | 33 |
| Leukogram | | |
| Leukocytes (10 ³ /mm ³) | 102.50 | 20.25 |
| Heterophils (/mm ³) | 3 895 | 12 352.5 |
| Lymphocytes (/mm ³) | 4 100 | 3 240 |
| Monocytes (/mm ³) | 512.5 | 227.5 |
| Basophils (/mm ³) | 1 845 | 2 430 |

^a PCV: Packed cell volume

^b MCH: Mean corpuscular hemoglobin

^c MCHC: Mean corpuscular hemoglobin concentration

giant cells in air sacs, revealing severe bacterial granulomatous air sacculitis. The cause of death appeared to be bacterial septic shock. The bird proved to be a juvenile female.

Only one report of veterinary care exists for albatrosses found along the coast of Brazil. Baldassin *et al.* (2007) reported biochemical blood findings of an Atlantic Yellow-nosed Albatross *Thalassarche chlororhynchos* found on the coast of São Paulo state, but no complete blood count was performed.

In the present study, we had the opportunity to observe a beached juvenile Black-browed Albatross under veterinary treatment for five days prior to dying. As there is no standard or even previous study reporting bloodwork for the species, we could only observe the differences between two samples taken during treatment. Between the first and second collections, the number of erythrocytes increased but they exhibited low hemoglobin, hematocrit, and mean corpuscular volume. Total leukocytes and the total number of lymphocytes and monocytes decreased, while heterophils and basophils increased. These data pointed to bacterial septic shock as a cause of death, as heterophils play an important role in combating systemic bacterial infection. Heterophils are generally the first defense cells released by the immune system and are the most abundant in this type of condition, accounting for approximately 80 % of inflammatory cells (Campbell 2015).

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MOVEMENTS AND ACTIVITY CHARACTERISTICS OF THE BROWN BOOBY *SULA LEUCOGASTER* DURING THE NON-BREEDING PERIOD

HIROYOSHI KOHNO^{1*}, AKIRA MIZUTANI¹, KEN YODA² & TAKASHI YAMAMOTO^{2,3}

¹Okinawa Regional Research Center, Tokai University, Taketomi, Okinawa 907-1541, Japan * (hiro-kohno@fan.hi-ho.ne.jp)

²Graduate School of Environmental Studies, Nagoya University, Nagoya, Aichi 464-8601, Japan

³Current Address: Research and Development Center for Data Assimilation, The Institute of Statistical Mathematics, Tachikawa, Tokyo 190-8562, Japan

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ABSTRACT

KOHNO, H., MIZUTANI, A., YODA, K. & YAMAMOTO, T. 2019. Movements and activity characteristics of the Brown Booby *Sula leucogaster* during the non-breeding period. *Marine Ornithology* 47: 169–174.

As the availability of individual-based tracking has increased, our understanding of seabird distributions outside the breeding season has advanced for a variety of species, but remains comparatively limited for species inhabiting the tropics. In this study, we investigated the at-sea movement and activity of eight Brown Boobies *Sula leucogaster* during the non-breeding period using light-level geolocators. Boobies spent the non-breeding season in the western Pacific across a large geographical range; however, at a regional scale, there was variation among individuals in their use of wintering habitats, with areas 6575 km apart between their northernmost (the East China Sea/Yellow Sea) and southernmost (northern New Guinea) destinations. Overall, during the non-breeding period, boobies spent $17.6\% \pm 5.0\%$ of their time on the water during the day and $11.1\% \pm 8.2\%$ of their time on the water at night. This low percentage of time spent on the water at night indicates that they may have rested on land or roosted on rocks, a behavior that might be an anti-predatory strategy. Although individuals exhibited spatiotemporal variations in their movements, all tracked birds were absent in the breeding region for periods of time coinciding with seasonal pulses of unfavorable local environmental conditions. This study is the first to explore individual-based at-sea movements and activity characteristics of *Sula* species during the non-breeding period. Our results provide insight into how breeding phenology relates to seasonal movements.

Key words: activity, Brown Booby, geolocation, non-breeding period, migration

INTRODUCTION

Bird migration is a well-known phenomenon that often involves long distance horizontal movements over hundreds to thousands of kilometers. Migration presumably occurs in response to changes in food availability and prevailing local weather (Dingle & Drake 2007, Newton 2012), which have critical consequences to survival and reproduction (Newton 2008). The recent development of tracking devices to monitor the movement of individuals, specifically those that use light-based geolocation methods (Wilson *et al.* 1992), has advanced our understanding of the at-sea movements and activity patterns of seabirds outside of the breeding season (Croxall *et al.* 2005, Shaffer *et al.* 2006, Yamamoto *et al.* 2010). To date, most studies have focused on species that inhabit polar and temperate regions; these species tend to exhibit distinct, seasonal, long-distance movements (reviewed by BirdLife International 2004, Shaffer *et al.* 2006, Newton 2008). In contrast, research into the behaviour of birds during the non-breeding season—among species that breed partially or completely in the tropics—has lagged despite these species representing half the number of all seabirds (Schreiber & Burger 2002). However, the number of studies on foraging behaviour during the breeding period for this group is increasing (Lewis *et al.* 2004, Mendez *et al.* 2017). Bird migration is thought to be driven by energy efficiency—the balance between the energetic costs associated with environmental conditions and distance travelled, and the benefits associated with access to seasonally available resources that are needed to fuel metabolism

(Newton 2008, 2012). In this way, migratory species can optimize energy acquisition (Somveille *et al.* 2018). Thus, elucidating the movement patterns of seabirds in the tropics, where seasonality is generally less pronounced (Longhurst & Pauly 1998), might provide insight into how migratory behaviour is shaped by environmental conditions.

The Brown Booby *Sula leucogaster* breeds in subtropical and tropical oceans between 25°S and 25°N (Nelson 1978). The breeding ecology and at-sea behaviour of this species during the breeding period have been examined at several breeding colonies (Nelson 1978, Lewis *et al.* 2005, Castillo-Guerrero *et al.* 2016), but information on their behaviour outside the breeding period remains limited. Nakanokamishima Island (southern Ryukyu Islands, Japan) is one of the study colonies for this species where many years of colony-based observations and application of animal-borne sensors have been conducted during the breeding period (Yoda & Kohno 2008, Yoda *et al.* 2011, Yamamoto *et al.* 2017, Kohno *et al.* 2018). Based on a small number of leg-ring recoveries (29 of 3029 rings recovered outside of Japan), Brown Boobies of Nakanokamishima were found mostly around the Philippines in winter (Yamashina Institute for Ornithology 2002). However, this result may be biased to areas where there are more people available to find the rings; it is also a better reflection of where the birds died than where they lived successfully.

In this study, we used light-level geolocators to record the at-sea movements and activity of individual Brown Boobies to understand

the behavioural characteristics of this tropical seabird species outside of the breeding season.

METHODS

Our study was carried out from 2009 to 2015 on Nakanokamishima Island (24°11'N, 123°34'E), a colony located close to the northern limit of the Brown Booby breeding range in the western Pacific Ocean (Nelson 1978). At night, from March to September, we captured 22 egg-incubating or chick-rearing boobies using a net, and attached geolocators (Mk-5, 3.6 g, British Antarctic Survey, UK or Mk-3006, 2.5 g, Biotrack Ltd., UK) to the tarsus of each bird using a plastic ring. The total weight of the unit was 8.5 g, which was < 1 % of the mean mass of the birds in our study (mean \pm SD: 1 435 \pm 201 g). After one to three years, we recovered geolocators from eight boobies. Some equipped birds were resighted, but we could not recapture them. The procedures used in this field study were approved by the

Ministry of the Environment, the Agency for Cultural Affairs, and the Nature Conservation Division, Okinawa, Japan.

Geolocators measured light levels at 60-s intervals and recorded the maximum value during each 10-min period. Immersion in seawater was checked every 3 s as 0 or 1 (out of or in water, respectively); information was compiled for each 10-min period (0–200), representing the proportion of time spent wet. Water temperature was recorded every 10 min only when there was continuous immersion for at least 20 min. We analyzed light-level geolocation data within a Bayesian framework using the Solar/Satellite Geolocation for Animal Tracking (SGAT) package (Wotherspoon *et al.* 2015) for program R (version 3.3.0; R Development Core Team 2016). Sunset and sunrise times were estimated using thresholds in the light curves. Day length and night length were used to estimate latitude, whereas the relative timing of local noon and midnight were used to estimate longitude, providing two position estimates per day (Wilson

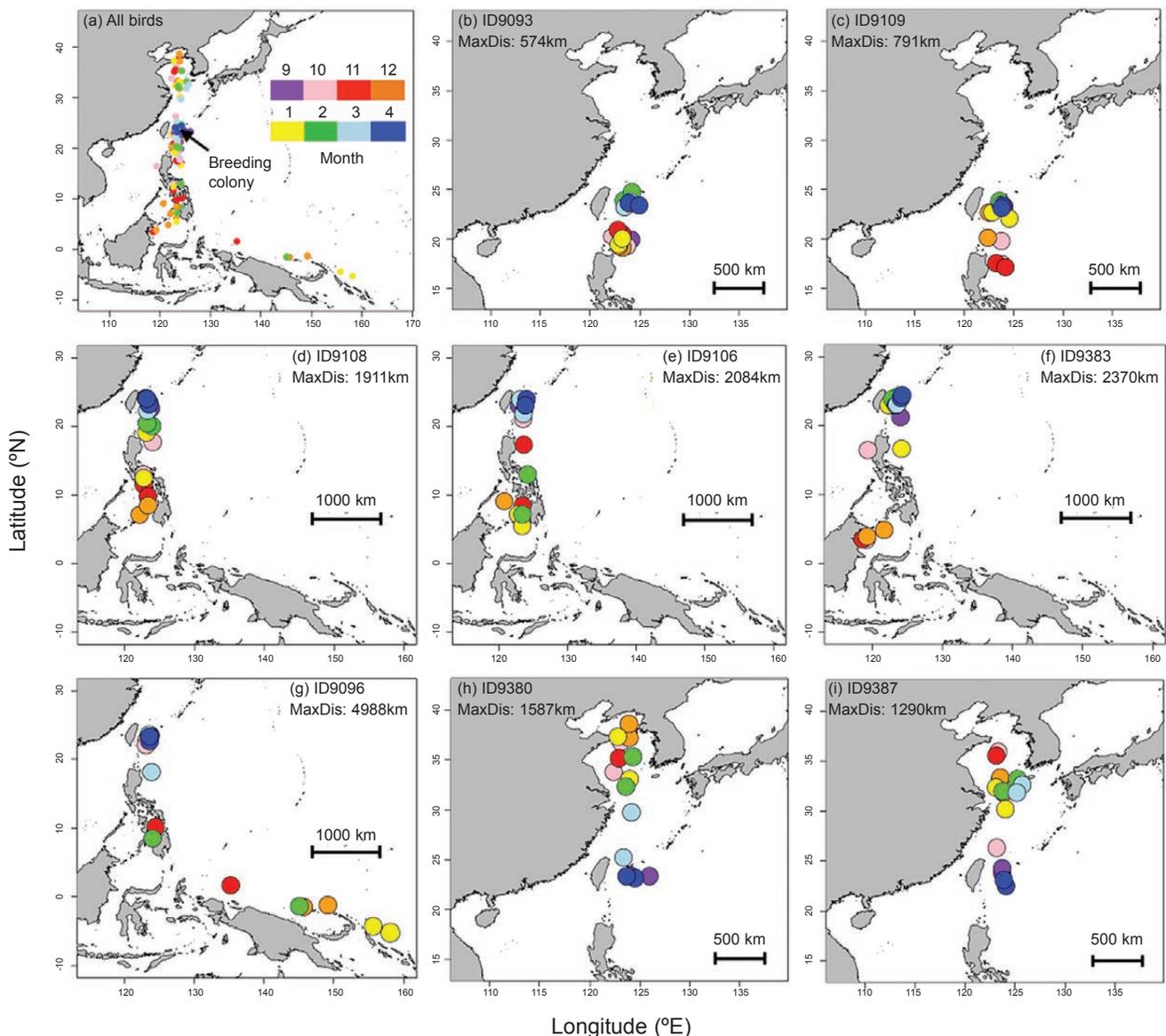


Fig. 1. At-sea movements of eight Brown Boobies breeding on Nakanokamishima Island, Japan, from September to April, including the non-breeding period. Position estimates are given for each half-month as spatial medians of daily data. Months are indicated by different colours: (a) all positions are pooled, and (b–i) different individuals are shown.

et al. 1992). SGAT uses Markov Chain Monte Carlo (MCMC) simulations to estimate locations and to quantify the error inherent in light-level geolocation based on behavioural models and spatial probability, accounting for bird flight speed, land mask (i.e., locations at sea are more likely than locations on land), and sea surface temperature mask (i.e., high probability in the range of the recorded water temperature). Despite these simulations, there was still some uncertainty in our location estimations. Therefore, we visualized overall movement patterns using half-monthly spatial medians of the latitude and longitude from September to April. This timing was chosen because fledgling independence typically occurs in early September, with egg laying occurring until mid-April (Kohno *et al.* 2018). Some boobies remained in areas around the breeding colony upon termination of breeding. Therefore, we were not able to use distance from the colony as an indicator of the beginning of the non-breeding period, despite its previous use as an indicator for other seabird species (Yamamoto *et al.* 2010).

Colony-based observations indicate that almost all boobies disappear from the colony by early November, and that peak egg-laying starts in February (Kohno *et al.* 2018). Hence, we calculated the daily proportion of time spent on the water, and the number of continuous periods of full-wet and full-dry events (i.e., periods spent on or out of the water, respectively, for 10 continuous minutes) (Yamamoto *et al.* 2010, Dias *et al.* 2012), from December to January, which represent the middle of the non-breeding period. Activities were calculated separately for light and dark periods each day; local sunset and sunrise times were assessed using light levels recorded by the geolocators.

RESULTS

The at-sea movements of Brown Boobies outside the breeding season occurred in a north-south direction (Fig. 1a). Their wintering areas were north of the Republic of the Philippines (Fig. 1b,c), in the Sulu/Celebes Sea (Fig. 1d,e,f), off northern New Guinea (Fig. 1g), and in the East China Sea/Yellow Sea (Fig. 1h,i). Most study birds stayed near the colony in September and started to move during October and the first half of November. They were most distant from the breeding site from November to January. The shortest direct maximum distance from the colony varied among individuals, ranging from 574–4988 km. Wintering habitats were located up to 6575 km apart between the northernmost and southernmost destinations. Boobies started to return to the breeding region in January, but the timing varied among individuals: ID9109, ID9108, and ID9383 in January; ID9093 in February; ID9106, ID9096, and ID9380 in March; and ID9387 in April (Fig. 1).

Within the non-breeding period, boobies spent $17.6\% \pm 5.0\%$ of their time on the water during the day and $11.1\% \pm 8.2\%$ of their time on the water at night (Fig. 2). Boobies rarely spent long periods of time sitting on water; continuous wet periods > 30 min for each individual represented just $1.1\% \pm 0.5\%$ (0.2% to 2.0%) of all events during the day and $4.4\% \pm 2.8\%$ (0% to 8.6%) of all events at night. Moreover, the longest period immersed was 2.6 ± 1.4 h (1 – 5.7 h) during the day and 4.0 ± 2.5 h (0.5 – 9 h) at night. In comparison, continuous dry periods (i.e., time spent out of water) typically lasted < 60 min during the day and > 3 h at night (Fig. 3).

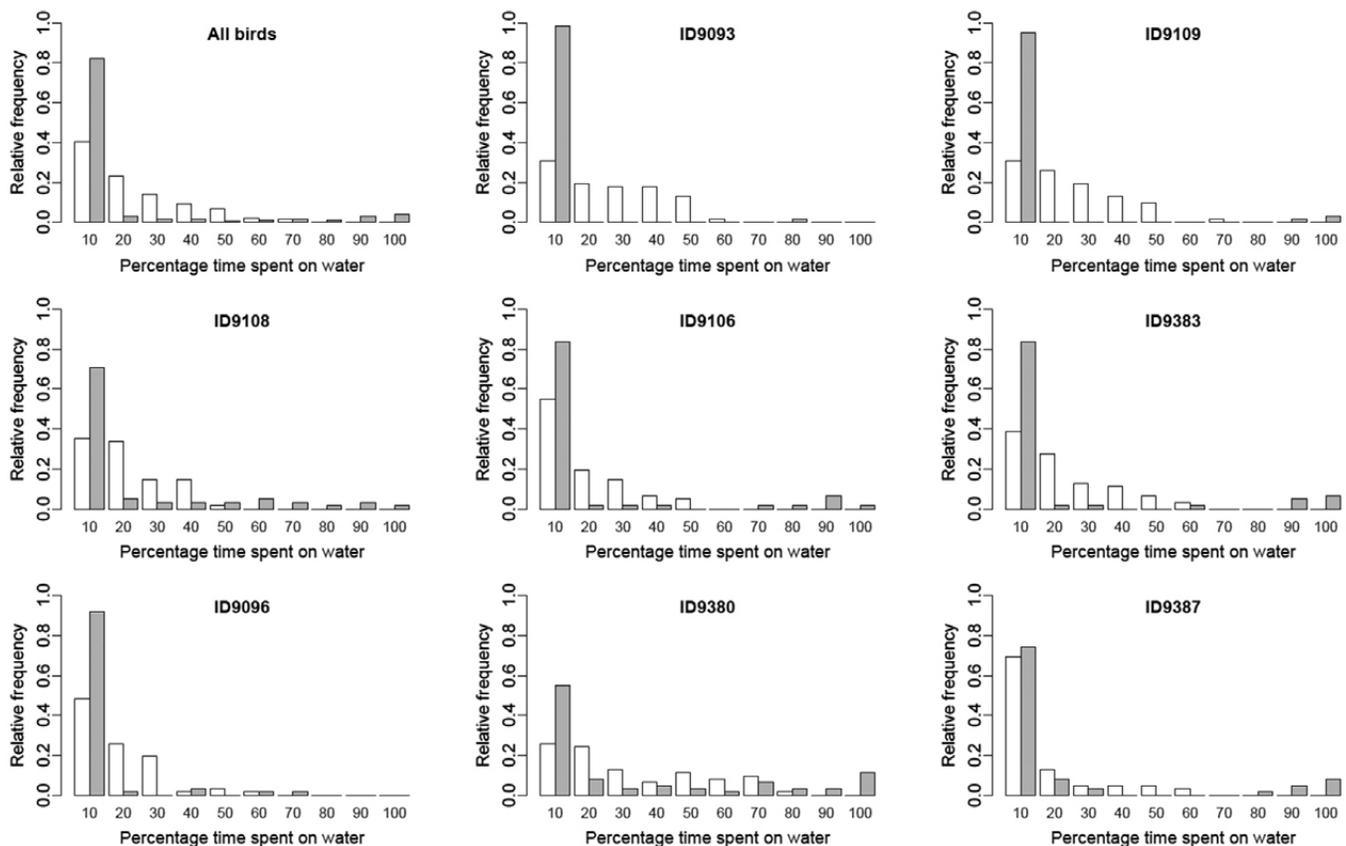


Fig. 2. Activity patterns of Brown Boobies during the wintering period from December to January. Graphs show the relative frequency of the proportion of time spent on the water during the day (white) and at night (grey), for all individuals (pooled) or each individual separately.

DISCUSSION

To our knowledge, this study is the first to explore the individual-based at-sea movements and activity characteristics of *Sula* species during the non-breeding period, although the sample size was limited to just eight birds. Brown Boobies from Nakanokamishima Island spent their non-breeding season across a large geographical range, with individuals exhibiting a large variation in wintering habitats at a regional scale. Species in temperate and polar regions primarily travel towards lower latitudes or similar latitudes in the opposite hemisphere, where the seasons are reversed (Phillips *et al.* 2005, Shaffer *et al.* 2006, Newton 2008). In contrast, a limited number of studies have shown that tropical pelagic seabirds exhibit longitudinal movements to remain in constant environmental conditions (Cтры *et al.* 2009, Pinet *et al.* 2011, Ramos *et al.* 2015, Zajková *et al.* 2017). In this study, Brown Boobies, a tropical seabird, exhibited broad north-south movements. This might be related to their reliance on land throughout the non-breeding period (see discussion below), with the continental coast running north-south. This may constrain their movements to coastal waters or to areas within archipelago regions. Interestingly, some individuals even moved north. We have no information on the factors that influence the choice of wintering habitats among individual boobies, but their movement patterns do indicate multi-directional movement. Multi-directional movements are typical of tropical seabirds owing to lower seasonality in surrounding environments (Spear & Ainley 2005, Ramos *et al.* 2015). On the other hand, our observations could reflect movement patterns typical of the Sulidae family (e.g., Northern Gannets *Morus bassanus*; Kubetzki *et al.* 2009).

Brown Boobies spent $17.6\% \pm 5.0\%$ of their time on the water during the day during the non-breeding period. Previous studies reported that Brown Boobies spent 3% to 30% of their time, on average, sitting on the water during a foraging trip (Lewis *et al.* 2004, Weimerskirch *et al.* 2009). The dominance of short, continuous wet and dry periods during the day indicates the frequent use of plunge dives during foraging, given that boobies conduct several dives per hour during the breeding period (Lewis *et al.* 2004, Weimerskirch *et al.* 2009). Thus, foraging activities during the non-breeding period are similar to those during the breeding period. Compared to temporal and polar seabird species, including Procellariiformes and Sulidae that generally spend > 80% of time on water at night during the non-breeding period (Cтры *et al.* 2009, Yamamoto *et al.* 2010, Garthe *et al.* 2012), the percentage of time spent on water at night was notably low in Brown Boobies, even when they were not associated with a specific island (i.e., breeding colony). Immersion records allowed us to determine if the birds were in or out of water, but they did not allow us to determine if the birds were in flight or resting on land (because both activities were recorded as dry). The Brown Booby is a diurnal feeder that usually spends the night on land during the breeding period (Lewis *et al.* 2004, Yoda & Kohno 2008, Miller *et al.* 2018). Furthermore, although some *Sula* species overnights at sea, they spend this time floating on the water surface rather than foraging and/or travelling (Mendez *et al.* 2017); this is likely because nocturnal foraging is constrained by the lack of ambient light. Thus, the increased continuous period of dry events at night recorded for Brown Boobies during the non-breeding period likely indicates that they were resting on land or roosting on rocks (Nelson 1978). In support of this hypothesis, the Brown Boobies in our study wintered in archipelago regions or close to the coast (Fig. 1). This behaviour might be related to anti-predatory behaviour (Weimerskirch *et al.* 2005, Mendez *et al.* 2017). Sharks are dominant predators in tropical

oceans (Johnson *et al.* 2006, Cairns *et al.* 2008), and they attack from underwater when seabirds are sitting on the water surface (Zavalaga *et al.* 2012). In fact, at the Nakanokamishima colony, Brown Boobies with foot injuries or missing feet have been observed during the breeding period (HK unpubl. data).

Colony-based observations have reported large variations in the breeding phenology of tropical sulids, as some populations breed annually while others breed irregularly or in all months (Nelson 1987, Schreiber & Norton 2002). In our study colony, the breeding period occurs broadly from February to November (Kohno *et al.* 2018). Although one bird used areas just 574 km from the breeding colony during the non-breeding period, this distance exceeded that of typical foraging excursions during the breeding period, which were a mean distance of 40 km from the colony and always within 100 km of the colony (HK unpubl. data; consistent with findings from other populations, in which distances from the colony were < 80 km: Weimerskirch *et al.* 2009, Miller *et al.* 2018). In the southern Ryukyu Islands, where Nakanokamishima is located, stormy seas prevail during November to February due to the East Asian Monsoon (Zhang *et al.* 1997, Kohno 2000, Ikema *et al.* 2013). These seasonal local environmental conditions, which may reduce prey detectability (Finney *et al.* 1999, Baptist & Leopold 2010, Dehnhard *et al.* 2013) and flight performance due to strong winds (Hertel & Ballance 1999, Zavalaga *et al.* 2012, Yamamoto *et al.* 2017), might force boobies to leave the breeding region. Therefore, the seasonal movements in this study might indicate, in part, that breeding phenology is shaped by changes in the local environment of the breeding region. Nonetheless, the timing of return to the breeding colony appeared to vary among individuals, which coincides with the observed variation in the breeding phenology of this population (e.g., among individuals, egg laying takes place over a two-month range; Kohno *et al.* 2018). The consequences of individual differences in wintering habitat may vary with differing energy or time costs, the time available for feeding, and the timing of the return to the colony (Phillips *et al.* 2017). Further investigations are needed to elucidate the advantages and disadvantages to survival or reproduction of each migratory characteristic, and to predict the effect of these differences on population dynamics.

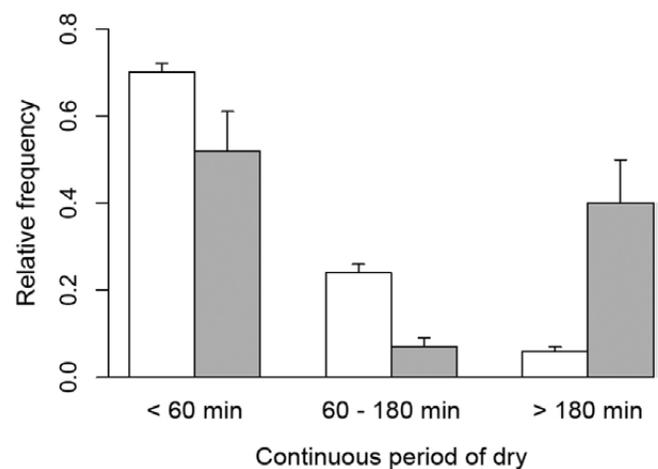


Fig. 3. Activity patterns of Brown Boobies during the wintering period from December to January. The graph shows the relative frequency of the proportion of the continuous period (mean \pm standard deviation) of dry during day (white) and night (grey). Data from all individuals are pooled.

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BILL MALFORMATION IN SCOPOLI'S SHEARWATER *CALONECTRIS DIOMEDEA* CHICKS

VITTORIA ROATTI¹, BRUNO MASSA² & GIACOMO DELL'OMO³

¹*Ornis italica, Piazza Crati 15, 00199 Rome, IT (vittoria.roatti@gmail.com)*

²*University of Palermo, Viale delle Scienze, 13, 90128 Palermo, IT*

³*Berta maris, 92031 Linosa, Agrigento, IT*

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ABSTRACT

ROATTI, V., MASSA, B. & DELL'OMO, G. 2019. Bill malformation in Scopoli's Shearwater *Calonectris diomedea* chicks. *Marine Ornithology* 47: 175–178.

We report three cases of bill malformation in Scopoli's Shearwater *Calonectris diomedea* on Linosa Island (Sicily, Italy) that were found during monitoring of the colony over a 13-year period. The cases were observed in pre-fledging chicks; two of the birds were also in poorer body condition compared with chicks of the same age. No adults in the colony have been found with similar bill malformations despite a much larger sample of recorded adults. We suggest that the observed malformations impair survival and that the chicks we encountered would likely starve after fledging. The frequency of bill malformation found on Linosa is less than one percent, which is consistent with cases reported in the literature for other species.

Key words: bill malformation, Scopoli's Shearwater, *Calonectris diomedea*, Procellariiformes, chicks, seabirds

INTRODUCTION

Bill deformities in wild birds are rare, with an estimated frequency of less than one percent (Pomeroy 1962, Nogales *et al.* 1990, Rockwell *et al.* 2003). However, higher frequencies have been observed (Kylin 2005, Handel *et al.* 2010, Buckle *et al.* 2014, Handel & Van Hemert 2015), and these can be either temporary or permanent (Pomeroy 1962). The bill of a bird consists of bones and a covering of cornified integument called the rhamphotheca, which is a modified layer of keratinized cells. The bill's proper functioning is essential for adequate foraging (Stettenheim 2000).

Isolated cases of bill deformities have been described among seabirds and most cases involve chicks. Chicks with deformed bills were reported in nine penguin species (Jones *et al.* 2015), Double-crested Cormorant *Phalacrocorax auritus* (Kuiken *et al.* 1999), Antarctic Shag *Leucocarbo bransfieldensis* (Casaux 2004), Black-legged Kittiwake *Rissa tridactyla* (Kylin 2005), and Common Tern *Sterna hirundo* (Gochfeld 1975). The only case of an adult bird involved a healthy King Penguin *Aptenodytes patagonicus*, which was able to survive with a highly anomalous bill, likely by adapting its diet (Corbeau *et al.* 2017).

In Procellariiformes, body deformities have been reported exclusively in chicks. For example, deformities in the feet and the eyes were described in chicks of Leach's Storm Petrel *Oceanodroma leucorhoa*, European Storm Petrel *Hydrobates pelagicus* (Nogales *et al.* 1990), and Southern Giant Petrel *Macronectes giganteus* (Martí *et al.* 2008). In Cory's Shearwater *Calonectris borealis*, bill deformities were described in three chicks ringed in 1988 on Selvagem Grande (Nogales *et al.* 1990). Two types of bill deformities were reported: Type 1 was described as a mandibular deviation of a certain angle (between 6° and 7.5°) from the central head axis to the right; Type 2 was described as both a mandibular deviation from the central head

axis and the lack of the final hooked part of the maxillae. These three cases were found among a total of 801 chicks (0.37 %).

Scopoli's Shearwater is a long-lived procellariiform that breeds in the Mediterranean Sea. The species shows high mate and nest fidelity and lays only one egg per year (Thibault 1993).

STUDY AREA AND METHODS

Linosa Island (35°30'11"N, 12°36'11"E) hosts the largest European colony of Scopoli's Shearwater, with 10000 breeding pairs estimated in 1986 (Massa & Lo Valvo 1986). The study area was in the largest part of the colony, on the northwestern side of the island in a coastal area called Mannarazza. The monitored nests were spread over a 1 km² area of volcanic rocks. Scopoli's Shearwater chicks were ringed in their nests during the daytime, and ringing occurred every year from 2011 to 2017 during the first and second weeks of October, just before fledging. Chicks were weighed with a 1000-g balance (Pesola®, precision ± 5 g) and bill measurements were recorded to the nearest 1 mm using a caliper.

RESULTS

Three chicks with bill deformities were found, one in each of three different years: 2011, 2015, and 2017. The first and second chicks were found in the same nest and had the same mother but different fathers. The mother was ringed in 2010, and her breeding success was monitored every year until 2018. Her eggs were predated in 2014 and 2016; apart from the two deformed chicks, she produced five healthy chicks during this period. The third chick was found in a nest 60 m away from the first nest. The parents of this chick were ringed in 2017, so their previous breeding history was unknown; in 2018, they produced a chick with a normal bill. All parents had normally developed bills and no other visible deformities.

The bill deformities observed in the chicks were similar to those described by Nogales *et al.* (1990). Following these authors' classification, the first and the third chick showed a Type 2 malformation: the bill could not close normally due to a mandibular deviation from the central head axis, and the hook at the top of the maxillae was either about to detach (first chick, Fig. 1) or missing completely (third chick, Fig. 3). The second chick showed a Type 1 malformation: the bill could not close normally due to a mandibular deviation from the central head axis to the right, and the hook at the top of the maxillae was present except for the tip. Its maxillae (46 mm, measured from attachment to tip along the central axis of the upper bill) were also shorter than the mandibles (53 mm, measured from attachment to tip along the central axis of the lower bill) (Fig. 2).

The first chick was observed at the beginning of August. Its weight (360 g) was in the lower range of a normal weight for chicks during August 2011 (Table 1). In October, this chick was observed to have a little bit of down left, but it seemed to be in poorer condition than other chicks of the same age. The second and the third chicks were found in the first half of October, when chicks normally have the appearance of an adult except for a little down, if any, left on the head and/or belly. While the second chick was normally developed and its weight (735 g) fell in the range of other chicks, the third chick appeared delayed in its growth (weight = 390 g) compared to the other chicks of a similar age (Table 1). The third chick was still covered with grey down and had not grown any contour or flight feathers.

The three chicks did not have other visible deformities and did not show any anomalies in other keratinized parts of the integument (feathers and claws), nor did they exhibit any sort of skin disease. From molecular sexing, we know that the second chick (from 2015) was a male and that its parents produced a healthy female in 2017. We have no information on the sex of the other deformed chicks or of the normal chicks hatched by their parents.

No adults and other chicks with deformities were observed during the study from 2006 to 2018. In total, 3218 adult birds and 2323 chicks were ringed. The frequency of bill malformation in all ringed birds (5541) was 0.05 %, but if we consider only the chicks (2323), it was 0.13 %.



Fig. 1. Scopoli's Shearwater chick with a Type 2 bill malformation (as per Nogales *et al.* 1990), side view (left) and top view (right). Chick #1 was found in August 2011.



Fig. 2. Scopoli's Shearwater chick with Type 1 bill malformation (as per Nogales *et al.* 1990), side view (left) and top view (right). Chick #2 was found in October 2015.



Fig. 3. Scopoli's Shearwater chick with Type 2 bill malformation (as per Nogales *et al.* 1990), side view (left) and top view (right). Chick #3 was found in October 2017.

TABLE 1
Comparison between the weight (mean and range) of normal chicks with that of chicks having a deformed bill found during the same year and month

| Time period | | Normal chicks | | | Deformed chicks | | |
|-------------|---------|---------------|-----------|----------|---------------------------|------------|-------------------------|
| | | Weight (g) | | <i>n</i> | Malformation ^a | Weight (g) | Percentile ^b |
| Year | Month | Mean | Range | | | | |
| 2011 | August | 410 | 190–630 | 125 | Type 2 | 360 | 38th |
| 2015 | October | 748 | 550–1 000 | 88 | Type 1 | 735 | 47th |
| 2017 | October | 726 | 450–905 | 294 | Type 2 | 390 | 0th |

^a Malformation type is indicated according to Nogales *et al.* (1990).

^b Percentile indicates the position of the deformed chicks' weights relative to the distribution of the weights of normal chicks.

DISCUSSION

The frequency of bill malformation found on Linosa Island is consistent with other reports in the literature (Pomeroy 1962, Nogales *et al.* 1990, Rockwell *et al.* 2003). Given that the mandibles and the maxillae were crossed and that the maxillae were either missing the tip of the hook or weren't completely developed, these birds were probably unable to hunt successfully at sea, although they could survive when fed by parents (Nogales *et al.* 1990). Reports on the King Penguin (Corbeau *et al.* 2017) and the Black-capped Chickadee *Poecile atricapillus* (Handel *et al.* 2010) indicate that birds may survive until adulthood in some cases by altering their feeding habits, relying more on other types of food (Van Hemert *et al.* 2012, Corbeau *et al.* 2017). However, this seems to not be the case for Procellariiformes, since all reports of bill deformities in this group involve only chicks; on Linosa Island, we did not detect any bill deformity in an adult, despite the large number of birds ringed. For the first and third chicks, their delayed development and low body weight suggest that the malformation may have affected even their ability to receive food from their parents. Type 2 malformations appear to affect food intake more dramatically, which consequently affects growth. Another explanation could be the opposite: poor food supplied by the parents could influence bill development. Moreover, the first chick was found with the tip of the maxillae freshly broken and still partially attached, while in the third chick, the tip was already missing. Thus, we suggest that the absence of the last segment of the maxillae is not a congenital condition, but rather the result of a weakness in bill structure. As suggested by Nogales *et al.* (1990), since the juveniles hadn't already left the nest and were still fed with oil by the parents, the malformation is likely not the result of an accident, but rather is of infective, environmental, or genetic origin.

In terrestrial birds, bill deformities have sometimes been observed at very high rates in a limited number of sites. For example, bill anomalies caused by keratin deficiency have been reported in 30 bird species in Alaska (Handel *et al.* 2010). These deformities were attributed to an avian keratin disorder of unknown cause. Recent studies (Zylberberg *et al.* 2016, Zylberberg *et al.* 2018) indicate that a newly discovered picornavirus may be the causative agent for avian keratin disorder. Many other causes have been suggested to explain the presence of bill deformities: developmental problems like improper bone growth or malocclusion (Stettenheim 2000); trauma (Pomeroy 1962); nutritional deficiencies (Tangredi 2007); infections of bacterial (Gartrell *et al.* 2003), viral (Mans & Guzman 2007), fungal (Keymer 2008), or parasitic (Galligan & Kleindorfer 2009) origin. No samples were taken to determine if our chicks were subjected to an infection. However, we believe that it is unlikely that the deformities we observed can be ascribed to a keratin disorder, since no anomalies were observed in other keratinized tissues, as was reported for the deformed Alaskan birds (Handel *et al.* 2010).

Developmental anomalies can be caused by environmental conditions, such as nutritional deficiencies, exposure to contaminants, or disease pathogens. For example, bill deformities related to problems with vitamin and calcium metabolism have been reported in domestic chickens and turkeys (Romanoff 1972, Stevens *et al.* 1984, Tangredi 2007) and in cormorants raised under artificial light (Kuiken *et al.* 1999). Environmental contaminants, particularly organic pollutants and heavy metals, have been

related to outbreaks of craniofacial deformities (Kylin 2005, Buckle *et al.* 2014, Handel & Van Hemert 2015); however, we don't have information to either support or exclude this possibility here. Another possibility may be psittacine beak and feather disease, a viral disease that causes developmental anomalies in bills and feathers, but it is known to affect only parrots (Greenacre 2017). Support for the genetic origin might include the facts that two of our three chicks had the same mother and that the third chick was in a nest only 60 m away. In accordance with the high philopatry in this species (Thibault 1993, Rabouam *et al.* 1998), these findings could indicate that the individuals were somehow genetically related.

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EFFECTS OF EGG HARVEST ON EGG LAYING OF GLAUCOUS-WINGED GULLS *LARUS GLAUCESCENS*

ANNE L. SCHAEFER*, MARY ANNE BISHOP & KIRSTI JURICA

Prince William Sound Science Center, 300 Breakwater Ave, PO Box 705, Cordova, Alaska 99574, USA *(aschaefer@pwssc.org)

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ABSTRACT

SCHAEFER, A.L., BISHOP, M.A. & JURICA, K. 2019. Effects of egg harvest on egg laying of Glaucous-winged Gulls *Larus glaucescens*. *Marine Ornithology* 47: 179–183.

Subsistence harvest of wild bird eggs is a traditional activity across many parts of Alaska. We examined the impact of egg collection on Glaucous-winged Gulls *Larus glaucescens* nesting on Alaska's Copper River Delta by comparing egg laying patterns across two experimental plots. In one plot, we manually removed eggs from incomplete clutches and in the other we walked through the plot to create disturbance. Gulls in this study did not appear to increase the number of eggs laid to compensate for eggs experimentally removed from their nests, with only 10 % of gull pairs completing a full clutch following nest manipulation.

Key words: Glaucous-winged Gulls, *Larus glaucescens*, egg harvest, subsistence, egg laying

INTRODUCTION

In North America, Glaucous-winged Gulls *Larus glaucescens* breed in dense colonies along the Pacific and Bering Sea coasts, from northwestern Oregon to western Alaska (Hayward & Verbeek 2008, BirdLife International 2019). Like other ground-nesting gulls, Glaucous-winged Gulls are indeterminate egg layers (Parsons 1976), meaning that when eggs are depredated or taken from the nest during the period when clutches are being completed, the female continues to lay replacement eggs until the clutch is complete (three eggs on average; Hayward & Verbeek 2008). If the clutch is lost during incubation (typically 27 d; Hayward & Verbeek 2008), the female must wait 12–13 d for follicle development before laying a replacement clutch (Vermeer 1963, Verbeek 1986).

In Alaska, there is a long tradition of harvesting Glaucous-winged Gull eggs for subsistence purposes, although the collection of migratory bird eggs without permit became illegal after the passage of the Migratory Bird Treaty Act in 1918. Legal mechanisms allowing for subsistence egg take began on a regional basis in 2003 (USFWS 2002). Beginning in 2014 on the Copper River Delta in southcentral Alaska, gull eggs could be legally harvested for subsistence purposes from 01–31 May by all residents of the nearby town of Cordova and two small villages of Prince William Sound (Fig. 1; USFWS 2014).

Previous studies have documented reduced hatch success and colony failures within gull colonies after human disturbance and egg collection activities (Hunt 1972, Robert & Ralph 1975, Vermeer *et al.* 1991). In contrast, other studies indicate that infrequent harvests early in the breeding season can limit the impact on the hatch success of gulls (Zador 2001, Zador *et al.* 2006, Zador & Piatt 2007). To resolve this inconsistency, we examined the effects of experimental egg removal on the egg laying patterns of Glaucous-winged Gulls nesting in a colony that was recently made accessible for legal subsistence harvest in southcentral Alaska (Fig. 1).

STUDY AREA AND METHODS

This experiment took place 14 May–12 June 2018 in a large Glaucous-winged Gull colony (10000 individuals; North Pacific Seabird Data Portal 2018) on Egg Island (60.39°N, 145.98°W), a barrier island on the western edge of the Copper River Delta in southcentral Alaska (Fig. 1). Egg Island is uninhabited by humans and hosts the second highest population of Glaucous-winged Gulls in the Gulf of Alaska after nearby Middleton Island (North Pacific Seabird Data Portal 2018). We conducted our study in a subcolony on the southwestern tip of the island, an area that is visited infrequently by locals, reducing the confounding effects of disturbance unrelated to our study.

We established two treatment plots of approximately the same size in non-contiguous areas of the gull subcolony. In Plot A, we

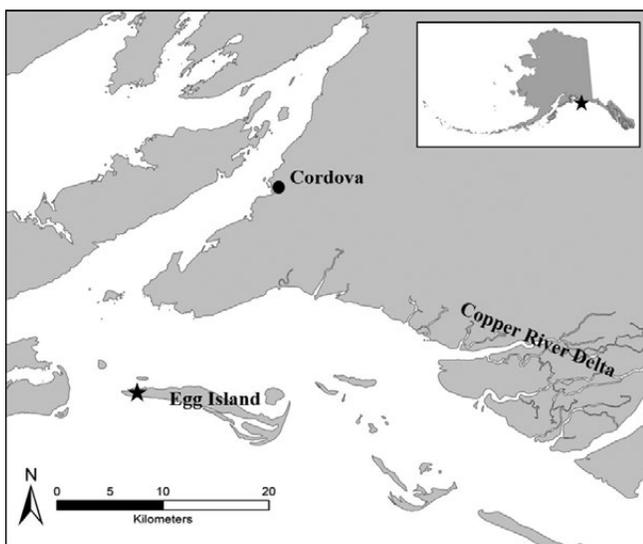


Fig. 1. Our experiment was conducted on Egg Island, a barrier island near the town of Cordova on the Copper River Delta in southcentral Alaska, USA. The location of study plots on Egg Island are indicated by the star.

removed one egg from each of 20 randomly selected nests having incomplete clutches (< 3 eggs) during the laying period to mimic traditional harvest practices. Eggs were removed from 10 one-egg nests and 10 two-egg nests. We then floated the eggs to estimate incubation stage following Schreiber (1970). Each nest was marked using GPS, and a small, flagged stake was placed 2–3 m away. We labeled eggs not selected for removal with a felt-tipped marker. In Plot B, our control, we monitored 12 randomly selected one-egg nests and eight two-egg nests. At the time of plot delineation there were only eight nests containing two eggs, hence the unbalanced sample size. Nests were marked and eggs labeled, but no eggs were removed. In both plots, we monitored nests twice during egg-laying (14 May, 15 May) and four times during incubation (23 May, 24 May, 03 June, 12 June). We noted any potential nest predators observed in the area and documented instances of nest predation following Anthony *et al.* (2004).

This research was conducted under the Prince William Sound Science Center IACUC protocol number PWSSC2018–01, USFWS permit number MB75979C–0, and ADFG permit number 18–154.

We used R version 2.12.1 (R Development Core Team 2010) to perform Mann-Whitney-Wilcoxon tests (Mann & Whitney 1947) to determine if differences in the mean total number of eggs laid per nest and mean final clutch size were statistically significant ($P \leq 0.05$) between study plots. Averages are reported with standard error unless otherwise specified.

RESULTS

Nest manipulation

Based on egg flotation patterns and the number of eggs in the nest, eggs were removed from the one- and two-egg nests within an estimated two and four days of laying, respectively. Within 24 h of egg removal, 35 % ($n = 7$) of the nests were abandoned and remained empty for the duration of the study. All abandoned nests were one-egg nests that became empty nests upon manipulation. Pairs continued to lay, on average, 0.80 ± 0.21 eggs after egg removal. Gull pairs in Plot A laid, on average, 2.30 ± 0.24 eggs in total and achieved a mean final clutch size of 1.30 ± 0.24 eggs (Table 1, Fig. 2). In all, only two of 20 monitored nests (10 %) in Plot A achieved a complete clutch of three eggs by laying a fourth egg. Both were one-egg nests at the time of egg removal.

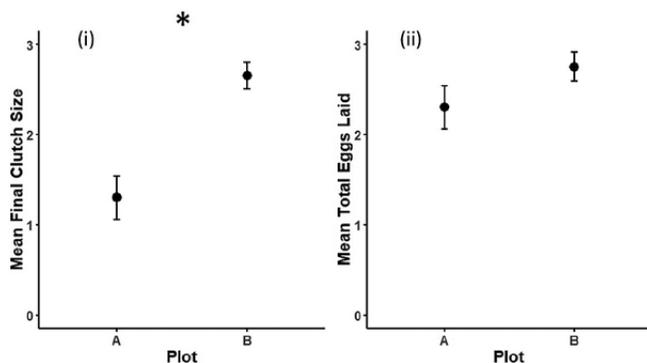


Fig. 2. Results from experimental nest manipulation comparing Plot A (manipulated) and Plot B (non-manipulated): i) final clutch size, and ii) mean total eggs laid. Statistical significance ($P \leq 0.05$), determined by Mann-Whitney-Wilcoxon tests, is indicated by an asterisk.

In Plot B, most pairs (85 %) continued to lay eggs after our initial visit, with 15 nests (75 %) achieving a complete clutch. Two nests were abandoned within the 24-h period following our initial visit and remained empty for the duration of the study. Pairs laid, on average, 2.75 ± 0.16 eggs in total and achieved a mean final clutch size of 2.65 ± 0.15 eggs (Table 1, Fig. 2). We found no significant differences in the total number of eggs laid per nest across plots ($P = 0.18$). However, the final clutch size in Plot B was significantly larger than the final clutch size in Plot A ($P = 0.000053$; Fig. 2).

Natural predation

Over the course of the study, no eggs from monitored nests in Plot A were lost to predation or other natural causes. In Plot B, we documented five instances of egg loss from monitored nests. In the 24-h period between nest visits on 14 May and 15 May, four nests lost an egg (three one-egg nests and one two-egg nest). No shells or egg remnants were observed in or around nests. The gull pair from the depredated two-egg nest laid one more egg and achieved a final clutch size of two eggs. Two of the one-egg nests were abandoned after predation and remained empty for the remainder of the study. The other depredated one-egg nest subsequently achieved a full clutch of three eggs by 23 May but had lost another egg by the time we visited the nest again on 03 June. No shell fragments were found in the nest, but a bloody half-shell was found ~ 4 m away.

DISCUSSION

Nest manipulation

Given that *Larus* gulls are reported to lay eggs indeterminately (Parsons 1976), we expected gull pairs in the manipulated plot to lay more eggs to compensate for the loss of an egg during the laying phase. Instead, we found no difference in the total number of eggs laid per nest across study plots. Glaucous-winged Gull pairs in the manipulated plot had significantly smaller final clutch sizes

TABLE 1
Comparison of the Glaucous-winged Gull nest manipulation experiment results across the manipulated (Plot A) and non-manipulated (Plot B) study plots on Egg Island, Alaska, May–June 2018

| | Plot A (1-egg nests/ 2-egg nests) | Plot B (1-egg nests/ 2-egg nests) |
|---|---|---|
| Number eggs removed | 10/10 | 0/0 |
| Number nests immediately abandoned | 7/0 | 2/0 |
| Number depredated eggs | 0/0 | 4/1 |
| Number depredated nests | 0/0 | 3/1 |
| Proportion of nests achieving complete clutch | 0.20/0.00 | 0.67/0.88 |
| Total number eggs laid | 46 ^a | 55 |
| Mean number eggs per nest | 2.30 (± 0.24) | 2.75 (± 0.16) |
| Mean final clutch size | 1.30 (± 0.24) | 2.65 (± 0.15) |

^a Includes experimentally removed eggs

compared with the non-manipulated plot, with mean clutch size in the non-manipulated plot more than double that of the manipulated plot. In fact, only two nests in the manipulated plot achieved a complete clutch of three eggs, compared with 15 nests in the non-manipulated plot.

After egg removal, seven manipulated one-egg nests were immediately abandoned. Unfortunately, we were unable to track whether gulls that had abandoned their nests after manipulation continued laying in another nest within their territory, as has been documented at other sites (Washington: Reid 1988; Alaska: Zador 2001). However, no pairs having a two-egg nest in the manipulated plot completed a full clutch after egg removal by laying a fourth egg, indicating that the gulls in this study did not compensate for eggs that were experimentally removed from their nests.

In contrast, at a colony in southeastern Alaska, Glaucous-winged Gulls completed a clutch of three by laying a fourth egg in 78 % of nests after their first egg was experimentally removed immediately after laying (Zador 2001). Furthermore, pairs with their first egg removed laid 1.24 and 1.06 more eggs (in the first and second year of the study, respectively) than gulls in the non-manipulated group. Similarly, Parsons (1976) reported that Herring Gulls *L. argentatus* with first eggs removed laid a fourth egg in 59 % of nests.

Forage availability is a limiting factor of seabird reproductive success (Cairns 1988, Suryan *et al.* 2002), including that of west coast Western Gulls *L. occidentalis* (Ainley & Boekelheide 1990) and Glaucous-winged gulls (Murphy *et al.* 1984, Blight 2011). Egg production is energetically costly for gulls (Houston *et al.* 1983), which are capital breeders, meaning females obtain the resources for egg production prior to the breeding season. Therefore, the inability of gulls to compensate for removed eggs in this study may be related to limited forage availability.

Immediately prior to the breeding season, gulls congregate in the town of Cordova to feed on fish offal discharged from local fish processing plants. Once nesting commences, breeding gulls leave

town and remain near their colonies on barrier islands of the Copper River Delta (MAB unpubl. data). These barrier islands border the North Pacific Ocean, a region which recently experienced a dramatic multi-year marine heatwave during 2014–2016 (Bond *et al.* 2015, Di Lorenzo & Mantua 2016). The persistently warm water mass altered food web dynamics and coincided with seabird colony failures across the Gulf of Alaska (Dragoo *et al.* 2017, 2018; Zador & Yasumiishi 2018), including the Egg Island Glaucous-winged Gull colony (MAB unpubl. data) and a nearby Caspian Tern *Hydroprogne caspia* colony (Suzuki *et al.* 2019). Although the heatwave had moderated by the 2018 breeding season, sea surface temperatures remained above the long-term mean (Zador & Yasumiishi 2018). The reduced clutch sizes of Glaucous-winged Gulls in our study, as well as the low reproductive success of surface-feeding Black-legged Kittiwakes *Rissa tridactyla* on nearby Middleton Island (~ 100 km south) in 2018, suggested that marine food web dynamics had not yet recovered (Institute for Seabird Research and Conservation 2018).

Natural predation

Although several potential predators are present on Egg Island (e.g., the Common Raven *Corvus corax*, Short-eared Owl *Asio flammeus*, and Northern Harrier *Circus hudsonius*), Bald Eagles *Haliaeetus leucocephalus* and cannibalistic adult Glaucous-winged Gulls appeared to be the main predators of gull eggs in our study, a finding that is similar to other study sites in North America (Zador 2001, Cowles *et al.* 2012, Hayward *et al.* 2014). Egg loss to depredation was minimal for the nests in our study, with only five instances of egg loss from four of 40 monitored nests. As has been recorded elsewhere (White *et al.* 2006), eagle attendance at the gull colony varied temporally and peaked during the egg hatching period. Interestingly, we only observed predation of eggs within the non-manipulated plot, which was slightly farther away from the local eagle nest (located ~ 500 m southeast of the study plots) compared to the manipulated plot.

CONCLUSIONS

Gulls in this study did not appear to increase the number of eggs laid to compensate for eggs experimentally removed from their nests. Given the ~ 15 000 Glaucous-winged Gulls breeding on the Copper River Delta (North Pacific Seabird Data Portal 2018), intraspecific competition may be high, thus limiting prey availability. Pressure from subsistence egg harvest in this area appears to be minimal—since its inception in 2014, the number of households in Cordova registered for the subsistence egg harvest, as well as the estimated number of eggs collected, has remained low (100–300 eggs per season, Fig. 3; Naves 2016, AMBCC unpubl. data). Further work on prey availability might reveal the degree of resiliency inherent in the gull populations of the region.

Due to the new harvest pressure in these colonies (i.e., egg harvest has only been legal since 2014), continued research and monitoring is warranted. Future studies should evaluate how varying levels of human disturbance (e.g., group size, time in colony, walking pace) affects the colony and should include methods to track whether gulls re-lay in new nest structures after manipulation.

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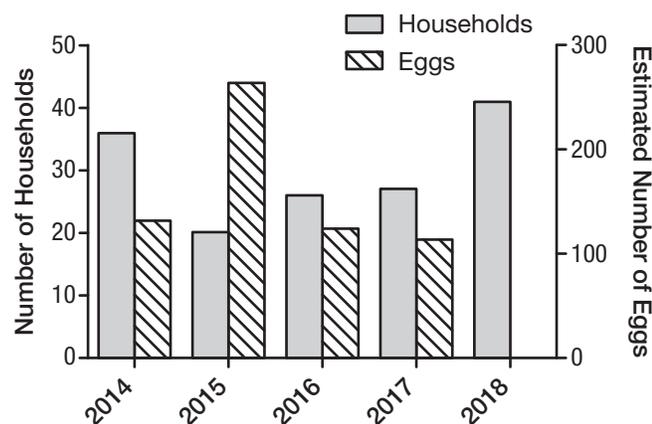


Fig. 3. Migratory egg subsistence harvest practices of Cordova, Alaska, USA from 2014 to 2018. Solid bars = number of households registered for the subsistence harvest; Hatched bars = estimated number of gull eggs harvested. The estimated number of gull eggs harvested was not available for 2018 at the time of publication. Data available from the Alaska Migratory Bird Co-Management Council (AMBCC 2018).

this research, the Native Village of Eyak for providing information regarding traditional harvest practices, Liliana Naves with the Alaska Department of Fish and Game for sharing subsistence harvest data, and Alaska Wilderness Air for safe transport to and from Egg Island. We would also like to thank David Ainley, Louise Blight, and an anonymous reviewer for their helpful comments that strengthened the manuscript.

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THE STATUS AND HISTORY OF THE BLACK TERN *CHLIDONIAS NIGER* IN CHILE

MANUEL MARÍN

Natural History Museum of Los Angeles County, Ornithology Department, 900 Exposition Boulevard, Los Angeles, CA 90007, USA
Current address: Casilla 15 Melipilla, Chile (mma95@hotmail.com)

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ABSTRACT

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Three Black Terns *Chlidonias niger* were observed and photographed in northern Chile in November 2018. Here, I summarize the occurrence of this species in Chilean territory and clarify the record for a specimen collected in 1859 during the *Novara* expedition: a typo in the original report led to a series of transcription errors that were perpetuated for ~150 years.

Key words: Black Tern, *Chlidonias niger*, southern distribution, Chile

The Black Tern *Chlidonias niger* is a seabird that breeds in the Northern Hemisphere, is widespread in North America and Europe, and exhibits post-breeding southward movements along the eastern and western coasts of the Americas. Its winter distribution in the Americas has been described as “from Mexico (rarely) to Panama S to Peru, and through the Gulf Coast to N South America; being accidental in Chile and Argentina” (Gochfeld & Burger 1996).

August von Pelzeln had the task of describing the birds collected during the voyage of the frigate *Novara* when it circumnavigated the globe (1857–1859). In his report, he mentioned the collection of *Hydrochelidon plumbea* (= *Chlidonias niger*) (NMW 38679) and he wrote “Chile - Ein Weibchen im See gefangen”, which translates to “Chile - a female caught in a lake”. No other information was provided (von Pelzeln 1865). The original label (Fig. 1) and the catalogue entry indicated “in See gefangen auf der Reise von

Valparaiso”, meaning that the bird was collected on the high seas during the trip from Valparaiso, Chile [to the Strait of Magellan], rather than on a lake or near the coast (H.-M. Berg pers. comm.). The *Novara* left Valparaiso on 11 May 1859. According to the ship track (von Pelzeln 1865), they were quickly moving south on 12 May, but between the 15th and 17th, they travelled west at a much reduced speed. Likely, winds had weakened, which facilitated the collecting of birds at sea; otherwise it would have been an extremely difficult task. The potential collection location would have been between 36°S and 37°S (off Concepción), between 77°W and 78°W, and at least 333 km from the coast. The specimen obtained was in the process of acquiring its breeding plumage (Fig. 1) and, without doubt, it was a straggler—instead of moving north to breed, it went south.

The spelling error of “im See gefangen” instead of “in See gefangen” in von Pelzeln’s 1865 publication concerning the collecting locality led to a series of misinterpretations. Using von Pelzeln’s citations as justification, Sclater (1867) included Black Tern on his list of Chilean birds under the name *H. fissipes*. This was based on the specimen reported by von Pelzeln as *H. plumbea*, and no other comment was added. Reed (1896), using the name *H. nigra*, mentioned only that it was not a common bird (information most likely based on Sclater). Hellmayr (1932) used the name *Chlidonias nigra surinamensis* and indicated that the only record of the Black Tern for Chile was collected on a lake in the vicinity of Santiago. Hellmayr (1932) regarded the species’ status in Chile as an “occasional winter visitor”, but the species would have been a summer visitor to Chile, not a winter visitor. Hellmayr misinterpreted von Pelzeln’s account, however, by adding the speculation that “the specimen was shot in the vicinity of Santiago”, a statement that led to a series of transcription errors that were perpetuated in the literature for over 150 years. The *Novara* naturalists visited Santiago and its surroundings in 1859 when there were several small swampy lakes around the city. The visit to Santiago by the naturalists combined with the text, which seemed to indicate to Hellmayr that the specimen was secured on a lake, led him to conclude that the vicinity of Santiago was the collecting locality. In their publications covering



Fig. 1. Specimen label of the Black Tern collected by the *Novara* expedition in Chile (NMW 38679). Courtesy of Natural History Museum Vienna/Bird Collection, photograph by H.-M. Berg.

Chilean birds, Murphy (1936), Housse (1945), Hellmayr & Conover (1948), Goodall *et al.* (1951), and Philippi (1964) added no new information but simply repeated that a bird was captured on a lake near Santiago, citing Hellmayr (1932). More recent authors summarizing the Chilean avifauna all followed Hellmayr's statements as well—e.g., Araya & Millie (2000), Jaramillo (2003), and Marín (2004). To further confuse things, Johnson (1967) added that “a single specimen in the Santiago Natural History Museum, was taken many years ago on a lake close to this city” [referring to a specimen of which there is no record in the museum's catalogues, exhibitions, or collections]. Furthermore, Couve *et al.* (2016) indicated that the specimen was collected during winter in a swamp near Santiago. This ignored Barros's attempt to straighten out the record, in which Barros misread (or misinterpreted or both) the actual published and unpublished information (Barros 2015). As examples: a) Hellmayr (1932) never mentioned that a bird was captured in winter [an assertion misinterpreted by many], but only noted in the range subheading that it was an “occasional winter visitor”; b) von Pelzeln (1865) did not mention the capture of the bird at sea, but he wrote “im See gefangen”, which translates to “caught in a lake”; c) the specimen label does not include a date, but the date was mentioned in the entry catalogue (inventory); and d) the label does not mention “near Valparaiso”, but only indicated collection on the high seas after departing from Valparaiso (see above and Fig. 1). Barros (2015) also mentioned an eBird sighting made by Jaramillo & Matus in February 2009 on the northern section of Chiloe Island, which is more than 500 km south of von Pelzeln's specimen and 3000 km south of the individuals observed near the town of Arica (*ca.* 18°28'S); however, we were unable to obtain this record from the database. There are only three accessible reports mentioned on eBird for Chile, at least one of which is mentioned by Barros (2018) (see also below).

Hughes (1988) mentioned that the Black Tern is an irregular visitor on the coastal lagoons of the Mollendo district of Peru, being absent in some years and very abundant in others. With that in mind, it was correctly suggested by Howell (2007) that the species should be expected to occasionally reach northern Chile, and he reported a sighting of a single individual on 23 October 1999 *ca.* 50 km west of Arica. The next record for Chile was a photograph of two individuals that was taken on 22 October 2016 by Fernando Diaz off Arica and reported by Barros (2018). As far as I know, there are no further published sightings of this species for Chile. Two other

unpublished records exist on eBird, one reported by I. Tejada on the same trip as F. Diaz and the other reported by C. Moreno on 22 May 2017, also off Arica.

During passages along the Chilean coast by vessel (from south to north in March 2018 and March 2019 and from north to south in November 2018), we encountered this species first on 15 March 2018 in Peruvian waters at *ca.* 17°52'S, very slightly north of the Chilean border, and I photographed a single bird perched on a floating log. The bird was about 43.5 km from shore and the water temperature was 20.6 °C. On 23 March 2019, we encountered many hundreds of Black Terns at 15°56'S, 76°06'W, *ca.* 126 km south-southwest from San Nicolas (Peru), and we recorded a water temperature of 21.3 °C. The birds were roosting on *Sargassum* “islands” on the western edge of the Peruvian Trench. We passed close enough to photograph 13 of those islands, each of which hosted up to 49 resting terns. I counted 337 terns in total on those 13 islands, with most in basic plumage but some entering their alternate plumage. Many more islands were evident in the distance. On the southbound trip, I observed and photographed three lone Black Terns on 16 November 2018, and all were perched on the carapace of floating loggerhead sea turtles *Caretta caretta* (Fig. 2A, 2B). In these encounters, the farthest position from land was 19°29'S, 70°59'W (*ca.* 74 km west of Pisagua) and the closest was 19°45'S, 70°40'W (*ca.* 55 km west of Pisagua and 140 km south-southwest of Arica). Water temperatures were 21.5 °C.

All recent Black Tern encounters in Chilean waters have been well offshore and in warmer waters. The bird collected in May 1859 by members of the *Novara* expedition was in cooler waters but well offshore and far from the main stream of the cold Humboldt Current. The year 1859 was hot and very dry in Chile, and the years immediately before and after were rainy (Ortlieb 1994). Coincidentally or not, the species was reported in 1999, 2016, 2017, and 2018, which were all dry years associated with La Niña events. During El Niño, the species may be more abundant in these waters, reaching further south. The individuals described here were observed in the months of October, November, March, and May. The *Novara* specimen (from May 1859) and some birds observed in March 2019 were entering their alternate or breeding plumage, while all other adult birds seemed to be in non-breeding plumage. In summary, the most recent data suggests that Black Terns visit Chile in warmer waters and well offshore, and it might well be a regular summer visitor rather than an occasional one or a vagrant.

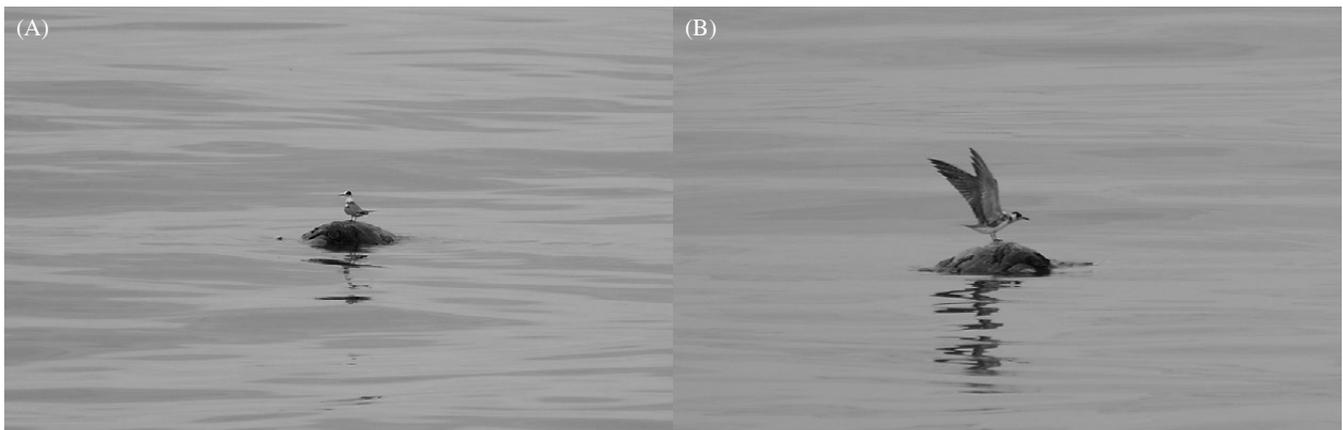


Fig. 2. Two Black Terns observed on 16 November 2018 at about (A) 74 km and (B) 55 km west of Pisagua, Tamarugal province, Chile.

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POPULATION SIZE AND CONDITION OF THE EMPEROR PENGUIN *APTENODYTES FORSTERI* COLONY OF SNOW HILL ISLAND, WEDDELL SEA, ANTARCTICA: OBSERVATIONS FROM 29 DECEMBER 2018

ROLF SCHIEL¹, FRANZISKA GÜPNER² & HANS-JOACHIM SPITZENBERGER³

¹Am Hasenpfahl 44, 31515 Wunstorf, Germany (rolf-schiel@t-online.de)

²Triq Kemmuna, GSM 1450, Ghajnsielem, Malta

³Haidland 15, 21218 Seevetal, Germany

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ABSTRACT

SCHIEL, R., GÜPNER, F. & SPITZENBERGER, H.-J. 2019. Population size and condition of the Emperor Penguin *Aptenodytes forsteri* colony of Snow Hill Island, Weddell Sea, Antarctica: Observations from 29 December 2018. *Marine Ornithology* 47: 189–192.

Snow Hill Island is of particular importance because it is the site of the northernmost colony of Emperor Penguins *Aptenodytes forsteri*. The colony was first discovered and counted in 1997 and has been visited sporadically, with counts conducted in 2004, 2009, and 2013, ranging from 1 200–4 000 breeding pairs. In December 2018, we photographed the entire colony. From photos, we counted 2 679 chicks and 339 adult Emperor Penguins, corresponding to a population of at least 2 700 breeding pairs. Although the census took place late in the breeding cycle when some chicks had already left the colony, the population size is well above the censuses of 1997 and 2009 but significantly below counts from 2004 and 2013. Snow Hill Island, located off the Antarctic Peninsula coast, is in an area strongly influenced by recent climatic developments. The Dion Island colony on the west side of the Antarctic Peninsula is also among the northernmost colonies, but it disappeared in 2009, presumably due to the climatic factors. Therefore, monitoring this Snow Hill colony is crucial.

Key words: Emperor Penguin, Snow Hill Island colony, Weddell Sea, Antarctica, population size, moulting chicks, sea ice cover, climate change

INTRODUCTION

The northernmost known Emperor Penguin *Aptenodytes forsteri* colony is located on the fast ice at the southeastern coast of Snow Hill Island, northeastern Antarctic Peninsula, and was first discovered during an overflight on 20 July 1997 (Coria & Montalti 2000). Before then, repeated sightings of single adults, as well as juvenile and immature Emperor Penguins in the northern Weddell Sea, suggested the existence of at least one breeding colony somewhere along the eastern coast of the Antarctic Peninsula (Kooyman *et al.* 2000). As early as 04 December 1893, Norwegian whaling captain Carl Anton Larsen described an Emperor Penguin colony south of

Snow Hill Island along the Jason Peninsula near the Larsen Ice Shelf (Todd *et al.* 2004). A colony in this area was only rediscovered, by satellite imagery, in 2014 (Fretwell *et al.* 2014). Overall three Emperor Penguin colonies have been identified in the northern section of the Antarctic Peninsula, although one of these colonies has recently disappeared, possibly relocating to Alexander Island (LaRue *et al.* 2015). The other 51 known Emperor Penguin colonies are situated further south along the coasts of the continent (Fretwell *et al.* 2012, Jenouvrier *et al.* 2014, LaRue *et al.* 2015, Teschke *et al.* 2016). Another colony that is farther south on the eastern side of the Peninsula also moved recently (Fretwell & Trathan 2019).

Due to the high pack ice concentration in the eastern Weddell Sea, only a few ships have been able to approach the southern end of Snow Hill Island. The icebreaker *Kapitan Khlebnikov* was the first expedition cruise ship to reach the colony, which it did on 09 November 2004 (Todd *et al.* 2004). This vessel has been as close as possible to the colony several times since, most recently in October and November 2018. The colony itself was approached by helicopter (and from there by foot, following the IAATO rules of conduct specifically developed for visits to the colony; IAATO 2015), which was launched from the vessel several kilometers from the colony. Crew and passengers of another expedition cruise ship, *M/V Ortelius*, have visited the colony repeatedly during the last couple of years. The results of four counts of the colony breeding population were published between 2000 and 2014, with counts ranging from 1 200 and 4 000 breeding pairs (Coria & Montalti 2000, Todd *et al.* 2004, Fretwell *et al.* 2012, Libertelli & Coria 2014).

Unusually favorable weather and ice conditions at the end of December 2018 (Table 1) made it possible for the expedition cruise

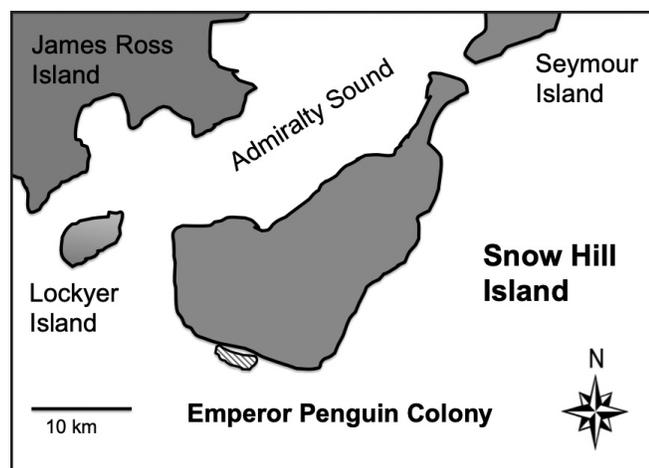


Fig. 1. Location of the Emperor Penguin colony of Snow Hill Island.

ship *M/V Bremen* to reach near to the Emperor Penguin colony, which is located on the fast ice at the southeastern coast of Snow Hill Island and covers an estimated 214 ha (2.14 km²) (BirdLife International 2019; Fig. 1). We were able to count Emperor Penguins during the journey around the southern part of the island, which provides valuable new knowledge about the colony; no such counts have been conducted there during the late phase of the breeding cycle.

In addition, our survey provides information on the distribution and composition of the groups of chicks and adults on the fast ice, as well as the moult stage of the chicks. The Snow Hill Island colony is of particular interest because, as the northernmost Emperor Penguin colony, it may be most vulnerable to climate change.

METHODS

Due to ice conditions—with nearly ice-free sea around the entire southeastern coastline of Snow Hill Island on 29 December 2018—we were able to reach the southeastern end of the island with the expedition cruise ship *M/V Bremen* (*Hapag-Lloyd Cruises*, Hamburg, Germany). We located the Emperor Penguin colony around 12h00. Because of the narrow pack ice belt in front of the fast ice, it was only possible to get within about 600–800 m of the colony.

Under sunny and windless weather conditions with very good visibility (Table 1), we observed the colony in its entirety from the ship for one hour and photographed it with high resolution digital cameras (digital SLR Canon EOS 7D with Canon EF 300mm f/4L IS USM lens; or Nikon D7200 with Tamron 300mm F/3.5-6.3 lens). Subsequently, we used our photos to count adults and juveniles; every individual was marked on each magnification to avoid double-counting individuals.

Subsequently, the *M/V Bremen* circumnavigated the island and Admiralty Sound between Snow Hill Island and James Ross Island. To our knowledge, this was the first time a non-icebreaker ship had done so. The three authors searched the observable water and ice surfaces continuously with binoculars for Emperor Penguins during the entire journey, from 10h00 to 16h00.

RESULTS

The penguins in the colony were distributed over an area of approximately three kilometers in length and a few hundred meters in width, along the edge of the fast ice. Almost all penguins were observed on level areas. No penguins were observed on ice ridges or in the rugged areas beyond the flat fast ice zone, nor were they observed on the ice-shelf or the mainland of Snow Hill Island.

We counted 29 penguin clusters consisting of either a) exclusively chicks (seven clusters), or b) exclusively adults (two clusters), or c) predominantly chicks with some adults (20 clusters). In most

clusters, the birds stood at some distance from each other, and in others they stood very close together. The largest gathering was a crèche of 144 chicks seen on the lee side of an iceberg (Fig. 2a).

We counted 2679 chicks and 339 adults, resulting in a total of 3018 individuals of different age groups. The chicks were in different stages of moult. The majority had completely moulted the abdominal area, with juvenile down still covering the dorsal body parts. Based on what could be seen clearly in the photos, only a few chicks (at least 187; 8.3 %) still carried a complete downy plumage; these chicks were usually smaller than chicks in a more advanced moult. The moulting process seemed to begin at the wings, then spread to the belly and finally over the back. Most chicks in the pack ice outside the colony still had a large number of down feathers, especially on their back (Fig. 2b). In a minority of chicks on ice floes, the moult was almost complete except for some remnants of downy plumage on the neck (Fig. 2c). The white face mask of the juvenile plumage was preserved in almost all chicks. We did not see any chicks that were completely down-free, and, as expected at this time of the year, we did not see any moulting adults.

While sailing along the eastern coast of Snow Hill Island, we observed single juvenile birds and small groups of recently fledged chicks (20 at most) in the pack ice and on ice floes. In total, we counted 50 individuals. Outside the colony, only 10 adults were



Fig. 2. (a) Crèches on the lee side of an iceberg at the Emperor Penguin colony of Snow Hill Island, (b) a group of juvenile chicks in the pack-ice at the eastern coast of Snow Hill Island, and (c) moulted juvenile Emperor Penguins on an ice-floe.

TABLE 1

Geographic position and weather data 12h00 on 29 December 2018 during the stay near the Emperor Penguin colony of Snow Hill Island

| Sunrise: 02:28 | | Sunset: 23:01 | | | Weather: sunny | |
|----------------|------------|-------------------|-------|---------------------|------------------|-------------|
| Noon position | | Temperature (°C): | | Air Pressure (hPa): | Wind (Beaufort): | Visibility: |
| Latitude: | Longitude: | Air | Water | | | |
| 64°33.3'S | 057°26.2'W | 1.5 | 0.0 | 991 | calm | clear |

spotted on pack ice floes or in the water. Interestingly, on the western coast of the island, as well as in Admiralty Sound between Snow Hill and James Ross islands, we observed just two Emperor Penguins with immature plumage that were adult in size and stature. Presumably, these penguins were from the previous breeding season. In total, we counted 3080 Emperor Penguins in the colony and in the wider environment.

In addition to the Emperor Penguins, a few Adelie Penguins *Pygoscelis adeliae*, Giant Petrels *Macronectes* spp., and Southern Black-backed Gulls *Larus dominicanus* were observed in proximity of the colony.

DISCUSSION

At the time of our visit, Emperor Penguin chicks were mostly moulting, which seemed to be in the same time sequence as described by Stonehouse (1953). At the time of our observation, the Snow Hill colony was already at the end of the breeding season and, therefore, in gradual disintegration. Therefore, only a few adults (339 in the colony and 10 on the eastern coast of the island) were found compared to other studies which took place earlier in the breeding season: July (Coria & Montalti 2000), August and September (Libertelli & Coria 2014), October (Fretwell *et al.* 2012), and November (Todd *et al.* 2004). Therefore, we used the counted chick numbers to estimate the population size of the colony.

Analyses of aerial photographs taken during the discovery of the colony in 1997 indicated a population of about 1200 pairs (Coria & Montalti 2000). Upon the first direct visit to the colony in November 2004, 3885 chicks were counted, on which an estimate of 4000–4200 breeding pairs was based (Todd *et al.* 2004). Counts from satellite images in October 2009 found 2164 breeding pairs (Fretwell *et al.* 2012). Libertelli & Coria (2014) photographed adult Emperor Penguins in the colony during a flight at the end of August 2013 and identified 7952 individuals, or about 4000 breeding pairs (numbers differ from the original publication but were confirmed by the author, Libertelli pers. comm.). A ground visit in mid-September 2013 produced a count of 3700 chicks (Table 2).

Colony numbers are expected to be at their maximum in October/November, when the breeding season is at its peak (Shirihai 2002). Nonetheless, the 2004 and 2009 censuses yielded significantly different counts, indicating that large variations in population size can occur between years. On the other hand, counts in 2004 and 2013 were very similar. Our count of 2679 juvenile penguins indicated at least 2700 breeding pairs, a number lower than that of Libertelli & Coria (2014) and Todd *et al.* (2004), but higher than Fretwell's estimate (Fretwell *et al.* 2012), further supporting the assumption of a fluctuating breeding population.

Given that the census methods that were used among studies were very different, over- or underestimation of penguin numbers cannot be ruled out. In our case, the large distance between observers and the colony, as well as the proximity of the individuals in the clusters, meant that penguins were likely overlooked rather than overestimated. Therefore, our count is likely a minimum estimate. In addition, many fledglings had presumably left the colony before our visit at the end of December, since fledging begins in early December (Emperor Breeding Cycle 2008, Wienecke 2008). However, it is unlikely that a substantial fraction of the 2018 chick cohort had left the colony by the end of December because relatively few penguins were spotted in the wider, general area of the colony. Even if we assume that several hundred chicks had already left the colony, and that a few hundred chicks may have died before reaching independence (there were about 100 dead chicks counted in 2004; Todd *et al.* 2004), the population size of the Snow Hill Island colony was significantly lower at the end of 2018 than in 2004 (3885 chicks; Todd *et al.* 2004) and 2013 (7952 adults, 3700 chicks; Libertelli & Coria 2014), but much higher than in 1997 (1200 pairs; Coria & Montalti 2000) and 2009 (2164 pairs; Fretwell *et al.* 2012).

Sea ice is of crucial importance for the breeding success of Emperor Penguins (Barbraud & Weimerskirch 2001, Ainley *et al.* 2010, Trathan *et al.* 2011, Fretwell *et al.* 2012, Jenouvrier *et al.* 2014). Therefore, the variability in the annual sea ice cover is a possible cause of population fluctuation in this species. Whether the low pack ice cover in the northeastern Weddell Sea in the austral summer of 2018/19 had an impact on the population size of the Snow Hill Island Emperor Penguins is unknown. It also remains to be seen whether the low sea ice cover was an exception or if it will continue in the next few years. The pack ice cover seems to have been increasing in most areas of the Weddell Sea in recent years, except in the northwestern part—the area of Snow Hill Island (Teschke *et al.* 2016). The extent to which possible changes in sea ice cover will affect the Snow Hill Island colony, as well as the impact of human disturbance, must be investigated in future studies (Jouventin 1975, Jouventin *et al.* 1984, Ainley *et al.* 2010, IAATO 2015, LaRue *et al.* 2015).

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TABLE 2
Published counts and estimates of the population size of the Emperor Penguin colony of Snow Hill Island

| Month & Year of Census | Number of Individuals | Number of Breeding Pairs | Author |
|------------------------|-----------------------|--------------------------|-------------------------------|
| July 1997 | | 1200 | Coria & Montalti (2000) |
| November 2004 | 3885 (chicks) | 4000–4200 | Todd <i>et al.</i> (2004) |
| October 2009 | | 2164 | Fretwell <i>et al.</i> (2012) |
| August 2013 | 7952 (adults) | ~ 4000 | Libertelli & Coria (2014) |
| September 2013 | 3700 (chicks) | | Libertelli & Coria (2014) |

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NEST DESERTION: AN ANTI-PREDATOR STRATEGY OF THE AUSTRALIAN FAIRY TERN *STERNULA NEREIS NEREIS*

CLAIRE N. GREENWELL^{1*,2}, JAMES N. DUNLOP^{1,3} & NEIL R. LONERAGAN^{1,2}

¹*Environmental and Conservation Sciences, Murdoch University, 90 South Street, Murdoch, Western Australia 6150, Australia*
*(C.Greenwell@murdoch.edu.au)

²*Centre for Sustainable Aquatic Ecosystems, Harry Butler Institute, Murdoch University, 90 South Street, Murdoch, Western Australia 6150, Australia*

³*Conservation Council of Western Australia, Lotteries West House, 2 Delhi Street, West Perth, Western Australia 6150, Australia*

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ABSTRACT

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This study describes nest desertion as a probable but previously undescribed anti-predator strategy for the Australian Fairy Tern *Sternula nereis nereis*. Deserted nests were observed at night for up to nine nights following the laying of the first eggs at a colony in southwestern Australia. Nocturnal nest desertion may provide the terns with a mechanism for assessing the occurrence of potential nest predators, maintaining reproductive synchrony, and reducing the total time a colony is detectable by predators. Additionally, temporary diurnal nest desertion for up to 80 minutes was observed following the predation of an adult tern. Diurnal nest desertion may be used to reduce the risk of adult mortality and, consequently, decrease colony visibility, thereby increasing reproductive success.

Key words: Egg neglect, Laridae, predation, reproductive success, *Sternula*

INTRODUCTION

Predation is one of the most influential selection pressures on animal reproductive strategies because it shapes the heritable behavioural and reproductive traits of a species (Lack 1968, Lima & Dill 1990, Martin 1992, Šmejkal *et al.* 2018). Birds have evolved various strategies that reduce predation during the breeding season to enhance adult survival and lifetime productivity and to increase the survival of offspring (Lack 1968, Martin 1992, Ward *et al.* 2011).

Surface-nesting seabirds, including members of the Laridae family, usually breed in groups or colonies, and active anti-predator behaviours such as nest synchronisation and social mobbing play an important role in reducing predation on the colony (Lack 1968, Gochfeld 1980). However, nest predation remains an important source of breeding failure. Colonies provide an opportunity to reward predators over an extended time because of the high density of nests, eggs, and adult birds, which may attract greater numbers of predators and repeat visits by predators over time (Gochfeld 1980, Burger & Gochfeld 1991, Martin 1992, Danchin & Wagner 1997, Ward *et al.* 2011). Where adults are not threatened directly (i.e., only eggs and chicks are targeted), the presence of a predator usually elicits aggressive aerial defence to drive off the intruder (Burger & Gochfeld 1991). However, where predators pose an immediate threat to adult survival, broods are routinely left unattended until the threat subsides; in extreme cases, a nesting attempt may be abandoned altogether (Burger & Gochfeld 1991, Levermann & Tøttrup 2007, CNG unpubl. data). For example, systematic predation of endangered Black-fronted Terns *Chlidonias albostratus* (probably by cats) in New Zealand resulted in the deaths of six adults (10 % of the population) and the subsequent abandonment of all 28 nests in the colony (O'Donnell *et al.* 2010).

In Greenland, the presence of a persistent arctic fox *Alopex lagopus* at a mixed colony of Arctic Terns *Sterna paradisaea* (311 pairs) and Sabine's Gulls *Xema sabini* (67 pairs) during a year of late sea ice break-up resulted in nesting attempts being delayed until the colony was eventually completely abandoned (Levermann & Tøttrup 2007). Prey availability was ruled out as a contributing factor, as courting birds were observed returning to the colony with a steady supply of large fish (Levermann & Tøttrup 2007).

Other anti-predator adaptations among surface-nesting seabirds include synchrony of egg-laying, crypsis of eggs and chicks, and nesting at densities that reduce the risk of predation to any one individual breeding adult (Lack 1968, Gochfeld 1980, Oro 1996, Brunton 1999). The eggs and chicks of surface-nesting seabirds have a mottled appearance and are very inconspicuous, and this crypsis is enhanced by parents routinely incorporating shells, small stones, and organic material in and around the nest (Lack 1968, Burger & Gochfeld 1991, Parrish & Pulham 1995). When faced with the threat of predation, chicks often lay flat against the substratum and rely on their cryptic colouration to reduce the probability of detection (Lack 1968, Burger & Gochfeld 1991).

Delayed nocturnal occupation of colony sites (prior to egg-laying) and nest desertion (after egg-laying) are two anti-predator strategies that are less studied, but they have been documented for several larids, including Least Tern *Sternula antillarum* (delayed nocturnal occupation; Atwood & Massey 1988, Wilson *et al.* 1991), Sandwich Tern *Thalasseus sandvicensis* (delayed nocturnal occupation; Veen 1977), and Common Tern *Sterna hirundo* (nocturnal nest desertion; Marshall 1942, Nisbet 1975, Shealer & Kress 1991). Roosting away from colony sites before the peak egg-laying period and/or deserting nests at night during the egg-laying and hatching periods

probably decrease predation by reducing both adult mortality and the length of time that the colony is detectable to nocturnal predators (Nisbet 1975, Atwood 1986). Predation of adult Common Terns by Great Horned Owls *Bubo virginianus* at a colony in Massachusetts is believed to have been the proximate cause of nocturnal nest desertion; this resulted in the delayed hatching of eggs by about six days and increased predation of unattended chicks (Nisbet 1975).

Our study describes nocturnal and diurnal nest desertion behaviour of the Australian Fairy Tern *Sternula nereis nereis* during the early egg-laying and the post-laying periods. To our knowledge, this behaviour has not been reported previously for the Fairy Tern.

MATERIALS AND METHODS

Study species

The Fairy Tern is one of two small terns, along with the Little Tern *Sternula albifrons*, to nest in Australia. In 2011, the Fairy Tern was listed as Vulnerable, in accordance with s266B of the Environment Protection and Biodiversity Conservation Act 1999 (Cwlth), due to a substantial population contraction (24 % between 1974 and 2007) and to a lack of evidence demonstrating that threats affecting Fairy Terns were abating (DE 2011, TSSC 2011). In the approved Conservation Advice for Fairy Terns, major threatening processes included introduced predators (e.g., red foxes *Vulpes vulpes*, cats *Felis catus*, and black rats *Rattus rattus*) and increased natural predators, whose populations are exacerbated due to human impacts (e.g., Silver Gulls *Chroicocephalus novaehollandiae*, Australian Ravens *Corvus coronoides*) (DE 2011).

Study area

We focused on two sites that are managed for Fairy Tern conservation in southwestern Australia, both located within 100 km of the Perth metropolitan centre (Fig. 1). The first site was situated in Mandurah (32°31'14.24"S, 115°43'00.26"E) and managed by the City of Mandurah (Fig. 1). It covers an area of ~2460 m², has a uniform elevation of ~2.0 m above sea level, and is separated from the adjoining beach by a 1.5-m limestone sea wall. The second site is located on reclaimed land at Rous Head, North Fremantle (32°02'25.83"S, 115°44'23.69"E) and is managed by the Fremantle Ports (Fig. 1). It covers a total area of ~3250 m² of which ~1650 m² is suitable for nesting, has an elevation of ~5.0 m above sea level, and is surrounded by coastal vegetation. The perimeters of both sites are fully enclosed by a chain-wire fence that is 1.2 m high and lined with shade-cloth to provide protection to nesting terns and their young. A layer of shell material was added to the ground surface at both sites by land managers in previous years to increase substrate complexity, thus enhancing the attractiveness of the sites to breeding terns and increasing crypsis to predators.

Observations of nocturnal nest desertion were made at Mandurah 19–24 October 2018 prior to sunrise and 20–30 October after last light. Nest desertion was observed at North Fremantle on 10–11 November and on an ad hoc basis from 29 November to 06 December 2018, either after last light or before sunrise. Observations of diurnal nest desertion were documented at North Fremantle between 05 December and 07 January 2019 during regular visits to the site in the morning (~04h30–09h00) and afternoon (~16h00–19h30). The monitoring at North Fremantle was less extensive and more opportunistic than at Mandurah in the

early nesting period due to logistical constraints. Three wildlife cameras (Swift 3C, Queensland) were installed on 22 October 2018 to monitor colony development at the North Fremantle site.

All observations were conducted in accordance with Murdoch University Animal Ethics Committee Approval (Protocol 546, Permit RW3077/18).

RESULTS

Nocturnal nest desertion (Mandurah)

Night desertion of nests was first observed at Mandurah on 19 October 2018, with terns not returning to the colony site until the following morning. The first three nests were recorded on 19 October (Nest 1 = N1), 22 October (Nest 2 = N2), and 23 October (Nest 3 = N3), and eggs were not incubated continuously during the day. The colony site was abandoned in the late afternoon, usually between 17h00 and 18h30, and the terns did not return to resume incubation until after sunrise the following morning. Fairy Terns were not observed after dark at the nest site until 29 October, so the eggs appear to have been left unattended for up to nine consecutive nights (N1). Fairy Terns were observed roosting on the adjacent beach at first light on 22 October and on the evening of 25 October. On 24 October, Fairy Terns were heard in the distance but were not seen on the beach.

The egg from N1 had hatched by 21 November (~33 d after it was laid), and the observed chick was estimated to be ~1–2 d old. Eggs from N2 were damaged during a hail storm and did not hatch. It is unclear whether the eggs from N3 were incubated and hatched.

Nocturnal nest desertion (North Fremantle)

Evidence of nocturnal nest desertion was also recorded in the early egg-laying period (29 November to 03 December 2018) at North Fremantle. On 29 November, three Fairy Terns were present following last light, but no terns were present prior to sunrise on 01 December, despite two nests being evident. Three birds were incubating eggs on 02 December at first light (6 nests recorded), as were two birds on 03 December (11 nests recorded).

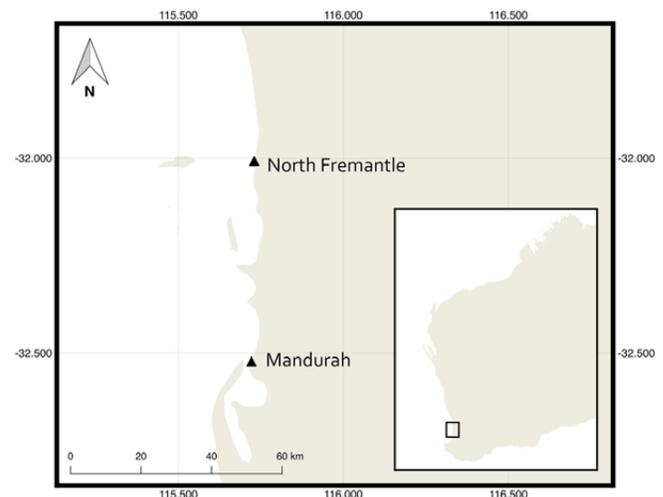


Fig. 1. Map showing the locations of two managed sanctuary sites for the Australian Fairy Tern in the Perth metropolitan area, southwestern Australia.

Diurnal nest desertion (Rous Head)

On 17 December 2018 at 06h05 an Australian Hobby *Falco longipennis* swooped into the Rous Head colony and captured a nesting adult Fairy Tern. This event resulted in the up-flight of the entire colony and temporary abandonment of the site. Highly synchronised group flight behaviour, similar to that exhibited by small shorebirds and described by Atwood (1986) for Least Terns at night roost locations, was observed for several minutes until the birds were so far away that they could no longer be observed from the colony site. At 06h56 the terns returned to within close proximity of the colony site and their flight behaviour remained highly synchronised, although several small groups broke away before re-joining the main group. Several group passes were made over the colony site between 07h03 and 07h14. Some birds landed momentarily before the group swooped synchronously down over the sea wall and out over the water, before circling back over the colony site. Unlike regular noisy up-flights that occur with no apparent stimuli, the flock remained almost completely silent while in flight. By 07h25 most birds had settled back onto the site, before up-flying again, en masse, with no apparent stimulus between 07h31 and 07h33.

An attempted predation event by a hobby was also observed on the previous day (16 December) at 07h08. The falcon swooped into the colony, this time failing to capture a tern. This attempt resulted in all but one of the nesting Fairy Terns up-flying and deserting the colony site, after which the falcon departed the area. Synchronised group flight behaviour was observed, but on this occasion, the birds remained within sight of the colony and the flight was initially silent, becoming noisier over time. The birds remained in flight for ~27 min, with most individuals landing at 07h35. Despite these events, the colony was successful, with a maximum of ~220 active nests established; it produced an estimated mean of 0.74 fledglings per pair (CNG & JND unpubl. data).

DISCUSSION

This study describes temporary nest desertion by Fairy Terns at the beginning of egg-laying, a strategy probably used to reduce adult predation, shorten the period of adult exposure to predators, and assess egg and chick predators during the breeding season. To our knowledge, this behaviour has not previously been described for Fairy Terns.

Nocturnal nest desertion

Nocturnal colony desertion and egg abandonment was observed for up to nine consecutive nights (19–29 October 2018) at Mandurah. Despite this abandonment, the first egg laid was viable, hatching ~31 d after the initial laying date. This egg was incubated continuously for ~22 d following the initial nine nights of no incubation. Note that the average incubation period for Fairy Tern eggs is 21 d ($n = 82$; CNG unpubl. data). Therefore, the temporary abandonment of eggs at night probably delayed hatching for the length of time that the egg was not continuously incubated (i.e., ~9 d). Nest desertion was also observed in the North Fremantle colony, although it is difficult to quantify the extent of this behaviour because this site could not be monitored to the same degree as Mandurah. These observations highlight the potential for eggs to remain viable in the early egg-laying period despite long periods (≥ 14 h) without incubation and to remain undetected by potential egg predators, such as Nankeen Night Heron *Nycticorax caledonicus*.

Plasticity in incubation is not widely described among coastal foraging seabirds, but notable examples of egg neglect do occur, particularly among pelagic-foraging birds such as auklets, murrelets, and storm petrels (Sealy 1976, Boersma 1979, Murray *et al.* 1980, Blight *et al.* 2010). Such behaviour in pelagic seabirds is believed to be an adaptation to patchily distributed food resources; this enables adults to spend more time foraging, especially in the early post-egg laying period, without compromising egg viability (Boersma 1979, Blight *et al.* 2010). For example, eggs of the Fork-tailed Storm Petrel *Oceanodroma furcata* were commonly neglected for up to two days at a time (mean cumulative egg-neglect period = 11 d), but in some instances, viable eggs were deserted for periods of 4–7 d (Boersma 1979). For coastal seabirds, whose food resources are typically more abundant and easier to access than pelagic seabirds, nocturnal nest desertion or egg neglect may be a strategy to pre-emptively avoid predation (Nisbet 1975, Nuechterlein & Buitron 2002).

Nocturnal nest desertion by Fairy Terns in the early egg-laying period is probably a mechanism to reduce predation in three ways: (1) it provides a mechanism for assessing potential nest predators, (2) it enhances reproductive synchrony in the early egg-laying period, and (3) it reduces the total time the colony is detectable to potential predators (Nisbet 1975, Gochfeld 1980, Atwood 1986, Jovani & Grimm 2008). Note that we recorded no instances of egg predation during the nocturnal desertion period, despite the site being accessible to mammalian egg-predators. However, predation by cats or black rats may have occurred for previous nesting attempts in Mandurah, and cats are suspected of preying on chicks and adults later in the 2018/19 season. A cat was detected at North Fremantle on 22 October, long before any eggs were laid, and it was removed by animal control agents. Baiting for black rats in the sea wall adjoining the sanctuary during the colony's formation period at both sites may have helped to relieve pressure from this well-known egg predator.

Habitat selection by nesting birds represents a compromise between maximising resources and minimising losses to adverse environmental conditions and predation. The first birds to lay eggs at any given location take the greatest risk, as the individual risk of predation is higher than for birds nesting mid-season (Ashmole 1963, Nisbet 1975). Nocturnal nest desertion was first described in Common Terns by Marshall (1942) in Ohio and subsequently by Nisbet (1975) in Massachusetts. While an explanation for nocturnal nest desertion was not apparent in Ohio, predation by Great Horned Owls is thought to have been the proximate cause of temporary desertion in Massachusetts (Marshall 1942, Nisbet 1975).

The lack of egg predation following nocturnal desertion may provide the terns with information about an absence of nest predators. Night observations of the North Fremantle colony prior to egg-laying revealed night-prospecting (i.e., flying over the site without landing) by Fairy Terns for short periods of time, but terns did not land on the site. Night-prospecting may also be used to provide terns with information on site suitability and the presence of potential predators. On an evolutionary timescale, predation by alien species is a relatively recent threat to breeding seabirds (Weidinger 1998). However, small terns frequently shift colony sites from one breeding attempt to the next (Nisbet 1973, Burger 1984, Cabot & Nisbet 2013). This regular shifting of colony sites in response to predation, by either native or introduced species, demonstrates a well-developed mechanism for rapid reaction through learning (Burger 1984, Weidinger 1998) among the small terns.

Nocturnal desertion of eggs increases the time to hatching (Nisbet 1975), but such behaviour may also be used to enhance reproductive synchrony. The adaptive value of synchronous hatching is thought to increase survival through: (1) collective group defence; (2) predator swamping, whereby high prey-population densities reduce individual risk by overwhelming the predator population's ability to consume them; and (3) predator confusion, which reduces the efficiency of prey capture (Lack 1968, Hamilton 1971, Estes 1976, Ims 1990). As Nisbet (1975) points out, predators have the potential to take a larger proportion of prey when fewer individuals are present. Thus, nesting in the middle of the season may increase the chance of survival for an individual when a larger proportion of birds are nesting (Nisbet 1975).

Observations of nocturnal nest desertion at multiple colony sites in the absence of nocturnal predators suggests that this is an innate, adaptive behavioural strategy used to enhance reproductive success, rather than a direct behavioural response to nocturnal adult predation (Nisbet 1975).

Diurnal nest desertion (North Fremantle)

Diurnal nest desertion and flocking by Fairy Terns is, presumably, a strategy used to increase adult survival, despite the potential cost to eggs and chicks (Thompson *et al.* 1974, Caraco *et al.* 1980, Burger & Gochfeld 1991). Seabirds are long-lived, with high adult survivorship (Hunt 1980)—for example, the current longevity record for the Australian Fairy Tern is ~22 years (banded in 1997 by JND; Australian Bird and Bat Banding Scheme pers. comm.). Therefore, the potential to replace themselves can be achieved by numerous nesting attempts over their long lifespan (Furness & Monaghan 1987, Schreiber & Burger 2001, Bried & Jouventin 2002). Thus, a reduction in short-term reproductive investment far outweighs any risk to future survival associated with a single mating attempt (Boersma 1979, Bried & Jouventin 2002, Drent & Daan 2002).

The flocking behaviour of birds is widely thought to decrease the chance of predation, with larger flocks having a higher probability of detecting potential predators and a lower risk of individual predation (Siegfried & Underhill 1975, Caraco *et al.* 1980). In the Common Starling *Sturnus vulgaris*, flocks became increasingly compact and synchronised with increased predation pressure, and predation rates by Peregrine Falcon *Falco peregrinus* were greatest at roosts where flocking behaviour was less marked (Carere *et al.* 2009). Therefore, the highly synchronised group flight behaviour and deliberate offshore movement by Fairy Terns is likely undertaken to reduce adult predation (Carere *et al.* 2009).

Secondly, nest desertion likely reduces nest detection by potential predators, which increases the chances of reproductive success, particularly for early- and mid-season nesters (Coulson 1966, Atwood 1986). Each breeding attempt is energetically costly, and birds breeding earlier in the season (closer to peak food availability) are typically more successful than those that lay later or birds laying for the second time (Coulson 1966). Therefore, reducing colony detectability, as opposed to completely abandoning the colony site, may be a strategy used to enhance reproductive success (Safina & Burger 1983). This behaviour overcomes the need to invest time and energy in the re-laying of eggs at an alternative site, which may yield low reproductive success (Safina & Burger 1983).

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MITOCHONDRIAL DNA REVEALS POPULATION GENETIC STRUCTURE WITHIN ATLANTIC BUT NOT PACIFIC POPULATIONS OF A HOLARCTIC SEABIRD

DREW SAUVE^{1*}, ANOMA PATIRANA², JOHN W. CHARDINE^{3*} & VICKI L. FRIESEN¹

¹*Department of Biology, Queen's University, Kingston, ON K7L 3N6, Canada* **(0as69@queensu.ca)*

²*Environment and Climate Change Canada, 401 Burrard St, Vancouver, BC V6C 3S5, Canada*

³*Science and Technology Branch, Environment Canada, PO Box 6227, Sackville, NB E4L 1G6, Canada*

^{*}*Retired*

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ABSTRACT

SAUVE, D., PATIRANA, A., CHARDINE, J.W. & FRIESEN, V.L. 2018. Mitochondrial DNA reveals genetic structure within the Atlantic but not Pacific populations of a holarctic seabird, the Black-legged Kittiwake *Rissa tridactyla*. *Marine Ornithology* 47: 199–208.

To predict evolutionary processes, such as speciation and local adaptation, we need to understand the mechanisms causing genetic differentiation of populations. We used mitochondrial control region sequence variation to investigate the genetic structure within and between Atlantic and Pacific populations of Black-legged Kittiwake (*Rissa t. tridactyla* and *R. t. pollicaris*, respectively). We predicted that genetic divergence of these populations, as in other northern hemisphere seabird species, might have been caused by glacial vicariance in the late Pleistocene. Further, because of regional differences in the morphology of kittiwakes, and the hypothesized historical vicariance, we predicted that genetic structure would exist within Atlantic but not Pacific populations. Population genetic and phylogenetic analyses of 756 base pairs of control region sequence for 398 kittiwakes indicated that Atlantic and Pacific populations are genetically differentiated from one another. Phylogenetic analyses indicated historical divergence of two mtDNA clades within the Pacific population and four mtDNA clades within the Atlantic population. Population genetic analyses indicated that colonies within the Atlantic were strongly differentiated from one another, which could be explained by restrictions in contemporary gene flow and historical fragmentation in historical refugia. Population genetic analyses provided little evidence for genetic structure in the Pacific population, which we attributed to longer time since vicariance, allowing more migration between colonies. Our results agree with current subspecies designations of Atlantic and Pacific populations.

Key words: coalescence, gene flow, mitochondrial control region, historical demography, mtDNA, Pleistocene glaciation

INTRODUCTION

Population geneticists have well developed theories on how evolutionary processes—such as selection, genetic drift, gene flow, and mutation—can result in population divergence and speciation (e.g., Endler 1977, Coyne & Orr 2004). However, the relative importance of each of these evolutionary forces in the process of genetic divergence or speciation in the natural world is not well known. For example, contemporary patterns of genetic variation are shaped by both present-day and historical forces, making patterns of genetic variation difficult to interpret. Understanding these processes is particularly important for many seabirds because historical fragmentation of their ranges by Pleistocene glaciations, and the long generation times of seabirds, make it probable that genetic patterns of northern hemisphere species are shaped, at least partially, by historical isolation of refugial populations (e.g., Morris-Pocock *et al.* 2008, Tigano *et al.* 2015).

Seabirds provide interesting study systems to investigate mechanisms of population differentiation. Genetic differentiation commonly occurs between seabird populations separated by land, but genetic differentiation can also occur between populations with no contemporary land barrier (Friesen *et al.* 2007, Friesen 2015). When seabird populations are not separated by land (within an ocean basin), genetic differentiation of populations is expected to be weak because of the high potential for dispersal—and therefore gene flow—in

seabirds (Friesen *et al.* 2007, Friesen 2015). However, many seabird populations exhibit restricted gene flow and genetic differentiation within ocean basins. Genetic differentiation among seabird colonies within an ocean basin could be the result of historical fragmentation. Historical demographic influences, such as population bottlenecks and spatial fragmentation by Pleistocene glaciers, are recognized as dominant forces shaping present-day diversity and distributions of many northern hemisphere species (Hewitt 2000). For example, genetic structuring in Atlantic Common Murres *Uria aalge* and Razorbills *Alca torda* likely reflects historical separation in multiple glacial refugia (Moum & Arnason 2001, Morris-Pocock *et al.* 2008). Differentiation among populations within ocean basins could also represent contemporary processes. Many seabirds are highly philopatric (but see Coulson 2016), and philopatry could restrict gene flow among colonies (Quinn & Dittman 1990, Friesen *et al.* 2007, Friesen 2015). Similarly, differences in selective pressures (e.g., due to ocean regime) may deter migration among colonies or reduce the fitness of immigrant individuals. Therefore, genetic differentiation among colonies of seabirds could be the result of a combination of historical fragmentation, natural selection, or philopatric behaviour.

The extent of genetic structure within Atlantic or Pacific seabird populations is difficult to predict. In the Atlantic, genetic structure is found in Common Murres, Razorbills, and Black Guillemots *Cepphus grylle*, whereas little genetic structure is found in Northern Fulmars *Fulmarus glacialis* or Thick-billed Murres *Uria lomvia*

(Kidd & Friesen 1998, Moum & Arnason 2001, Morris-Pocock *et al.* 2008, Kerr & Dove 2013, Tigano *et al.* 2015). Similarly, within the Pacific, genetic structure is found in Thick-billed Murres and Pigeon Guillemots *Cephus columba* but not in Northern Fulmars or Common Murres (Kidd & Friesen 1998, Morris-Pocock *et al.* 2008, Kerr & Dove 2013, Tigano *et al.* 2015). Reviews of seabird species suggest multiple environmental and ecological factors could interact to produce genetic structure (Friesen *et al.* 2007, Friesen 2015). For example, genetic structure in Black Guillemots is primarily attributed to small population sizes and low dispersal, whereas genetic structure in Atlantic Common Murres is attributed to fragmentation during the Pleistocene glaciation (Kidd & Friesen 1998, Morris-Pocock *et al.* 2008). Determining the relative importance of these factors in shaping genetic structure will require the accumulation of genetic, ecological, and environmental data on multiple species within ocean basins.

Black-legged Kittiwakes *Rissa tridactyla* are small, pelagic, cliff-nesting gulls that have a subarctic and arctic breeding distribution and show regional variation in morphometrics and plumage (Sluys 1982; Chardine 2002). Two subspecies are generally recognized: *R. t. pollicaris*, confined to Alaska and the Bering, East Siberian, and Chukchi Seas; and *R. t. tridactyla*, restricted to arctic Canada, Norway, Western Greenland, Western Russia, and the Northeast Atlantic (Cramp & Simmons 1983). Pacific Black-legged Kittiwakes generally have a longer bill, slightly larger body size, and more black on the primaries (Cramp & Simmons 1983; Chardine 2002).



Fig. 1. Map of Black-legged Kittiwake sampling sites. Diamonds depict the Atlantic and circles depict the Pacific subspecies. Black squares indicate major sampling gaps. Sample sizes and coordinates are given in Table 1.

TABLE 1
Locations, coordinates, sample sizes (*n*), haplotype diversities (H_S), nucleotide (π) diversities, Tajima's *D* statistics, and Fu's F_S test of neutrality for Atlantic and Pacific kittiwake colonies^{a, b}

| Location | Population | Coordinates | <i>n</i> | H_S (SE) | π (SE) | Tajima's <i>D</i> | Fu's F_S |
|----------------|--------------------|-------------------|------------|------------|--------------|-------------------|-------------|
| Alaska, USA | Barren Islands* | 58°53'N, 152°00'W | 45 | 0.91(0.03) | 0.010(0.005) | -0.54 | -6.0 |
| | Kachemak Bay* | 59°30'N, 151°29'W | 16 | 0.91(0.08) | 0.015(0.008) | -0.7 | -0.8 |
| | Buldir Island | 52°21'N, 175°55'E | 12 | 0.86(0.09) | 0.012(0.006) | -0.9 | 0.6 |
| | Cape Lisburne | 68°53'N, 166°21'W | 24 | 0.98(0.02) | 0.012(0.006) | -1.1 | -8.2 |
| | Cape Thompson | 68°09'N, 165°58'W | 13 | 0.98(0.01) | 0.013(0.007) | -0.6 | -3.5 |
| | Chisik Island* | 60°08'N, 152°33'W | 9 | 0.97(0.06) | 0.012(0.007) | 0.4 | -1.5 |
| | Chowiet Island | 56°02'N, 156°42'W | 15 | 0.96(0.05) | 0.009(0.005) | -0.8 | -2.0 |
| | Duck Island* | 60°09'N, 152°33'W | 13 | 0.96(0.05) | 0.011(0.006) | 0.0 | -2.8 |
| | Koniuji Island* | 52°15'N, 175°07'W | 16 | 0.97(0.03) | 0.011(0.006) | -0.4 | -5.5 |
| | Middleton Island | 59°26'N, 146°20'W | 26 | 0.96(0.02) | 0.011(0.006) | -0.5 | -4.2 |
| | St. George Island* | 56°39'N, 169°47'W | 20 | 0.95(0.04) | 0.010(0.006) | -1.1 | -4.9 |
| Canada | Avalon Peninsula | 47°21'N, 053°19'W | 30 | 0.87(0.04) | 0.009(0.005) | -0.6 | 0.3 |
| | Prince Leopold I. | 74°02'N, 090°05'W | 7 | 0.83(0.13) | 0.004(0.003) | -0.6 | -0.8 |
| Greenland | Hakluyt | 77°27'N, 071°48'W | 11 | 0.81(0.08) | 0.004(0.003) | -1.5 | 2.1 |
| United Kingdom | Shetland Islands | 60°20'N, 001°14'W | 8 | 0.64(0.18) | 0.003(0.002) | -1.5 | 0.8 |
| | Isle of May | 56°11'N, 002°33'W | 30 | 0.71(0.07) | 0.003(0.002) | -1.0 | -1.1 |
| France | Brittany | 48°42'N, 003°48'W | 17 | 0.75(0.09) | 0.005(0.003) | -1.1 | 0.1 |
| Norway | Hornøya | 70°23'N, 031°09'E | 30 | 0.80(0.05) | 0.005(0.003) | -0.3 | 0.0 |
| | Svalbard | 78°54'N, 012°00'E | 29 | 0.61(0.10) | 0.003(0.002) | -1.2 | -0.9 |
| Russia | Kola Peninsula | 67°18'N, 041°06'E | 27 | 0.85(0.05) | 0.007(0.004) | -0.9 | 0.4 |
| Total | | | 398 | | | | |

^a Significant Tajima's *D* and Fu's F_S values are in bold. The alpha used for evaluating F_S significance was 0.02 (Fu 1997).

^b Asterisks indicate birds collected near breeding colonies during the breeding season instead of actively nesting adults or chicks hatched at a colony.

Kittiwakes in the North Atlantic differ regionally in the extent of black on the tips of primary feathers (Chardine 2002) and biometrics (wing, culmen, and tail length; Sluys 1982). Wing-tip patterns of Atlantic kittiwakes suggested that there are two geographic groups: 1) Arctic Canada and West Greenland; and 2) Newfoundland, United Kingdom, and Barents Sea (Chardine 2002). To the best of our knowledge, a regional analysis of the variation of phenotypes present in the Pacific has not been conducted. Variation in plumage between and within ocean basins suggests that significant genetic differences and restricted gene flow may exist among kittiwakes from different ocean basins and to some extent within the Atlantic Ocean (Chardine 2002; Coulson 2016). Variation in microsatellite markers indicate that Atlantic and Pacific colonies are genetically different, whereas colonies within the Atlantic are not (McCoy *et al.* 2005).

In the present study, we analyzed sequence variation in the mitochondrial control region of Black-legged Kittiwakes sampled from colonies throughout most of their range. The mitochondrial control region exhibits a high mutation rate and small effective population size compared to nuclear DNA, and it is therefore sensitive to restrictions in gene flow and population size (Avice 1994). Because many conspecific seabird populations are genetically differentiated between ocean basins (Friesen *et al.* 2007, Friesen *et al.* 2015), and microsatellite markers indicate that Pacific and Atlantic kittiwakes differ genetically (McCoy *et al.* 2005), we predicted that mitochondrial sequences would differ between Black-legged Kittiwakes in the Atlantic versus Pacific Oceans. If so, Atlantic and Pacific populations act as natural replicates for tests of mechanisms of population differentiation within ocean basins.

Evidence from morphometrics suggests that genetic structure exists within the Atlantic but not the Pacific population of Black-legged Kittiwakes. Therefore, we predicted that population genetic structure

in mtDNA would contrast with nuclear DNA of Black-legged Kittiwakes because of restrictions in contemporary gene flow.

Because genetic variation may allow species to adapt to changing environmental conditions, estimates of genetic structure and differentiation may have conservation implications (Allendorf *et al.* 2013). If populations differ genetically, then loss of a population may result in loss of overall genetic variation. Therefore, genetic differences should be considered in the assessment of management units. Genetic information guiding management of kittiwakes is pertinent because rapid and sustained declines in population sizes of Black-legged Kittiwakes in the Atlantic have resulted in the species being listed as vulnerable by the International Union for the Conservation of Nature (BirdLife International 2017).

METHODS

DNA extraction and amplification

We extracted DNA from blood samples, muscle tissue, or pin feathers from 398 Black-legged Kittiwakes from 20 colonies (Fig. 1, Table 1) using standard protease-k, phenol-chloroform protocols (Friesen *et al.* 1997). Although samples from Duck Island, Kachemak Bay, and Chisik Island are geographically close to each other, they were analyzed separately to reveal any fine-scale structure.

We assayed variation in the 5' and 3' ends of the mtDNA control region in two nonoverlapping fragments following Patirana *et al.* (2002), using the primers RbL20 and RtH400 (Domains I and II), and RtL500mt and RtH900 (Domains II and III). We discarded sequences with more than three ambiguous sites from downstream analyses. We then collated sequences from the two fragments for each bird. We quantified genetic variability using gene diversity (H_s ; Nei 1987) and nucleotide diversity (π ; Nei & Tajima 1983) in Arlequin (3.5.22; Schneider *et al.* 2000).

We calculated Tajima's D (Tajima 1989) and Fu's F_s (1997) using Arlequin (Excoffier *et al.* 2007) to test whether sequence variation deviated significantly from the assumption of a neutral model of evolution. Tajima's D is expected to be negative under a model of population expansion or under a selective sweep and positive under rate heterogeneity or diversifying selection (Tajima 1989). Fu's F_s is more sensitive to population expansion than Tajima's D , and is expected to be negative following a population expansion or selective sweep; positive values might indicate a population bottleneck (Fu 1997).

Tests of population differentiation

We conducted the analyses described below in Arlequin unless otherwise noted. We used an analysis of molecular variation (AMOVA) to calculate ϕ_{st} statistics (Excoffier *et al.* 1992) and to deduce the statistical significance of geographic variation in mitochondrial haplotypes. We ran these analyses using Kimura two-parameter distances with the alpha (α) parameter of the gamma distribution set to 0.42 (Marshall & Baker 1997). We tested the significance of ϕ_{st} estimates by comparison to values generated from 10 000 random permutations of sequences among populations.

To test for restrictions in gene flow due to distance (Wright 1943), we performed Mantel's tests using the R package "ecodist" (Goslee & Urban 2007) within each ocean basin to determine whether a

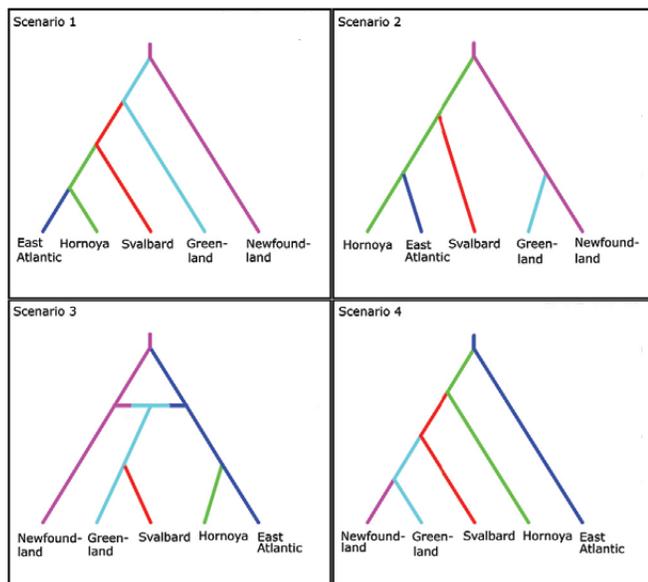


Fig. 2. Population history scenarios tested in DIYABC. Scenarios include a refugial Newfoundland population that successively spread East (Scenario 1), Eastern and Western refugial populations that successively spread to form the Atlantic colonies (Scenario 2), Eastern and Western populations that experienced an admixture event that led to the Svalbard and Greenland populations (Scenario 3), and a refugial European population that successively spread West (Scenario 4).

positive correlation existed between Slatkin's linearized ϕ_{st} and log-transformed geographic distance.

Population history

We used DIYABC (2.1.0) to test for genetic support for alternative models of population history within the Atlantic population (Cornuet *et al.* 2014). We did not conduct DIYABC analyses for the Pacific because there were no biologically significant population genetic groupings in the Pacific. Populations were clustered based on pairwise ϕ_{st} values. Because the Kola Peninsula, Brittany, Isle of May, and Shetland colonies had significant pairwise ϕ_{st} with all other colonies in the Atlantic except each other (see Results), we combined these colonies into a single population ("East Atlantic"). We excluded the colony at Prince Leopold Island from the analysis due to small sample size. We tested four different population scenarios based on possible Pleistocene refugia in the Atlantic (Fig. 2): 1) an eastward expansion from a single western Atlantic glacial refugium; 2) allopatric divergence followed by expansion of eastern and western Atlantic populations into the Arctic; 3) allopatric divergence, with a gene flow event between eastern and western refugial populations giving rise to the Greenland and Svalbard colonies; and 4) a westward expansion from a single eastern Atlantic glacial refugium.

We generated a reference table containing 1×10^7 simulated datasets for each scenario and used 0.1 % of the simulated datasets closest to the observed genetic dataset to estimate posterior probabilities for each scenario using a logistic approach. All genetic parameters available in DIYABC were simulated for each scenario and compared to the observed genetic parameters of the dataset (Supplementary Table S3, available on the website). To validate confidence in scenario choice, we calculated the posterior predictive error. The posterior predictive error is reported as the proportion of incorrectly identified scenarios out of 500 simulated datasets. Finally, we used a model-checking analysis to evaluate whether our posterior model fit the data.

Phylogeographic structure

To infer the relationships among control region haplotypes and to estimate the divergence time between Atlantic and Pacific mitochondrial lineages, a gene tree was constructed using BEAUti (2.3.1) to import data, BEAST (2.3.1) to perform the analysis, TREEANNOTATOR (2.3.1) to produce a summary tree, TRACER (1.6) to examine trace file output, and FIGTREE (1.4.3) to generate gene tree figures (Heled & Drummond 2010, Bouckaert *et al.* 2014, Drummond & Bouckaert 2015). In BEAST, a burn-in period of 10^5 iterations was used on a total of 10^8 Markov Chain Monte Carlo iterations. Sequence of the closely related Red-legged Kittiwake *Rissa brevirostris* mitochondrial control region was used to root the Black-legged Kittiwake sequences (Patirana *et al.* 2002). Nucleotide substitution models were determined by JMODEL test (Darriba *et al.* 2012), and a strict molecular clock was used. A constant coalescence prior was applied to the gene tree. Convergence of the MCMC process was monitored using TRACER (Version 1.6; Drummond & Rambaut 2007), and we ensured effective sample sizes (ESSs) were all higher than 200. Additionally, a haplotype network was constructed using statistical parsimony (Clement *et al.* 2002) in PopArt (<http://popart.otago.ac.nz>).

Maximum and minimum divergence times (t) were calculated using δ/r , where δ is the average of all pairwise δ_s between Atlantic and

Pacific colonies (or between clades within the Atlantic or Pacific) and r is the sequence divergence rate for the control region in years (Wilson *et al.* 1985). The divergence rate is not known for the mitochondrial control region of kittiwakes. Quinn (1992) estimated a divergence rate of 20.6 % per million years (Ma) for the hypervariable Domain I of geese, and Wenink *et al.* (1996) determined an overall divergence rate of 14.8 %/Ma for Domains I and II of the Dunlin *Calidris alpina*. Similarly, Vigilant *et al.* (1991) estimated the mean divergence rate for the entire human mitochondrial control region to be between 11.5 %/Ma and 17.3 %/Ma. Thus, we applied conservative maximum and minimum divergence rates of 11.5 %/Ma and 5 %/Ma for the entire control region.

RESULTS

Characterization of control region variation

Analysis of 756 base pairs (bp) of the mitochondrial control region identified 134 haplotypes and 102 variable sites among 398 Black-legged Kittiwakes. One Atlantic kittiwake from Hakluyt, Greenland possessed a haplotype (U2K) that otherwise occurred only among Pacific kittiwakes. Apart from this bird, no other haplotypes were shared among individuals from different ocean basins. Otherwise, 38 haplotypes (defined by 46 variable positions) were found among the 189 Atlantic samples. Among the Atlantic haplotypes, 44 polymorphic sites were found in Domain I (335 bp), with no variable sites in Domain II (100 bp), and two variable sites in Domain III (321 bp). Thirty-nine transitions and 10 transversions were evident, with three insertion/deletions (indels). The number of substitutions between haplotypes varied from one to 26, corresponding to Kimura two-parameter distances of 0.13 % to 3.5 %. The mean pairwise sequence divergence between Atlantic haplotypes was 0.66 % (five substitutions). Each sampling site had either one or two common haplotypes, and two (Greenland) to seven (Newfoundland) private haplotypes, at low frequency. For example, the most common haplotypes within the Northeast Atlantic were BF and EE, which were shared among 16 % and 11 %, respectively, of the 189 individuals. Haplotypes B4F and G2F were unique to Hornøya, where they were found among 36 % and 23 % of individuals, respectively, at that colony. In Svalbard, 62 % of individuals shared haplotype F2F, which was also present in Greenland at a much lower frequency (20 %). Similarly, 51 % individuals in Newfoundland shared haplotype A6F, while 15 % of individuals shared A6F in the Kola Peninsula. Several haplotypes were shared among populations (e.g., K2F, K3F, AF, F1F) but occurred in only one or two birds at each colony.

Of the 134 haplotypes, 96 (defined by 86 variable positions) were identified exclusively among the 209 Pacific kittiwakes (Supplementary Table S2, available on the website). Among Pacific haplotypes, 73 polymorphic sites were in Domain I (335 bp), three were in Domain II (100 bp), and 10 were in Domain III (321 bp). Among these haplotypes, 74 transitions, 10 transversions, and 10 indels were evident. The mean pairwise sequence divergence between Pacific haplotypes was 1.06 % (eight substitutions). Haplotypes differed by one to 23 substitutions, corresponding to Kimura two-parameter distances of 0.13 % to 3.0 %, respectively. The most common Pacific haplotype (U2K) was shared among 14 % of the 203 individuals and was found across all sampling sites except for Kachemak Bay and Duck Island (Supplementary Table S2). The second most common haplotype (UK) was found in 7.6 % of the individuals and was restricted to Gulf of Alaska

samples. All other haplotypes were unique to one or two populations and occurred in only one or two individuals.

The Pacific had higher haplotype diversity than the Atlantic ($F = 18.85$, $P < 0.001$), ranging from 0.86 to 0.91 in the Pacific and 0.61 to 0.87 in the Atlantic (Table 1). Nucleotide diversities were also higher in Pacific colonies compared to Atlantic colonies, ranging from 0.005–0.015 in the Pacific and 0.003–0.009 in the Atlantic ($F = 30.52$, $P < 0.0001$).

Tajima's D was negative but non-significant for both the Atlantic ($D = -1.1$, $P = 0.12$) and Pacific ($D = 1.3$, $P = 0.06$), while Fu's F_s was negative and significant for both the Atlantic ($F_s = -14.5$, $P = 0.002$) and Pacific ($F_s = -24.5$, $P < 0.0001$) samples. Tajima's D and Fu's F_s were mostly negative but not statistically different from zero for any Atlantic colony (Table 1). In Pacific colonies, Tajima's D was negative and significant at the Barren Islands, and Fu's F_s was negative and significant at Cape Lisburne, Koniuji Island, and St. George Island (Table 1).

Test of population differentiation

AMOVA indicated significant population genetic structure within Black-legged Kittiwakes (global $\phi_{st} = 0.53$; $P < 0.00001$). Significant genetic structuring was found among both Atlantic ($\phi_{st} = 0.23$; $P < 0.0001$) and Pacific ($\phi_{st} = 0.06$; $P < 0.0001$) colonies. Mantel's tests did not detect significant associations between log geographic distance and Slatkin's linearized ϕ_{st} within either the Atlantic (Mantel $r = 0.25$, $P = 0.24$) or Pacific (Mantel $r = -0.14$, $P = 0.34$) colonies.

Population history

DIYABC identified Scenario 3 (historical isolation of eastern and western Atlantic colonies followed by admixture; Fig. 2) as the most likely historical scenario in the Atlantic (Posterior Probability = 0.9; 95 % Confidence Interval = [0.78–1.0]). Scenario 2 (historical isolation of eastern and western Atlantic colonies without admixture) was the next most likely tested scenario (Posterior Probability = 0.2; 95 % Confidence Interval = [0.06–0.30]). Model checking indicated that observed summary statistics for Scenario 3 were not significantly different from statistics simulated from the DIYABC model ($P < 0.01$; Supplementary Table 3).

Phylogeographic structure

The gene tree for Atlantic and Pacific haplotypes (Fig. 3.) shows six strongly supported monophyletic clades. Within each clade, relationships were poorly resolved; no nodes had greater than 75 % posterior probability. Kittiwakes from the Atlantic comprised four haplotype groups, whereas Kittiwakes from the Pacific comprised two haplotype groups. The statistical parsimony network clearly separated haplotypes from the Atlantic and Pacific Ocean basins. However, the gene tree and haplotype network provide little evidence for strong phylogeographic clustering within ocean basins. Assuming divergence rates of 11.5 %/Ma and 5 %/Ma, respectively, between the Atlantic and Pacific Ocean basins, corrected pairwise sequence divergence ($\delta = 3.2$ %; Fig. 3) between the two ocean basins suggests that their mtDNA lineages diverged 0.64 to 0.28 Ma years ago. Corrected pairwise sequence divergence indicated that major divergences occurred in both the Atlantic and Pacific around

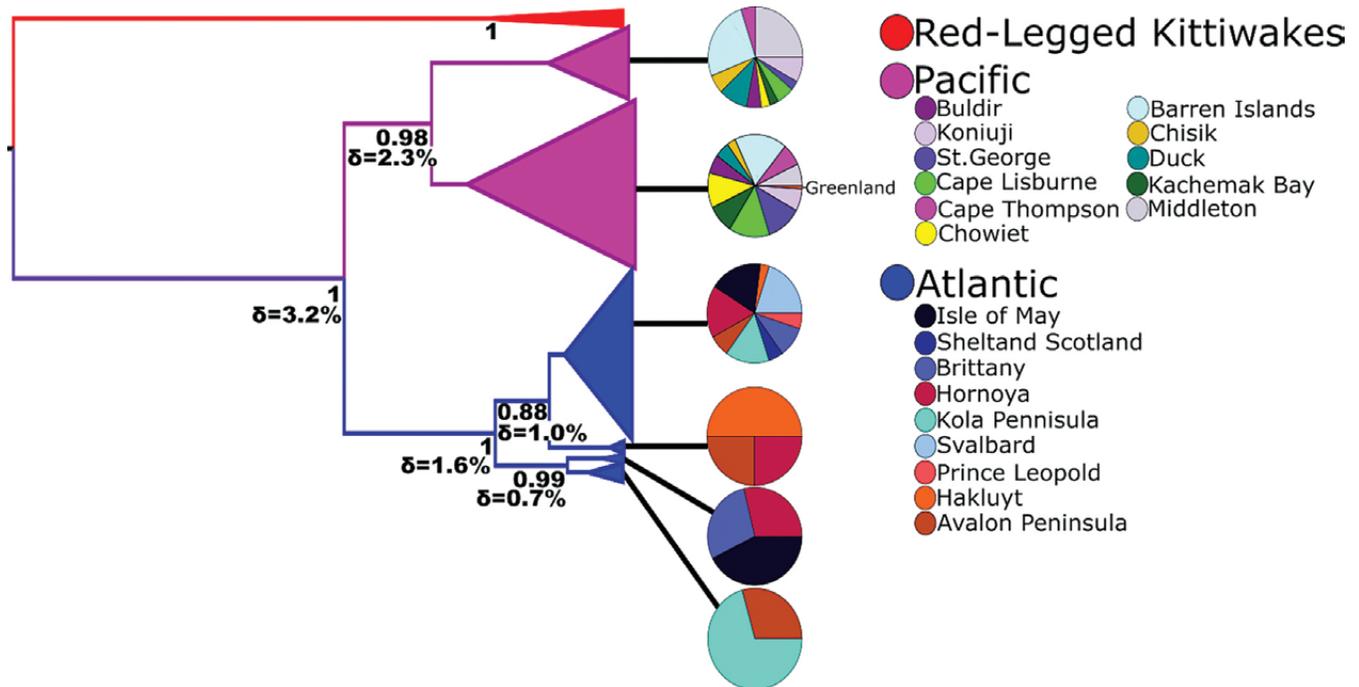


Fig. 3. Bayesian rooted gene tree of Black-legged Kittiwake mitochondrial control region sequences. The collapsed nodes represent the Red-legged Kittiwake outgroup (red), Atlantic (blue), and Pacific (purple) haplotypes. Posterior probabilities are displayed on nodes of the tree and divergence rates (δ) are displayed underneath posterior probabilities. Colony composition of each haplotype clade is displayed in pie graphs.

0.32 to 0.14 Ma ($\delta = 1.6\%$) and 0.46 to 0.20 Ma ($\delta = 2.3\%$), respectively (Fig. 3).

DISCUSSION

Differentiation between Atlantic and Pacific populations

Geographic variation in control region sequences, microsatellite markers (McCoy *et al.* 2005), and phylogenetic relationships among mtDNA haplotypes (Figs. 3, 4) provided evidence for genetic differentiation between Atlantic and Pacific kittiwake subspecies. Other than one common Pacific haplotype that was found in one Atlantic kittiwake, haplotypes of Atlantic and Pacific kittiwakes formed strongly supported reciprocally monophyletic groups separated by at least eight substitutions. An estimated divergence time of 0.64 to 0.28 Ma correlates with the isolation of Atlantic and Pacific oceans by the Bering Landbridge and Pleistocene glaciers (Kürten & Anderson 1980). Subdivision by Pleistocene glaciers, the Bering Landbridge, or both, is thought to have contributed to population differentiation and speciation in several other arctic and north temperate seabirds (Friesen *et al.* 2007, Morris-Pocock *et al.* 2008; Friesen 2015). Estimates of the divergence time of Atlantic and Pacific mtDNA lineages of kittiwakes in our study are very similar to those found between Atlantic and Pacific Common Murres (Morris-Pocock *et al.* 2008). The similar divergence timing

of the Common Murres and Black-legged Kittiwakes could indicate that similar glacial processes drove genetic divergence in these largely co-distributed seabird species.

Population structure of Atlantic kittiwake colonies

Results from AMOVA indicate that significant genetic differences exist among kittiwakes from different Atlantic colonies (Table 2). Furthermore, some Atlantic colonies were characterized by population-specific haplotypes that were found in a substantial proportion of individuals. Kittiwakes from Isle of May, Brittany, Shetland, and the Kola Peninsula appear to be genetically similar to each other, whereas kittiwakes from all other colonies are genetically different. The genetic similarity of European colonies and the Kola Peninsula is surprising given the distance between the Kola Peninsula colony and the sampled European colonies. Overlapping non-breeding distributions or foraging distributions are sometimes a predictor of genetic divergence (Friesen 2015). Geolocation data from Atlantic kittiwakes indicate that some Russian birds may have overlapping winter distributions with British colonies in the North and Labrador seas (Frederiksen *et al.* 2012). However, many Atlantic colonies in our study have overlapping non-breeding distributions, indicating that wintering distributions are not necessarily good predictors of mtDNA structure (Frederiksen *et al.* 2012).

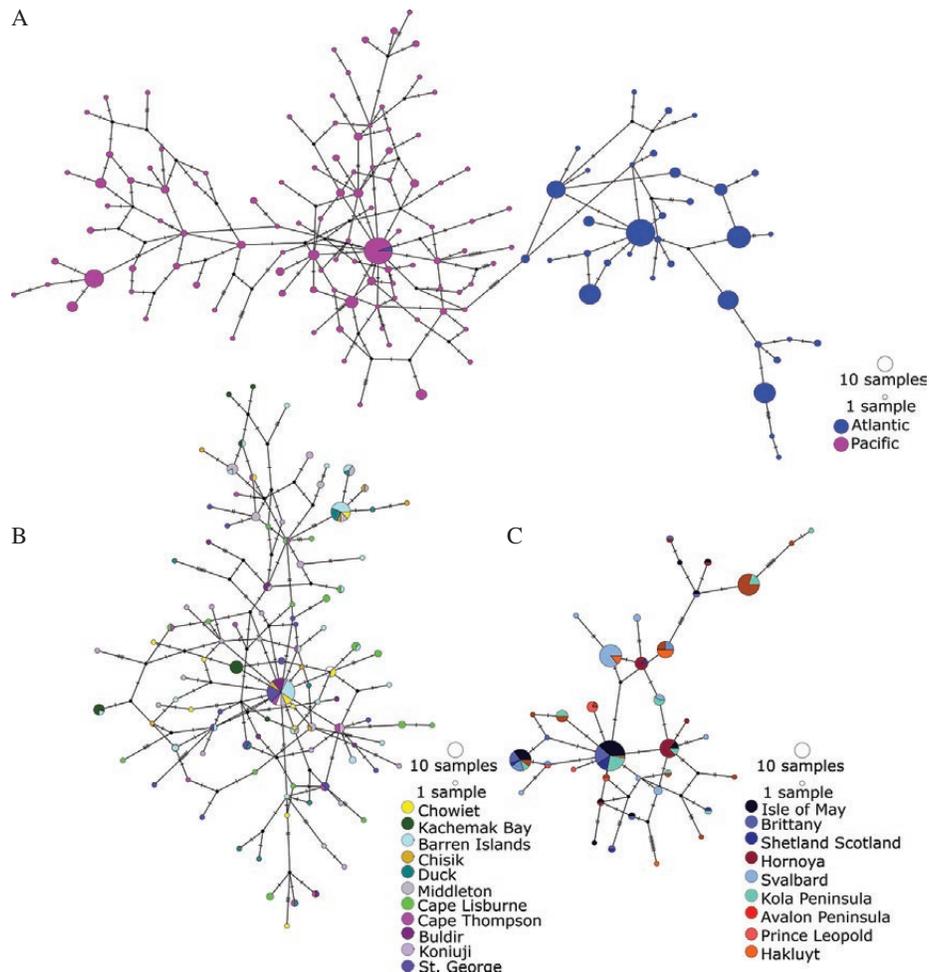


Fig. 4. TCS haplotype network of A) the global, B) Atlantic, and C) Pacific haplotypes. Colours represent different sampled colonies.

Population genetic structure could also be explained by philopatry (Coulson 2016), a behaviour that would reduce gene flow among colonies. Philopatry alone putatively led to population genetic structure in several seabird species, including Stewart Island shags *Leucocarbo chalconotus* (Rawlence *et al.* 2014), Brant Goose *Branta bernicula* (Shields 1990), Fairy Prions *Pachyptila turtur* (Ovenden *et al.* 1991), and Red-legged Kittiwakes (Patirana *et al.* 2002; reviewed in Friesen *et al.* 2007; Friesen 2015). Importantly, mtDNA is maternally inherited, but in Black-legged Kittiwakes females are less philopatric than males. Sex-biased dispersal of female kittiwakes may reduce the speed at which mtDNA markers sort among colonies.

Significant genetic structure may also arise through isolation by distance, wherein gene flow among populations decreases with increasing geographic distance, resulting in greater genetic difference with distance (Wright 1943). Mantel’s test for a correlation between ϕ_{st} and distance among Atlantic colonies was not significant; thus, there is either an n-island (random) model of dispersal, or mitochondrial DNA is not yet in migration-drift equilibrium (Hutchison & Templeton 1999). Genetic differentiation metrics assume that the diversifying effects of genetic drift and the

homogenizing effects of gene flow are at equilibrium; violation of this assumption means that differentiation metrics are not representative of contemporary processes. Evidence of recent population expansions provided by negative Fu’s F_s statistics and DIYABC results suggest that populations in the Atlantic are not in migration-drift equilibrium. Tajima’s D values agreed with Fu’s F_s in direction but not significance. Simulations of both test statistics indicate that Fu’s F_s is more sensitive to population expansion (Fu 1997). Therefore, the observed geographic pattern of genetic variation could be caused by a combination of contemporary and historical processes.

Population structure of Pacific kittiwake colonies

In contrast to Atlantic colonies, little evidence of population genetic structure was found within the Pacific Ocean. Haplotypes did not cluster by site on the gene tree (Fig. 3.), and few pairwise estimates of ϕ_{st} were significant (Table 3). The weak population structure in Pacific kittiwakes is similar to some other species in this region. For example, Shields & Wilson (1987) found little differentiation in mtDNA among populations of Canada Geese *Branta canadensis* in the Aleutian Islands, and Pacific Common Murres have little genetic

TABLE 2
Pairwise ϕ_{st} values between Atlantic kittiwake colonies^a

| | Kola Peninsula | Hornøya | Svalbard | Shetland | Isle of May | Brittany | Hakluyt | Prince Leopold |
|-------------------------|----------------|-------------|-------------|-------------|-------------|-------------|-------------|----------------|
| Hornøya | 0.10 | | | | | | | |
| Svalbard | 0.22 | 0.19 | | | | | | |
| Shetland | 0.02 | 0.15 | 0.29 | | | | | |
| Isle of May | 0.02 | 0.15 | 0.32 | 0.0 | | | | |
| Brittany | 0.02 | 0.14 | 0.29 | -0.03 | -0.04 | | | |
| Hakluyt | 0.16 | 0.18 | 0.18 | 0.25 | 0.26 | 0.21 | | |
| Prince Leopold | 0.09 | 0.22 | 0.40 | 0.10 | 0.11 | 0.09 | 0.34 | |
| Avalon Peninsula | 0.18 | 0.33 | 0.41 | 0.32 | 0.31 | 0.27 | 0.26 | 0.35 |

^a Comparisons that were significant after a Benjamini-Yekutieli correction with an alpha of 0.05 are in bold.

TABLE 3
Pairwise ϕ_{st} values between Pacific kittiwake colonies^a

| | Buldir | Koniuji | St. George | Cape Lisb. | Cape Thomp. | Chowiet | Chisik | Barren Islands | Duck | Kachemak Bay |
|-----------------------|--------|-------------|-------------|-------------|-------------|-------------|--------|----------------|-------------|--------------|
| Koniuji | 0.00 | | | | | | | | | |
| St. George | 0.01 | 0.03 | | | | | | | | |
| Cape Lisb. | -0.02 | 0.01 | 0.0 | | | | | | | |
| Cape Thomp. | -0.02 | -0.02 | -0.02 | -0.02 | | | | | | |
| Chowiet | -0.01 | 0.00 | 0.0 | -0.01 | -0.02 | | | | | |
| Chisik | 0.03 | 0.02 | 0.07 | 0.06 | 0.03 | 0.0 | | | | |
| Barren Islands | 0.01 | 0.02 | 0.03 | 0.04 | 0.00 | 0.00 | -0.03 | | | |
| Duck | 0.12 | 0.12 | 0.18 | 0.14 | 0.11 | 0.10 | -0.01 | 0.07 | | |
| Kachemak Bay | 0.06 | 0.09 | 0.03 | 0.05 | 0.06 | 0.04 | 0.09 | 0.06 | 0.18 | |
| Middleton | 0.11 | 0.07 | 0.16 | 0.14 | 0.09 | 0.20 | -0.02 | 0.07 | 0.03 | 0.20 |

^a Comparisons that were significant after a Benjamini-Yekutieli correction with an alpha of 0.05 are in bold.

structuring in the mitochondrial control region (Morris-Pocock *et al.* 2008). In contrast, other seabird species in this region, such as Marbled Murrelets *Brachyramphus marmoratus* (Congdon *et al.* 2000), Pigeon Guillemots (Kidd & Friesen 1998, Poland *et al.* unpubl. data), and Kittlitz's Murrelets *Brachyramphus brevirostris* (Birt *et al.* 2011), show significant structuring in mtDNA (reviewed in Friesen *et al.* 2007, Friesen 2015).

Overlapping non-breeding distributions between Black-legged Kittiwakes in the Bering Sea and Gulf of Alaska might explain some of the lack of genetic structure found in the Pacific. Tracking data from two colonies in the Bering Sea (St. George & St. Paul) indicate a broad non-breeding distribution of Black-legged Kittiwakes in the Northern Pacific (Orben *et al.* 2015a, 2015b), which potentially overlaps with some individuals from colonies in the Gulf of Alaska (Shoup Bay & Passage Canal; McKnight *et al.* 2011). If the tracking results from these studies are generalizable to other colonies in the Bering Sea and Gulf of Alaska, there may be substantial overlap of non-breeding distributions.

Evolutionary histories of Atlantic versus Pacific kittiwakes

The low genetic structure in the Pacific compared to the Atlantic may be due to differences between ocean basins in refugial histories. We found evidence that clade divergences are more recent in the Atlantic compared to the Pacific, and that contemporary Atlantic populations are derived from the expansions of two refugial populations (Fig. 3). In contrast, our gene tree suggests that Pacific clades may be older and have, therefore, had more time for admixture to occur. Differentiation caused by this separation may have been erased by admixture. Alternatively, the genetic structure could be hidden from our current analysis because of the lack of samples derived from Western Pacific and Siberian populations.

Within both the Atlantic and Pacific, both the gene trees and haplotype networks were characterized by incomplete lineage sorting between colonies (Fig. 4). All lineage divergences within each ocean were estimated to have occurred during the Pleistocene, with the most ancient divergence in the Pacific occurring 0.46 to 0.20 Ma and the most ancient Atlantic divergence occurring 0.32 to 0.14 Ma years ago. During the late Pleistocene, five major and two minor glaciations occurred (Head *et al.* 2008). Much of the present breeding range of kittiwakes was covered by glaciers until about 10 000 years ago (Pielou 1991). Thus, glaciations would have forced kittiwakes into one or more southerly refugia. The most supported scenario from DIYABC involved historical isolation of eastern and western Atlantic populations, followed by admixture and divergence of the admixed population into the Svalbard and Greenland colonies as the eastern Atlantic populations diverged into the British and Hornøya colonies (Fig. 2; Scenario 3). This scenario corresponds to two glacial refugia in the Atlantic Ocean. Geological and palaeoclimatic evidence suggests that the coasts of Newfoundland, the Gaspé Peninsula, and Grand Banks remained unglaciated in the late Pleistocene (Pielou 1991), providing one possible refugium. Like other Atlantic taxa (e.g., Common Murres; Morris-Pocock *et al.* 2008), Black-legged Kittiwakes may have had a second, southeastern refugium, possibly off Iberia (Hewitt 2000).

Comparison of nuclear versus mitochondrial variation

Nuclear markers suggest that little genetic structure exists among the Atlantic black-legged kittiwakes (McCoy *et al.* 2005), which

contrasts with the strong geographic structure in mtDNA. Greater structure in mtDNA compared to nuclear DNA is common. Assuming a constant mutation rate, mtDNA variation is expected to sort four times faster than nuclear DNA (Birky *et al.* 1989). However, comparing microsatellite markers to mtDNA is difficult because mutation rates are not equivalent. High mutation rates in microsatellite loci could drive fast sorting, while homoplasy might result in decreased genetic structure. The high mutation rate of microsatellites results in a low magnitude of differentiation statistics (Birky *et al.* 1989, Hedrick 1999).

Geographic variation in morphology among Atlantic colonies

Because geographic variation in plumage and morphometrics was previously described for Atlantic kittiwakes (Sluys 1982, Chardine 2002), we expected to find geographically ordered mtDNA variation and restricted gene flow between colonies. Despite only two phenotypic groupings of Atlantic populations (one in Arctic Canada and West Greenland, and one in Newfoundland, United Kingdom, and Barents Sea; Chardine *et al.* 2002), we observed extensive genetic structure in mtDNA. Therefore, although geographic patterns of variation in morphology and mtDNA exhibit some similarities, cryptic genetic variation exists that does not match patterns of morphology among Atlantic kittiwake colonies.

Taxonomy and conservation

Despite earlier skepticism of subspecies designations due to considerable phenotypic overlap (Vaurie 1965, Sluys 1982), mtDNA data correlate with differences in morphology and microsatellite variation between kittiwakes from the two oceans (McCoy *et al.* 2005, Cramp & Simmons, 1983). Original subspecies designations of Atlantic and Pacific Black-legged Kittiwakes are therefore supported by mtDNA, nuclear DNA, and morphological data. For conservation and management, the Atlantic and Pacific subspecies should be considered evolutionarily significant units. Further, mtDNA results indicate that Atlantic colonies should be managed as separate management units. Genetic structuring of these colonies indicates that loss of one colony may result in an overall loss of genetic diversity.

CONCLUSIONS

Analyses of genetic variation in the mitochondrial control region in Black-legged Kittiwakes indicates that Atlantic and Pacific subspecies are highly differentiated and form monophyletic groups that are essentially reciprocal. Within the Atlantic, most colonies differ genetically. In contrast, Pacific colonies have weak genetic structure. This difference may be due to differences in the timing of major clade divergence between ocean basin populations. Genetic structure in the Atlantic could be partially attributed to historical fragmentation, and differentiation between subspecies may have arisen during a period of isolation during the mid to late Pleistocene. Future studies should assess the genome-wide genetic structure of colonies in the Pacific Ocean, and should increase sampling ranges to include more western Pacific and Arctic colonies to determine whether mtDNA and nuclear DNA are concordant. Future studies should also include more detailed analyses in the Pacific Ocean.

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SURVIVAL AND RECRUITMENT DYNAMICS OF BLACK-LEGGED KITTIWAKES *RISSA TRIDACTYLA* AT AN ALASKAN COLONY

ALY MCKNIGHT¹, ERIK J. BLOMBERG², DAVID B. IRONS³, CYNTHIA S. LOFTIN⁴, SHAWN T. MCKINNEY⁴

¹*School of Biodiversity Conservation, Unity College, Unity, ME 04988, USA (aly.mcknight@gmail.com)*

²*Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, Orono, ME 04469, USA*

³*US Fish and Wildlife Service, Migratory Bird Management Office, Anchorage, AK 99503, USA*

⁴*US Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, Orono, ME 04469, USA*

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ABSTRACT

MCKNIGHT, A., BLOMBERG, E.J., IRONS, D.B., LOFTIN, C.S. & MCKINNEY, S.T. 2019. Survival and recruitment dynamics of Black-legged Kittiwakes *Rissa tridactyla* at an Alaskan colony. *Marine Ornithology* 47: 209–222.

Most seabirds breed colonially and exhibit considerable site fidelity over the course of their long lifespans. Initial colony selection can therefore have substantial fitness consequences, but factors contributing to recruitment into colonies and subsequent fidelity remain unclear. We used multi-state capture-recapture models to test several hypotheses related to apparent fledgling survival, probability of recruitment to natal colonies, and apparent post-recruitment survival in Black-legged Kittiwakes *Rissa tridactyla*, using data from individuals banded as chicks and subsequently resighted at a colony in south-central Alaska over a 20-year period. Competitive models suggested that apparent fledgling survival declined throughout our study. This decline was likely driven by intrinsic, cohort-specific processes and was not explainable by post-fledging weather or climate conditions. Independent resightings at other colonies suggest the apparent decline may have been at least partially influenced by permanent emigration (natal dispersal), which occurred more frequently when the colony size was large. Recruitment was primarily age-dependent, with no detectable effects from early life experience or from annual changes in four factors: colony size, colony productivity, climate, or average weather conditions. We estimated an average recruitment age of seven years, which is older than typically reported for Atlantic kittiwake populations and which supports a more conservative life history strategy for kittiwakes in the Pacific. Variation in the apparent survival of recruits was cohort-specific and did not correlate with age or annual changes in the factors listed above. Instead, apparent survival of recruits was best explained by colony size during a cohort's second year, suggesting a degree of negative density dependence in post-recruitment survival or fidelity. This information could prove useful to managers deciding how to allocate resources among small, growing colonies and large, well-established colonies.

Key words: Black-legged Kittiwake, *Rissa tridactyla*, colonial breeding, survival, recruitment, capture-mark-recapture analysis, demographic modeling

INTRODUCTION

Colonial breeding is nearly ubiquitous among seabirds (Coulson 2002). The behavior may provide an informational advantage for birds foraging in a patchy and unpredictable environment (Clode 1993, Buckley 1997, but see Rolland *et al.* 1998), but any such advantage comes at a cost that may be proportional to the size of the colony. Dense colonies can attract seabird predators (Coulson 2002, but see Hernandez-Matias *et al.* 2003) that can substantially influence nest-site choice (Martin 1995, Eggers *et al.* 2006) and breeding success (e.g., Regehr & Montevecchi 1997, Whittham & Leonard 1999). Coloniality can also increase intraspecific competition (Tella *et al.* 2001), risk of ectoparasitism (Møller 1987, Mangin *et al.* 2003), and pathogen transmission (Clancy *et al.* 2006).

Patterns of colony recruitment and fidelity likely reflect life history strategies. The age of recruitment greatly influences lifetime reproductive success (Stearns 1992) but is subject to significant tradeoffs with future reproductive potential (e.g., Reed *et al.* 2008, but see Aubry *et al.* 2011). These tradeoffs may favor different strategies in populations under dissimilar constraints, leading to diverse recruitment patterns. Fitness tradeoffs may also determine fidelity to particular colonies or nest sites following recruitment;

there is some relationship between life expectancy and breeding site fidelity for some seabird taxa (Bried & Jouventin 2002). This relationship suggests that a longer lifespan is associated with a “stay and tolerate occasional costs” strategy, whereas a shorter lifespan is linked to greater variability in breeding site choices from year to year. Colony quality (i.e., the probability of reproductive success for a typical colony member) can be quite variable and may depend on factors such as local foraging-ground characteristics (e.g., Paredes *et al.* 2012, Renner *et al.* 2012) and the degree of inter-colony competition (Cairns 1989, Ainley *et al.* 2003, Grémillet *et al.* 2004); thus, breeding colony choice and subsequent fidelity represent high-stakes decisions for individual birds.

In turn, events occurring at colonies undoubtedly influence population dynamics. Nest-site availability at colonies may limit the number of breeders in a population (e.g., Porter & Coulson 1987). Further, species like the Red-legged Kittiwake *Rissa brevirostris* nest in only a few large colonies so that a single breeding site can contain most of the global breeding population (Byrd & Williams 1993). In these cases, colony success can drive larger population dynamics. Dispersal among colonies could also potentially influence regional population dynamics, both through direct effects on production as well as through alterations to genotype distribution and abundance patterns.

Intrinsic processes clearly play a regulatory role within seabird colonies. Density-dependent relationships between colony size and reproductive success are well-documented (e.g., Hunt *et al.* 1986). Such relationships stem at least partially from localized prey depletion (e.g., Lewis *et al.* 2001, Forero *et al.* 2002), which forces birds nesting in large colonies to forage farther from the colony (Ainley *et al.* 2003, Grémillet *et al.* 2004), presumably at greater cost. Density dependence can also influence recruitment (e.g., Crespin *et al.* 2006). The role of density dependence in breeding site fidelity patterns, however, remains somewhat more enigmatic. In Black-legged Kittiwakes *Rissa tridactyla* (“kittiwake” hereafter), breeding patch success (i.e., success within distinct colony subsections) rather than breeder density is the dominant consideration in movement decisions (Danchin *et al.* 1998). Although new, small colonies can be more productive than large, established colonies, birds may be reluctant to form new colonies (Kildaw *et al.* 2005), suggesting that there are hidden costs

associated with new colony formation or that strong fidelity may sometimes represent an evolutionary trap. We know even less about how extrinsic processes shape colony dynamics, though seabird recruitment patterns have been tied to climate patterns (Crespin *et al.* 2006) and predator density (Finney *et al.* 2003)

Our goal here was to explore return and recruitment dynamics of seabird colonies. We focused on three questions: (1) What factors contribute to the return of fledglings to their natal colony? (2) What influences fledgling recruitment to these colonies? (3) Once recruited, what factors contribute to their continued return? We approached these questions with a suite of specific hypotheses related to apparent fledgling survival, recruitment, and apparent recruit survival of kittiwakes at a south-central Alaskan colony (Table 1). We tested these hypotheses with multi-state capture-mark-recapture (CMR) modeling. Our objectives were to determine whether intrinsic or extrinsic processes drive these vital rates and

TABLE 1

Hypotheses explaining apparent fledgling survival, recruitment, and post-recruitment fidelity in Black-legged Kittiwakes from the Shoup Bay colony in Prince William Sound, Alaska, USA, along with variables and their sources used in multi-state capture-recapture models representing each hypothesis

| Hypotheses and variables | Source |
|---|---|
| Vital rate is a function of cohort-specific factors. | |
| <i>Carryover effects (fledging survival only)</i> | |
| Herring spawn activity within colony foraging range during: (1) hatch year, (2) previous breeding season (parental effect) | Moffitt 2016; see McKnight (2017) for details |
| Modeled age-1 herring abundance in PWS region during: (1) hatch year, (2) previous breeding season (parental effect) | HRMT 2014 |
| <i>Early life experience</i> | |
| Colony size in cohort’s hatch year | US FWS monitoring data, unpubl. data |
| Colony productivity in cohort’s hatch year | US FWS monitoring data, unpubl. data |
| Post-fledging environmental conditions | |
| Mean first winter* PDO index values | JISAO 2016 |
| Mean first winter ENSO 3.4 index values | ESRL 2016a |
| Mean monthly modeled first fall**, winter, and spring*** winds in northern Gulf of Alaska (58°N, 147°W) | ESRL 2016b |
| Mean monthly first winter SST in northern GOA (58°N, 147°W) | ESRL 2016c |
| <i>Prospecting experience</i> | |
| Natal colony size at cohort ages 2 or 3 | US FWS monitoring data, unpubl. data |
| Natal colony productivity at cohort ages 2 or 3 | US FWS monitoring data, unpubl. data |
| Vital rate is a function of time-varying factors. | |
| Natal colony size in current, previous year | US FWS monitoring data, unpubl. data |
| Natal colony productivity in previous year | US FWS monitoring data, unpubl. data |
| Environmental conditions in current, previous year (listed above) | JISAO 2016, University of Washington unpubl. data |
| Vital rate is a function of age (recruitment and post-recruitment fidelity only). | US FWS monitoring data, unpubl. data |
| Vital rate is constant. | |

* Averaged monthly data from November through February prior to the breeding season

** Averaged monthly data from September and October

*** Averaged monthly data from March through April prior to the breeding season

to evaluate evidence for a more conservative life history strategy in Pacific vs. Atlantic kittiwakes, as has been suggested by other authors (Hatch *et al.* 1993, Golet *et al.* 2004).

METHODS

Ethics statement

Seabird monitoring activities in 2008 were conducted under US Fish and Wildlife Service Region 7 IACUC #2008007.

Focal species

The kittiwake provides an ideal case study to investigate questions regarding natal colony recruitment and fidelity. As such, it has been the focus of numerous studies on breeding habitat selection in marine birds (e.g., Cadiou 1999, Ainley *et al.* 2003, Kildaw *et al.* 2005, Coulson & Coulson 2008). The kittiwake is a small, long-lived, piscivorous gull with a northern circumpolar distribution and a global population size of 17–18 million (Delany & Scott 2006). Kittiwakes are colonial cliff-nesters that rear one, two, or (rarely) three young per breeding season. As in many seabird species, parents share incubation and chick-rearing duties equally (Coulson & Wooller 1984). When breeding patches are successful, both mate (Coulson & Thomas 1985) and nest-site fidelity are high (Danchin *et al.* 1998, Boulinier *et al.* 2008); this facilitates long-term CMR studies. Kittiwake numbers within our study region of Prince William Sound (PWS) fluctuate dramatically: the breeding-season population size ranged from 28 000 to 110 000 from 1989 to 2007 (McKnight *et al.* 2008). Colony occupancy and productivity in PWS are also dynamic—more than 40 colonies were monitored from 1985 to 2012 and during this period, 14 new colonies were initiated while 16 colonies were abandoned (DBI unpubl. data).

Study area

The Shoup Bay kittiwake colony is in northeastern PWS, Alaska (61°10'N, 146°35'W; Fig. 1). Shoup Bay is a small fjord that adjoins the larger Port Valdez fjord with a tidewater glacier that terminates at Shoup Bay's western end. The fjord connects to Port Valdez via

a reversing tidal river that is 0.8 km in length. The kittiwake colony is located primarily on the south-facing side of a rocky island that is 0.4 km in length and 100 m from the mainland. The colony formed sometime after the island emerged from the receding Shoup glacier, which still covered the nesting cliffs in the early 1960s; the colony was well-established by the 1980s and peaked at ~20 000 individual breeders in the early 2000s. Through the early 2000s, the fjord was frequently filled with large icebergs that had calved from the glacier; by the late 2000s, the glacier retreated mostly onto land. Predators at the colony are predominantly avian and include Bald Eagles *Haliaeetus leucocephalus*, Peregrine Falcons *Falco peregrinus*, Northern Ravens *Corvus corax*, Northwestern Crows *Corvus caurinus*, and Black-billed Magpies *Pica hudsonia*. Occasional mammalian predators include American mink *Neovison vison* and wolverine *Gulo gulo*.

Field data collection

Capture/resight sampling

In 1979 and annually from 1988 to 2008, we banded 369 ± 74 (95 % confidence interval (CI)) 12- to 32-day-old kittiwake chicks at the Shoup Bay colony by temporarily removing them from nests by hand. We individually marked chicks with unique color band combinations. From 1992 to 2010, four to eight observers read color bands using binoculars and 60× spotting scopes (hereafter referred to as resighting) during mornings and evenings in May, when breeders were actively building nests. Major breeding patches ($n = 10$) were delineated by cliff features, and birds were resighted within each patch an average of 9.8 ± 0.35 (95 % CI) times within each nesting season.

We evaluated individual breeding status based on the number of times a bird was recorded at a specific nest location. Holding a nest site is the essential condition that affects kittiwake survival, irrespective of reproductive success (Aubry *et al.* 2011), and thus provides a reasonable representation of breeding intent in our survival models. Birds seen at a particular nest site three or more times were considered to be probable breeders ("breeders" hereafter). Birds seen fewer than three times on a single site were noted as probable non-breeders ("non-breeders" hereafter), i.e., they were present but not engaged in intensive nesting behavior. While predation was substantial during some years, the majority of predation affected nestlings and occurred after the period during which we resighted marked individuals at the colony; thus, predation did not appreciably influence breeding status assignments by removing banded breeders prior to their third sighting.

We constructed encounter histories for each individual based on annually summarized encounters and breeding state designations. Each year represented a single occasion in which the individual either was or was not encountered. If encountered, breeding state was designated in the encounter history according to the description above.

Breeding population size and productivity

We included metrics describing colony size and productivity in our modeling to assess the role of intrinsic colony processes in determining vital rate patterns. From 1985 to 2012, we visited the Shoup Bay kittiwake colony twice annually as part of a larger effort to document breeding effort and productivity at all PWS kittiwake colonies. In late May/early June, when birds had begun incubation, we used binoculars to count all active nests (i.e., those attended by

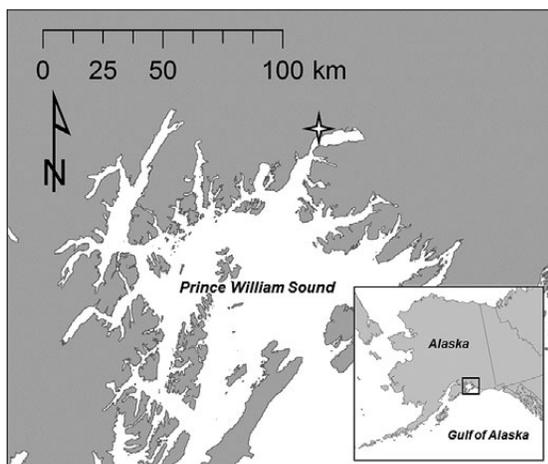


Fig. 1. Location (indicated by star) of the Shoup Bay kittiwake colony in Prince William Sound, Alaska, USA. Inset map shows the location of Prince William Sound within Alaska.

at least one bird) on all faces of the colony from an eight-meter fiberglass boat floating 100–200 m from the cliff faces. We returned in late July/early August each year and used the same method to count chicks and fledglings at a stage of development when most chicks were large enough to be easily visible in the nests. We also included several measures of prey availability: herring spawn activity within foraging range (40 km) of the colony (Moffitt 2016; see McKnight 2017 for details) and modeled age-1 herring abundance for the PWS region (HRMT 2014).

Environmental variables

In addition to the metrics described above for breeding kittiwakes, we also considered extrinsic factors that might affect kittiwake survival and recruitment. We suspected that winter conditions were important, although given the Shoup Bay kittiwakes' diverse migratory strategies, choosing a single metric to represent winter posed a challenge. Because kittiwakes migrate in some years but remain in the northern Gulf of Alaska in others (McKnight *et al.* 2011), we hypothesized that birds may face a tradeoff between costs associated with migration and constraints associated with reduced winter day lengths in the high latitudes. Migratory decisions may therefore be made based on local conditions affecting forage efficiency—specifically, wind and sea surface temperature (SST). We therefore used several metrics to represent both winter and spring weather conditions on the northern coastal shelf of the Gulf of Alaska. First, we calculated the mean winter (November–February) Pacific Decadal Oscillation (PDO) index, which is based on the first principal component of monthly SST anomalies in the North Pacific (i.e., north of 20°N) (JISAO 2016). We similarly computed the mean winter El Niño Southern Oscillation (ENSO) index based on a five-month running mean of SST anomalies in the region between 05°N and 05°S and between 170°W and 120°W (ESRL 2016a). Both the PDO and ENSO indices are known to correlate with winter weather patterns in Alaska (Papineau 2001). For an index of fall (September–October), winter (November–February), and spring (March–April) weather conditions on the northern coastal shelf of the Gulf of Alaska, we extracted the monthly modeled wind magnitudes for 59°N, 147°W (ESRL 2016b) and used the average value for each period. We also averaged monthly SSTs for the same region of the Gulf of Alaska from the National Oceanic and Atmospheric Administration's optimally interpolated SST data (ESRL 2016c). We used Z-standardization to center and scale all continuous time- and cohort-varying covariates prior to modeling.

Data analysis

Multi-state modeling

We used multi-state Cormack-Jolly-Seber models (Nichols & Kendall 1995) to test hypotheses about factors governing apparent survival of fledglings, recruitment, and apparent survival of recruits (Table 1) in a kittiwake population. Multi-state modeling allowed us to simultaneously estimate the resighting probability (p), the probability of transitioning between pre-defined states (ψ), and the apparent survival probability (ϕ). We acknowledged that this population was not completely closed and that permanent emigration was possible during our study. Thus, we interpret survival estimates as apparent survival, which reflects a combination of true mortality and permanent emigration from the study colony (i.e., true survival is likely underestimated).

Because the sequence of parameter modeling can affect model selection (e.g., Lawson *et al.* 2017, but see Hadley *et al.* 2007), we followed a consistent modeling scheme whereby we first selected the best structure for “nuisance” parameters before applying those structures in our hypothesis testing. We conducted our analyses in three stages to determine the most parsimonious model structure for p , ψ , and ϕ . In the first stage, we evaluated a set of resighting probability models while allowing a fully general model structure for survival and transition probabilities. During the second stage of analysis, we applied the best resighting structure to a candidate set of transition models with fully state- and time-dependent survival structures to test hypotheses regarding transition probabilities. Finally, in stage three, we used the best resighting and transition probability structures to build candidate models representing hypotheses addressing apparent survival.

Using this general framework, we employed a two-phase approach within each stage of the analysis to evaluate fundamentally different sources of variation in each vital rate. During phase I, we evaluated general sources of variation for each parameter (p , ψ , ϕ) by fitting five alternative models: constant (intercept only), year (as a categorical variable), age or juvenile vs. adult age classes (i.e., all records for that age or age class combined across years), cohort (determined by hatch year), and breeding state, along with any additive and interactive combinations of these factors that were appropriate to the parameter. We further considered that year, cohort, and age effects may interact with breeding state, and that year and cohort may interact with age class. For phase II, we used the best-supported model structure from phase I; however, for the more general model components that were supported in phase I, we substituted explanatory covariates that were consistent with our sub-hypotheses and associated with the best-supported structure (Table 1). For example, if year was supported as a fixed effect in phase I of hypothesis testing, then during phase II, we substituted covariates that varied annually (e.g., colony size) and could provide a biological mechanism for the annual variation supported in phase I.

We performed all demographic modeling using the “RMark” package (Laake 2013) in R (R Core Team 2016) to interface with MARK (White & Burnham 1999). We adjusted Akaike's Information Criterion (AIC) values to the corrected version (AIC_c), which accounts for small effective sample sizes. We assessed goodness-of-fit of the most general model (with p , ψ , and ϕ structures all set to full state- and time-dependence) using the median \hat{c} test in MARK, and we used the test results to calculate a variance inflation factor, adjusting AIC_c values to quasi-AIC_c values (QAIC_c) for the entire model set, as appropriate. We used QAIC_c model selection procedures to evaluate support for competitive models (Burnham & Anderson 1998). We considered any model structure to be competitive if it successfully converged, if the 85 % confidence intervals of beta estimates associated with the model's core hypothesis did not overlap 0.0 (Arnold 2010), and if QAIC_c scores fell within 2.0 units of the best model from the candidate set. We considered a hypothesis to be supported over alternate hypotheses if its model Akaike weight was greater than all other models combined. For models with full annual time-varying structure in both p and ϕ or ψ , we avoided interpretation of parameter estimates for the final time period, during which survival/transition and resight probabilities are confounded in the model likelihood. We report 95 % confidence intervals for real parameter estimates as the 2.5 (lower) and 97.5 (upper) percentiles of bootstrapped ranges (10000 iterations), calculated using the logit back-transformed beta coefficients. Finally, we performed a sensitivity analysis on each model set to determine the effect

of different variance inflation factors on top model support. This was done by recalculating and comparing each QAIC_c value using variance inflation factors of 1.0, 1.5, 2.0, 2.5, and 3.0.

Model construction

We performed two separate analyses (detailed in the sections below) on two different variations of the data set: 1) an analysis to test hypotheses regarding fledgling survival and recruitment using all records; and 2) an analysis to test hypotheses regarding apparent post-recruitment survival (a combination of true survival and fidelity), which omitted individuals that failed to recruit.

1. Apparent fledgling survival and recruitment

To test hypotheses regarding apparent fledgling survival and recruitment (i.e., permanent transition from the pre-breeder state to the breeder state), we constructed models with data from chicks banded in 1991 and 1995–2006 ($n = 5090$). Using 2006 as our end year ensured that all birds were at least four years of age during the final year of resighting; 90 % of returning chicks from the 1991–1999 cohorts ($n = 1329$) had returned at least once by age four. In every year a bird was detected, we assigned it to one of two states: “pre-recruits”, which included chicks and any birds present but not documented as breeders in the current or previous years, or “recruits”, which included birds classified as breeding during the current or previous year. To facilitate modeling, we simulated the release of all birds as age-1 pre-recruits to eliminate the mathematical gap between the banding year (age 0) and the earliest possible sighting for most birds (age 2); age-1 returns were negligible ($n = 8$ of 5090 individuals). Cohort-specific covariates (e.g., colony size during the hatch year) were included as individual covariates with a common value applied to all members of a cohort. In addition to investigating age effects (e.g., one year old, two years old, etc.), we also assigned birds to one of two age classes in each year (juvenile = 0–2 years; adult = 3+ years), acknowledging that the transition between age classes occurred before most individuals returned to the colony for the first time. This distinction allowed us to calculate separate parameter estimates for fledglings in their first two years of life. The juvenile survival estimates thereby represented the cumulative probability of apparent survival associated with the first two years combined, and detection probabilities from juvenile birds reflected the joint probability of detection and first return to the colony, assuming survival. We fixed the following two parameters to zero to improve estimation: (1) the probability of transitioning from a breeder to a pre-recruit, and (2) survival and resighting probabilities for missing cohorts (i.e., 1992–1994 when intensive chick banding did not occur). Because 95 % of all recruiting individuals had recruited by age 12, we also fixed the probability of transitioning from pre-recruit to a recruit to 0.0 after age 12. The transition from pre-recruit to recruit was calculated via maximum likelihood estimation in MARK, and the probability of remaining within a state was calculated via subtraction.

To calculate the average recruitment age, we first used estimates from the best-supported model to calculate a cumulative transition probability, γ , which gave the probability that a bird would recruit to the breeding population at or before age j , according to

$$\gamma_j = \sum_{i=1}^j [\psi_j * \prod_{i=1}^{j-1} (1 - \psi_i)]$$

where γ is the probability that a bird would recruit to the breeding population at or before age j . The calculated value γ is also the probability that recruitment at a given age was conditional both

on not recruiting during any prior year and on survival. The age at which cumulative recruitment probability first surpasses 0.5 represents the average recruitment age, ω , of the sampled cohorts.

We also assessed the probability of survival to the average recruitment age. To do this, we used the coefficients from the best-supported model to calculate the cumulative probability, η , of pre-recruits surviving to the average age of recruitment, ω , for each cohort k , according to

$$\eta_k = \prod_{A=0}^{\omega_k} \varphi_A$$

We then calculated the geometric mean of these cumulative probabilities over all cohorts that reached the mean recruitment age during the study in order to approximate the mean probability of recruitment.

2. Apparent post-recruitment survival

We used resighting data from only the 1991 and 1995–2004 cohorts to test hypotheses regarding apparent post-recruitment survival (a combined measure of survival and fidelity); members of later cohorts were less likely to have recruited by the time resighting ceased in 2010. Further, we were interested solely in factors associated with apparent survival following recruitment to the colony (i.e., not natal fidelity *per se*), so we included only those individuals that eventually recruited to the Shoup Bay colony ($n = 997$) in the modeled data set. In this separate apparent-survival analysis that included only successful recruits, we identified three breeding states: “pre-recruit” (as described above), “breeder” (observed three times on the same nest site), and “non-breeder” (a former breeder observed fewer than three times on a single nest site). We released all individuals as two-year-olds to facilitate estimation, for reasons described above. Because the modeled data set included only eventual recruits, we lost little information in eliminating records of pre-recruit returns at age 2, as the number of reported two-year-old breeders was negligible ($n = 5$ of 997 individuals). Parameter estimates for the first modeled time period therefore represented cumulative probabilities across a three-year period. Once again, we assigned each bird sighting as either a juvenile or adult, as defined previously. This distinction allowed us to separate the recruitment probability of three-year-olds from that of older birds. As in the fledgling survival analysis, we fixed several parameters to improve model estimation: we fixed all impossible transition probabilities to 0.0 (e.g., non-breeder to pre-recruit), all survival probabilities of pre-recruits to 1.0, and all survival and resight probabilities for missing cohorts to 0.0. Transition probabilities between states were determined via maximum likelihood estimation, while the probabilities of remaining within a state were determined via subtraction.

Assessing permanent emigration

Our data did not allow us to estimate post-recruitment fidelity directly. However, we conducted a cursory assessment of permanent emigration, using independent resighting work from two time periods within the larger study period to provide context for apparent survival estimates. To this end, we used ancillary resighting data, which were collected using comparable methods, from other PWS colonies (1997–1999; DBI unpubl. data) and from the new Valdez pipeline terminal dock colony (2007; dock is less than 10 km from the Shoup Bay colony) to assess the relative degree of emigration in the 1990s vs. the 2000s. We calculated the proportion of each cohort with

members aged 5–11 that were observed nesting outside of Shoup Bay over a three-year period (1997–1999) and at the pipeline terminal colony in 2007. We chose age 11 as the cutoff because annual banding began in 1988 at the Shoup Bay colony; birds in this cohort would have been 11 years old in 1999. We then calculated the percentage of the pipeline terminal group that had never been detected at the Shoup Bay colony; a similar calculation was not possible for the 1997–1999 group, as some members carried only cohort-specific marks and were not individually distinguishable from other members of their cohorts.

RESULTS

Colony size and productivity

The size of the Shoup Bay colony ranged from 8400–19000 actively breeding kittiwakes during this study. It peaked in 2002 and declined to 14400 active breeders by 2010. Productivity (defined as the number of chicks per nest) varied widely during the same period, from a maximum of 0.62 in 1996 to a minimum of 0.00 in 2009, with a general decline over time (Fig. 2).

Apparent fledgling survival and recruitment

Of chicks banded in the 1991 and the 1995–2006 cohorts, 35 % ± 6 % (95 % CI) of each cohort was documented at least once at the Shoup Bay colony in the years following fledging, and 20 % ± 6 % of the 1991 and the 1995–2004 cohorts (i.e., birds that were at least age 6 during the last year of resighting) were detected breeding at their natal colony.

Apparent fledgling survival appeared to be driven by factors shared among members of a cohort. After we adjusted all AIC_c to QAIC_c with the estimated variance inflation factor $\hat{c} = 2.13$, the best-supported model structure for resighting probability included the additive effects of breeding state and age class ($w_i > 0.99$; Table S1 in Appendix 1, available on the website), and the best-performing model structure for transition probability contained only an age effect ($w_i > 0.99$; Table 2). The top-ranked general model of apparent fledgling survival included an interaction between age class and cohort ($w_i > 0.99$; Table S2), indicating that apparent fledgling survival is influenced by events that affect cohorts independently (e.g., events occurring during a sensitive age or immediately after the hatch year). Hypotheses involving time-varying factors were not supported; apparent fledgling survival was

not closely linked to annual variations in colony characteristics or environmental conditions. Of the models reflecting our specific cohort-based hypotheses, the top-ranked model included a negative effect of hatch-year population size ($w_i > 0.99$; Table 3). However, none of the models reflecting specific cohort-based hypotheses outperformed the general cohort structure. Apparent survival of fledglings generally declined over cohorts from a peak of 0.81 (95 % CI 0.73–0.87) for the 1995 cohort down to 0.23 (95 % CI 0.10–0.47) for the 2005 cohort. However, once individuals reached adulthood, apparent survival was variable, with no obvious trend and with a mean annual survival of 0.82 (0.77–0.87; Fig. 3). The cumulative probability of survival to age 7 (average modeled recruitment age) for the 1991 and 1995–2003 cohorts (i.e., birds were at least seven years of age during the final resighting effort in 2010) was 0.23 (95 % CI 0.17–0.31).

The resight probability was 0.53 (95 % CI = 0.47–0.57) for pre-recruitment adults and 0.81 (0.77–0.83) for post-recruitment adults, whereas the resight probability for juveniles was 0.09 (0.08–0.10) for pre-recruits and 0.27 (0.24–0.29) for two-year-old breeders. The probability of recruitment peaked between ages 5 and 6 at 0.21 (0.17–0.25), then declined until age 10, when the cumulative probability of recruitment had reached 0.69 (Fig. 4). The average recruitment age was seven years old.

Our sensitivity analysis on the variance inflation factor revealed no

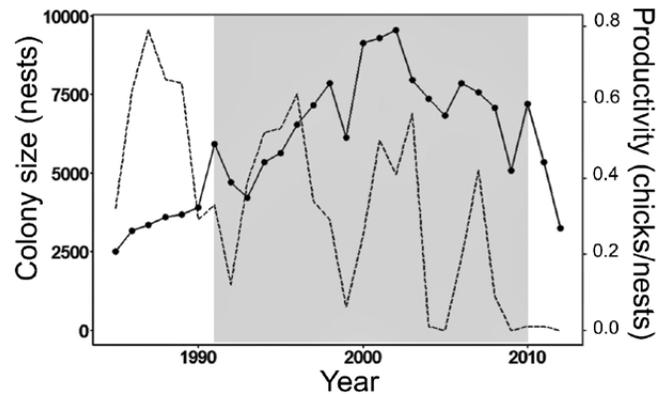


Fig. 2. Total nests (left axis; solid line) and productivity measured as total chicks divided by total nests (right axis; dotted line) at the Shoup Bay kittiwake colony in Prince William Sound, Alaska, 1985–2012. Gray box denotes the time period assessed in the present study

TABLE 2

Fledgling survival and recruitment modeling: recruitment probability. Performance of competing models exploring the best general structure for multi-state models estimating the probability of state transition (ψ), where states were pre- vs. post-recruitment, for Black-legged Kittiwakes banded as chicks at the Shoup Bay colony, Prince William Sound, Alaska, 1991–2008

| Model* | Hypothesis | $\Delta QAIC_c$ | w_i | K |
|---|--|-----------------|--------|----|
| Recruitment probability varies ... | | | | |
| $\Psi_{(age)}$ | ... among ages only. | 0.00 | > 0.99 | 51 |
| $\Psi_{(time)}$ | ... among years only. | 160.24 | < 0.01 | 57 |
| $\Psi_{(cohort)}$ | ... among cohorts only. | 230.67 | < 0.01 | 57 |
| $\Psi_{(constant)}$ | Recruitment probability does not vary. | 293.75 | < 0.01 | 40 |

* Model structure for resight probability was set to the best competing structure (recruitment state + age class) and survival was set to general state and time dependence (by year). Model weights are denoted by w_i and K represents the number of estimable parameters in each model, adjusted for any parameters that were fixed during analysis. $\Delta QAIC_c$ values reflect ΔAIC_c values adjusted according to a median \hat{c} estimate of 2.13.

change in model selection outcomes for variance inflation factors between 1.5 and 3.0.

Apparent post-recruitment survival

Factors shared among members of a cohort also drove apparent post-recruitment survival, which incorporates both true survival and colony fidelity. After we adjusted all AIC_c to $QAIC_c$ based on

a variance inflation factor of $\hat{c} = 1.76$, the best-supported model structure for resighting probability included the additive effects of breeding state and time ($w_i > 0.99$; Table S3). The best-performing model structure for transition probability contained the interactive effects of breeding state and year ($w_i > 0.99$; Table S4). The top-ranked variability structure in apparent survival included the additive effects of breeding state and cohort ($w_i = 0.94$; Table S5), which supports our hypothesis that post-recruitment apparent

TABLE 3
Fledgling survival and recruitment modeling: apparent survival probability. Performance of competing multi-state models testing hypotheses to explain the observed cohort effect on apparent survival (φ ; survival + fidelity) of Black-legged Kittiwakes banded as chicks at the Shoup Bay colony, Prince William Sound (PWS), Alaska, 1991–2008, with the top-ranked general model (italicized) included for reference

| Model ^a | Hypothesis | $\Delta QAIC_c$ | w_i | K |
|--|---|-----------------|--------|----|
| Apparent survival varies ... | | | | |
| $\varphi_{(age\ class * cohort)}$ | ... between age classes and among cohorts, with a different cohort pattern between age classes. | -78.47 | n/a | 41 |
| $\varphi_{(age\ class * HY\ pop\ size)}$ | ... between age classes and by hatch year colony size, with a different colony size pattern between age classes. | 0.00 | > 0.99 | 19 |
| $\varphi_{(age\ class * pre-HY\ herring\ spawn)}$ | ... between age classes and by herring spawn activity within colony foraging range in breeding season prior to hatch, with a different herring spawn pattern between age classes (parental effect). | 68.40 | < 0.01 | 19 |
| $\varphi_{(age\ class * HY\ herring\ spawn)}$ | ... between age classes and by herring spawn activity within colony foraging range during hatch season, with a different herring spawn pattern between age classes. | 68.40 | < 0.01 | 19 |
| $\varphi_{(age\ class * age\ 2\ pop\ size)}$ | ... between age classes and by colony size during the cohort's second year, with a different colony size pattern between age classes. | 73.12 | < 0.01 | 19 |
| $\varphi_{(age\ class * HY\ age\ 1\ herring)}$ | ... between age classes and by PWS-modeled age-1 herring abundance in hatch year, with a different herring pattern between age classes (parental effect). | 79.75 | < 0.01 | 19 |
| $\varphi_{(age\ class * pre-HY\ age\ 1\ herring)}$ | ... between age classes and by PWS-modeled age-1 herring abundance in breeding season prior to hatch, with a different herring pattern between age classes (parental effect). | 79.76 | < 0.01 | 19 |
| $\varphi_{(age\ class * age\ 3\ pop\ size)}$ | ... between age classes and by colony size during the cohort's third year, with a different colony size pattern between age classes. | 87.70 | < 0.01 | 19 |
| $\varphi_{(age\ class * age\ 3\ prod)}$ | ... between age classes and by colony productivity during the cohort's third year, with a different productivity pattern between age classes. | 98.22 | < 0.01 | 19 |
| $\varphi_{(age\ class * AHY\ spring\ winds)}$ | ... between age classes and average spring winds in the northern GOA following the cohort's first winter, with a different wind pattern between age classes. | 105.08 | < 0.01 | 19 |
| $\varphi_{(age\ class * HY\ prod)}$ | ... between age classes and by colony productivity during the cohort's hatch year, with a different productivity pattern between age classes. | 115.61 | < 0.01 | 19 |
| $\varphi_{(age\ class * first\ winter\ winds)}$ | ... between age classes and by average hatch year winter winds in the northern GOA, with a different wind pattern between age classes. | 126.79 | < 0.01 | 19 |
| $\varphi_{(age\ class * AHY\ PDO)}$ | ... between age classes and by the PDO value from the cohort's first winter, with a different PDO pattern between age classes. | 128.37 | < 0.01 | 19 |
| $\varphi_{(age\ class * age\ 2\ prod)}$ | ... between age classes and by colony productivity during the cohort's second year, with a different productivity pattern between age classes. | 129.63 | < 0.01 | 19 |
| $\varphi_{(age\ class * HY\ PDO)}$ | ... between age classes and by the PDO value from the winter prior to the cohort's hatch, with a different PDO pattern between age classes. | 133.52 | < 0.01 | 19 |
| $\varphi_{(age\ class * HY\ fall\ winds)}$ | ... between age classes and by average hatch year fall winds in the northern GOA, with a different wind pattern between age classes. | 134.11 | < 0.01 | 19 |
| $\varphi_{(age\ class * first\ winter\ SST)}$ | ... between age classes and by average hatch year winter SST in the northern GOA, with a different SST pattern between age classes. | 136.90 | < 0.01 | 19 |

^a Asterisks denote interactive models, which include both additive and interactive effects. Model structure for resight probability was set to the best-competing structure (recruitment state + age class, where the states were pre- vs. post-recruitment), and transition model structure was set to the best-competing structure from transition modeling (age). For further explanation of column headings, see footnote in Table 2.

survival is driven by factors shared among a cohort. The analysis did not support hypotheses that apparent survival was a function of age or temporal variation. Of the models reflecting specific cohort-based hypotheses, the top-ranked model included a term for the colony size during the cohort's second year ($w_i = 0.74$; Table 4). Models containing a term for population size for the cohort's second or third year, by which time 63 % and 85 %, respectively, of all individuals that eventually returned had been detected at the colony, had a combined Akaike weight of 0.99.

Pre-recruit resight probabilities were lower and spanned a wider range (0.45–0.80) than those of post-recruits (0.70–0.94). Non-breeders had greater resight probabilities than breeders, likely owing to the more stringent observation criteria for breeders, though the confidence intervals overlapped substantially. Juvenile transition probabilities (0.11–0.55) were greater and more variable than those of adults (0.02–0.23). The colony size at age 2 had a negative influence on a cohort's apparent post-recruitment survival (Fig. 5).

Our sensitivity analysis on the variance inflation factor revealed no change in model selection outcomes for variance inflation factors between 1.0 and 2.5.

Emigration assessment

At least some part of the decline in apparent survival at the Shoup Bay colony was likely caused by declining fidelity, as dispersal appears to have increased since the 1990s, including among established breeders. Only $1.6\% \pm 1.5\%$ (95 % CI) of the chicks banded in the 1988–1994 Shoup Bay colony cohorts were detected nesting at any other PWS colony between 1997 and 1999. In contrast, our single visit to the Valdez pipeline terminal colony in 2007 revealed that at least $3.1\% \pm 0.7\%$ (95 % CI) of the 1996–2003 Shoup Bay cohorts had established nests at that colony. Further, 38 % of these nesters had never been resighted at the Shoup Bay colony following banding, whereas 11 % had previously bred there; the remainder had been observed roosting at the Shoup Bay colony.

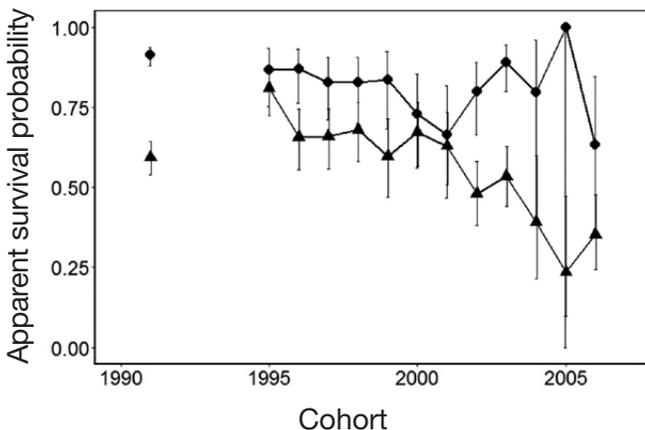


Fig. 3. Apparent survival probabilities (φ ; survival + fidelity) of juveniles (age 0–2; triangles) and adults (age 3+; circles) by cohort from the top-ranked multi-state survival model ($\varphi \sim$ age class \times cohort, $p \sim$ breeding state [pre-recruit vs. recruit] + age class, $\psi \sim$ age) for Black-legged Kittiwakes banded as chicks at the Shoup Bay colony in Prince William Sound in 1991 and 1995–2006. Error bars denote the 2.5 and 97.5 percentiles of bootstrapped estimate distributions (10 000 iterations).

Data accessibility

Manipulation and encounter history data is available from the Dryad Digital Repository (McKnight *et al.* 2019).

DISCUSSION

Trends in apparent fledgling survival: Evidence for increased dispersal over time

Estimating post-fledgling survival rates is challenging because of kittiwakes' tendency to remain at sea for the first two years of life and because of their propensity for dispersal from the natal colony (e.g., Coulson & Coulson 2008). Coulson & Ouellet (1988) estimated an overall survival rate of 0.34 from fledging until

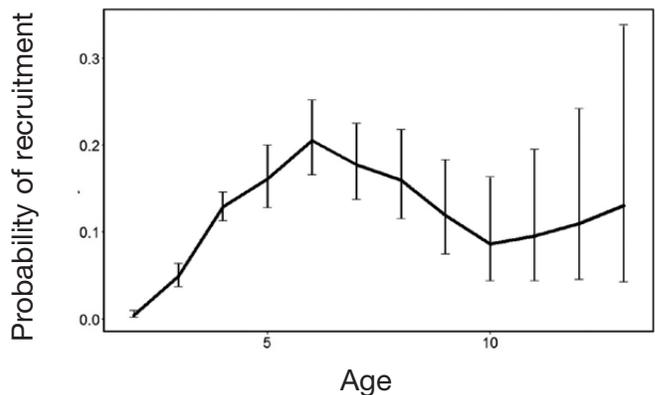


Fig. 4. Recruitment probabilities from the top-ranked multi-state model of apparent fledgling survival ($\varphi \sim$ age class \times cohort, $p \sim$ breeding state [pre-recruit vs. recruit] + age class, $\psi \sim$ age) for Black-legged Kittiwakes banded as chicks at the Shoup Bay colony in Prince William Sound in 1991 and 1995–2006. Error bars denote the 2.5 and 97.5 percentiles of bootstrapped estimate distributions (10 000 iterations).

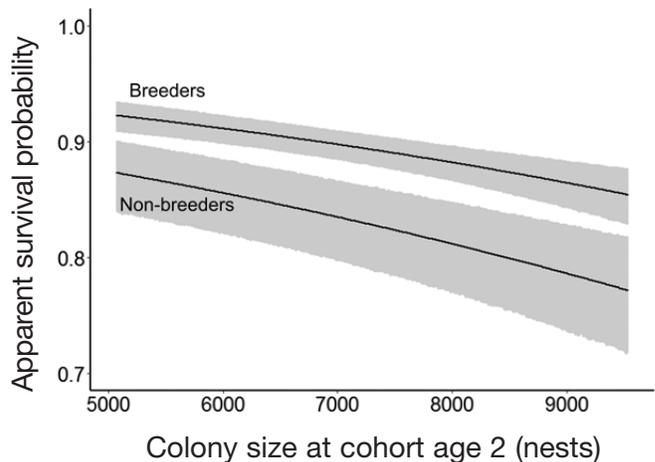


Fig. 5. Effect of natal colony size on the apparent survival of recruits from the top-ranked multi-state model explaining recruit fidelity to the natal colony as a function of natal colony size at age 2 in Black-legged Kittiwakes banded as chicks at and eventually recruiting to the Shoup Bay colony in Prince William Sound. The two states, breeders and post-recruitment non-breeders, are denoted by the solid black lines; the gray shading denotes the 2.5 and 97.5 percentiles of bootstrapped estimate distributions (10 000 iterations).

recruitment for individuals at a well-studied British colony, while Porter & Coulson (1987) reported that 11 % of each cohort returned to breed at the same colony. Our cumulative probability of survival (0.23, 95 % CI = 0.17–0.31) through the average age of recruitment was slightly less than that of Coulson & Ouellet (1988); this difference likely reflected the younger recruitment age in Atlantic kittiwakes (age 4.5: Coulson 1966, Wooller & Coulson 1977, Link *et al.* 2002) compared to birds in our study (age 7). Survival to recruitment age can also be influenced by both hatch order and the duration of the rearing period (Cam *et al.* 2003), which we were unable to account for in this work. Further, realized recruitment, which reflects the integration of both survival and the transition to a breeding state, can be a function of factors affecting survival prior to recruitment (Cam *et al.* 2005). Our approach assessed both components simultaneously; however, we suggest that, in the absence of such cohort-specific survival effects, recruitment is primarily age-dependent.

Boulinier & Danchin (1997) proposed that when the environment quality is patchy but breeding patch quality is stable and predictable, the optimal recruitment strategy has two parts: (1) prospecting before choosing to recruit to a patch and then (2) retaining or abandoning nest sites based on the patch's overall reproductive success rather than the individual's own breeding success. Indeed, individuals who prospect a patch prior to breeding may enjoy greater initial reproductive success (Schjørring *et al.* 1999), which likely influences the trajectory of future reproductive success (Cam *et al.* 2002) and thus patch fidelity. Unfortunately, we did not assess breeding success in this work and were therefore unable to account for it in our exploration of post-recruitment dynamics. When colony or patch quality is predictable, better-quality colonies or patches likely recruit through conspecific attraction (e.g., Oro & Ruxton 2001), performance-based conspecific attraction (Danchin *et al.* 1998), or natal philopatry (in which young birds recruit to the colony from which they successfully fledged, implying that it was of reasonably good quality). Varying degrees of natal philopatry

have been observed in many colonial birds (e.g., Thibault 1993, Aebischer 1995, Pyk *et al.* 2013, but see Coulson & Coulson 2008). One contributing factor appears to be the age of the colony: during the initial years of colony development, growth is dependent on immigration alone until the first generations of chicks produced at the colony have reached maturity (e.g., Pyk *et al.* 2013). Following this phase, colony growth is contingent upon some combination of natal philopatry and immigration.

Crespin *et al.* (2006) found a suggestion of negative density dependence in return rates (i.e., apparent survival was not corrected for imperfect detection) for the Common Murre *Uria aalge*, which may indicate a reduction in natal philopatry at large colonies. We found a similar suggestion in kittiwakes at the Shoup Bay colony: hatch-year colony size was the best predictor of apparent fledgling survival after the general cohort-varying model structure. This means that as colony size increases, new recruits may not have access to the best patches. Such limitation is likely responsible for slower growth in large colonies compared to small colonies (e.g., Porter & Coulson 1987, Chapdelaine & Brousseau 1989). In large colonies, dispersal away from the natal colony may then become the better strategy over philopatry. Steiner & Gaston (2005) documented greater reproductive success in Thick-billed Murres *Uria lomvia* that dispersed from their natal colony, presumably owing to a greater choice in mates and nest sites.

Such strategic dispersal likely contributed to the decline in apparent survival of fledglings that we observed at the Shoup Bay colony. Recruits from Shoup Bay were very rare at other PWS colonies in the late 1990s but were fairly common during a survey at a single neighboring colony in 2007, suggesting an increase in dispersal from Shoup Bay over that time period. Such a decline in natal philopatry could have further reduced recruitment to the Shoup Bay colony through negative feedback on immigrants. The number of non-breeders, including pre-recruits, attending a seabird colony can be a relatively good indicator of the colony's quality to other prospectors

TABLE 4
Post-recruitment survival modeling: apparent survival probability. Performance of competing multi-state models testing hypotheses to explain the observed cohort effect on apparent survival (φ ; survival + fidelity) of post-recruitment breeders and non-breeders (determined by nest-site attendance) for Black-legged Kittiwakes banded as chicks at and eventually recruiting to the Shoup Bay colony, Prince William Sound, Alaska, 1991–2006, with the top-ranked general model (breeding state + cohort; italicized) included for reference

| Model ^a | Hypothesis | ΔQAIC_c | w_i | K |
|--|---|-----------------------|--------|----|
| Apparent survival probability of recruits varies ... | | | | |
| $\varphi_{(\text{state} + 2\text{Y pop size})}$ | ... between breeding states and by colony size in a cohort's second year. | 0.00 | 0.74 | 73 |
| $\varphi_{(\text{state} + 3\text{Y pop size})}$ | ... between breeding states and by colony size in a cohort's third year. | 2.42 | 0.22 | 73 |
| $\varphi_{(\text{state} + \text{HY pop size})}$ | ... between breeding states and by colony size in a cohort's hatch year. | 6.69 | 0.03 | 73 |
| <i>$\varphi_{(\text{state} + \text{cohort})}$</i> | <i>... between breeding states and among cohorts.</i> | 8.74 | 0.01 | 82 |
| $\varphi_{(\text{state} + \text{HY PDO})}$ | ... between breeding states and by winter PDO value prior to a cohort's hatch year. | 14.67 | < 0.01 | 73 |
| $\varphi_{(\text{state} + \text{AHY PDO})}$ | ... between breeding states and by winter PDO value in a cohort's hatch year. | 15.96 | < 0.01 | 73 |
| $\varphi_{(\text{state} + \text{HY Prod})}$ | ... between breeding states and by colony productivity in a cohort's hatch year. | 16.96 | < 0.01 | 73 |
| $\varphi_{(\text{state} + 3\text{Y Prod})}$ | ... between breeding states and by colony productivity in a cohort's third year. | 17.01 | < 0.01 | 73 |
| $\varphi_{(\text{state} + 2\text{Y Prod})}$ | ... between breeding states and by colony productivity in a cohort's second year. | 17.29 | < 0.01 | 73 |

^a Model structures for resight and transition probability were set to the best-competing structures (state + time and state \times time, respectively; asterisk denotes interactive model). For further explanation of column headings, see footnote in Table 2, except that ΔAIC_c values were adjusted according to a median \hat{c} estimate of 1.76.

(Klomp & Furness 1990, Cadiou 1999); such non-breeders may contribute to a population's resilience by filling nest sites left vacant during periods of high adult mortality (Porter & Coulson 1987). The presence of natal pre-recruits at a colony would be an even better indicator of a colony's quality than the presence of late-stage chicks because chicks have some ability to buffer the effects of low food quality temporarily (Dahdul & Horn 2003), but they may suffer greater post-fledging mortality than well-fed counterparts. Szostek *et al.* (2014) found that Common Tern *Sterna hirundo* immigrants were attracted strongly by local recruits and pre-recruits at the colony. If such attraction also occurs in kittiwakes, then declining numbers of pre-recruits at the Shoup Bay colony could have had a negative effect on colony growth that was disproportionate to their actual numbers.

Pacific vs. Atlantic life history differences

Local adaptation may be responsible for apparent differences in kittiwake life-history strategies between the two ocean basins. Atlantic kittiwakes enjoy greater and more stable productivity compared to Pacific counterparts (Hatch *et al.* 1993) and exhibit reduced adult survival: 0.78–0.88 for Atlantic kittiwakes (Coulson & Wooller 1984, Coulson & Thomas 1985, Aebischer & Coulson 1990, Oro & Furness 2002, Ponchon *et al.* 2018) compared to 0.92–0.94 for Pacific kittiwakes (Hatch *et al.* 1993, Golet *et al.* 2004). However, survival estimates generated from single-site CMR studies should always be viewed with caution (Ponchon *et al.* 2018). The recruitment age we estimated for the Shoup Bay kittiwakes provides more evidence of this strategic difference. Our estimate of seven years agrees with the maturation age estimated using a different method for kittiwakes at a nearby (within 200 km) Gulf of Alaska colony that is located near the continental shelf break (Vincenzi *et al.* 2013). Together, these estimates stand in sharp contrast to a much younger maturation age of four to five years observed in Atlantic kittiwakes (Coulson 1966, Wooller & Coulson 1977, Link *et al.* 2002). Further study is needed to determine whether the contrast stems directly from biological differences or if it reflects greater freedom to spend time prospecting prior to breeding in longer-lived Pacific populations.

Patterns of juvenile mortality may shape tradeoff strategies (Goodman 1984, Young 1990), while patterns in adult mortality likely result from these strategies. Variable juvenile survival to adulthood can favor a “bet-hedging” strategy among iteroparous organisms, particularly when nest sites are limited (Sæther *et al.* 1996) or where the cost-savings associated with reduced reproductive effort during a vulnerable time may afford young adults a greater chance of surviving to take part in future reproductive opportunities. This delayed investment may lead to the tradeoff often seen between longevity and maturation age (e.g., Wooller & Coulson 1977, Orell & Belda 2002, Reed *et al.* 2008, Aubry *et al.* 2009). On one hand, early maturity can lead to greater probability of surviving to maturity, shorter generation time, and increased lifetime fitness. Such early maturation, however, may require a sacrifice of growth, fecundity, or offspring quality and may not be advantageous when bet-hedging is the optimal approach. Given its potential fitness tradeoffs, maturation age may be sensitive to selective pressure and thus may rapidly respond to local conditions (Stearns 1992). Alternatively, delayed maturation may reflect more time spent in prospecting potential colonies and breeding patches. This investment could lead to fitness payoff, as prospecting can improve initial breeding success (Schjorring *et al.* 1999) and overall fitness (Cam *et al.* 2002), though it may incur a survival cost via increased food competition during the prospecting period (Bosman *et al.* 2013).

Gill & Hatch (2002) proposed that the differences between the two populations may be driven by differences in food availability rather than local adaptation. However, several lines of evidence suggest that food is not as limiting within PWS as it may be elsewhere in Alaska. Kittiwake colonies within 10 km of the Shoup Bay colony that were geographically restricted to the same general foraging area grew and produced chicks during the Shoup Bay colony's decline (McKnight 2017), suggesting that food limitation was not the proximate cause. Instead, predation may have a greater influence on productivity in this region (McKnight 2017) compared to oceanic colonies such as the Pribilof Islands in the Bering Sea (DBI unpubl. data), where predation is minimal (Byrd *et al.* 2008) and where food is likely more limiting (e.g., Harding *et al.* 2013). Combined with the contrast between Alaskan and western Atlantic kittiwake recruitment ages, the fact that our recruitment age agreed closely with that of a Gulf of Alaska colony experiencing different prey and predator dynamics may reflect a true phenotypic difference in life history strategy between Pacific and Atlantic populations.

Density dependence in apparent survival of recruits

We have long been aware of the role of negative density dependence in population regulation (e.g., Hassell 1975). In seabirds, this dependence is evident in the negative relationship between colony size and reproductive success (e.g., Hunt *et al.* 1986), which at least partially reflects a direct cost of large colony size in the form of localized prey depletion (e.g., Lewis *et al.* 2001, Forero *et al.* 2002). Nest-site limitation can also dampen population growth potential when poorer sites (i.e., those that produce few fledglings) are used at high population densities (Kokko *et al.* 2004). Somewhat counterintuitively, nesting success can also exhibit positive density dependence if the decreased predator defense activity required by individuals allows for an increase in foraging effort, although this effect can be countered by increased intraspecific aggression towards unattended nestlings (Ashbrook *et al.* 2010). In our study, we have revealed another expression of negative density dependence: apparent survival of recruits was lower when natal colony size was large early in life (Fig. 5). This reduction was likely due in part to the increased dispersal of established breeders when the colony was at its largest, as suggested by the larger numbers of Shoup Bay emigrants detected in 2007 compared to the late 1990s.

Many species exhibit high site fidelity following recruitment (e.g., Atwood & Massey 1988, Coulson & Nève de Mévergnies 1992, Pyle *et al.* 2001, Kokko *et al.* 2004), with few established breeders switching colonies (e.g., Aebischer 1995). Emigration is not well understood but may occur more regularly when a colony or breeding patch is declining in quality (e.g., Martínez-Abraín *et al.* 2003), producing few chicks (e.g., Danchin & Monnat 1992), or experiencing a series of cumulative disturbances (Fernández-Chacón *et al.* 2013). Site fidelity in Atlantic kittiwakes is known to be strongly tied to both individual and conspecific reproductive success within the nesting patch (Danchin *et al.* 1998, Bouludier *et al.* 2008, Ponchon *et al.* 2015, Ponchon *et al.* 2017). Once dispersal begins, emigration can accelerate rapidly, suggesting that declining attendance may trigger other breeders to leave as well (Martinez-Abraín *et al.* 2003).

Nest site limitation may have contributed to emigration of recruited breeders in our work. If young recruits tend to establish nest sites on the periphery of the colony, peripheral nests established when the colony is small may become centrally located as the colony grows around them. Centrally located nests tend to have greater quality

(e.g., safety from predators) than nests at the periphery (Hamilton 1971, Vine 1971, Wittenburger & Hunt Jr. 1985, Kharitonov & Siegel-Causey 1988, but see Descamps *et al.* 2009 and Minias *et al.* 2012). Therefore, young individuals that recruited when the Shoup Bay colony was small may have eventually possessed nests in higher quality patches than individuals recruiting when the colony was large; greater success in these higher quality patches, in turn, may have led to greater fidelity (e.g., Danchin *et al.* 1998).

Dispersal of established breeders from productive colonies is uncommon among kittiwakes (e.g., Coulson & Nève de Mévergnies 1992); our relatively large apparent survival estimates for recruits (> 0.75) support this theme. When established breeders disperse, they tend to recruit to other existing colonies. Kildaw *et al.* (2005) documented a “threshold of reluctance” to establish new colonies, even though new colonies can be highly productive. Dispersal to new, unoccupied nesting areas may simply present too many risks for the average breeder: unknown factors include predator dynamics, long-term food availability, and microclimate effects, whereas existing colonies provide copious information to potential recruits regarding food abundance and nest safety (Forbes & Kaiser 1994). However, decreasing productivity at the Shoup Bay colony in the later years of our study may have signaled to breeders that patch quality was becoming less predictable, causing them to employ the “dispersal following patch failure” strategy (Boulinier & Danchin 1997). Frederiksen & Bregnballe (2001) found that productivity affected recruitment age in Great Cormorants *Phalacrocorax carbo sinensis*, where individuals waited longer to recruit after seasons of poor productivity. We found no such relationship for the Shoup Bay kittiwakes, potentially due to the ease of dispersal to more promising colonies within the PWS system. Dispersal of breeders may have become even more feasible after the establishment of nearby (i.e., within 10 km) colonies in Port Valdez beginning in the late 1990s. This was likely exacerbated by declining habitat quality at the Shoup Bay colony due to post-glacial successional changes in vegetation that may have benefited predators. Because any birds nesting within Port Valdez must travel into Valdez Arm and its associated fjords to forage, we suspect that foraging grounds overlap almost completely (but see Ainley *et al.* 2003), which would make a move more feasible for birds that are already familiar with feeding conditions in the area.

CONCLUSION

Given the recent and dramatic decreases in seabird populations around the globe (Palczy *et al.* 2015), understanding recruitment and emigration patterns is important not only for successful population management but also for the effective use of seabirds as ecosystem indicators (e.g., Cairns 1988, Piatt *et al.* 2007). In this work, we identified that intrinsic processes may drive apparent survival in fledglings and recruits at an Alaska seabird colony and that declines in apparent survival likely reflect greater dispersal when colony sizes are larger. This fidelity/colony size relationship could be a useful consideration for managers, as small, growing colonies may represent a better long-term investment for conservation projects than large, established colonies. Additionally, our results allowed us to estimate the average age of first reproduction for this population. Our estimate agreed with that calculated for another Pacific colony, and both were several years older than recruitment ages calculated for Atlantic populations. This strengthens the argument that Pacific kittiwakes follow a more conservative life history strategy than their Atlantic counterparts, which may confer

added resilience against the increased frequency or magnitude of short-term environmental perturbations associated with ecosystem change. Finally, while this study addresses a single colony of a single species, it provides demographic parameter estimates that can be applied in parameterizing models of population dynamics. Such models can provide us with valuable insights and realistic predictions about future dynamics in changing marine systems.

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STATUS OF BLACK-HEADED GULL *LARUS RIDIBUNDUS* IN INDONESIAN BORNEO

AHYADI HASYIM¹, MUHAMMAD IQBAL², ARUM SETIAWAN³ & INDRA YUSTIAN³

¹*Indocement Tunggal Prakarsa, Tbk. Plant-12 Tarjun, Kotabaru, Kalimantan Selatan, Indonesia*

²*Conservation Biology Programme, Faculty of Science, Sriwijaya University, Jalan Padang Selasa 524, Palembang 30139, Indonesia (kpbsos26@yahoo.com)*

³*Department of Biology, Faculty of Science, Sriwijaya University, Jalan Raya Palembang-Prabumulih km 32, Indralaya, Sumatera Selatan 30662, Indonesia*

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ABSTRACT

HASYIM, A., IQBAL, M., SETIAWAN, A. & YUSTIAN, I. 2019. Status of Black-headed Gull *Larus ridibundus* in Indonesian Borneo. *Marine Ornithology*: 47: 223–224.

Here, we report the second record of the Black-headed Gull *Larus ridibundus* in Indonesian Borneo. Although larids are uncommon in these waters, observations of these birds are increasing. Whether this is due to greater observer coverage remains to be determined.

Key words: Black-headed Gull, Borneo, changing status

The Black-headed Gull *Larus ridibundus* is a small (length 34–43 cm), elegant gull that breeds in Iceland, Faeroes, Britain, and throughout most of Europe and Asia, including on the shores of the Black and Caspian seas, east to the Sea of Okhotsk and the Kamchatka Peninsula, and across Eurasia (Harrison 1985). Northern populations are migratory, whereas lower latitude birds tend to be resident or dispersive; Asian birds winter in India and are vagrant in Malaysia and Philippines (Burger & Gochfeld 1996). The Black-headed Gull is also vagrant to Mexico, Hawaii, Socotra, Maldives, New Guinea, Wallacea, North Australia, Chad, Gabon, Mozambique, and South Africa (Olsen & Larsson 2003). In Indonesia, the Black-headed Gull has been reported in Sumatra, Sulawesi, Moluccas, and West Papua (MacKinnon & Phillipps 1993, Sukmantoro *et al.* 2007, Eaton *et al.* 2016, Gregory 2017).

Although it has been recorded in Borneo, the Black-headed Gull is absent in Indonesian Borneo and Kalimantan (Smythies 1999, Mann 2008, Myers 2016, Phillipps & Phillipps 2016). In this paper, we report the presence of the Black-headed Gull in Indonesian Borneo.

On 20 December 2018, a small white gull was observed and photographed by the first author on Semayap Beach, South Kalimantan, Indonesia. Based on observations and photographs, the bird was identified as a Black-headed Gull. The bird's body was whitish overall, with pale grey upperparts; a long, slender, dark red bill with black tip; and a white head with dark ear spot and pale grey around eyes. These characteristics indicate an adult non-breeding Black-headed Gull. The bird in question differed from other gulls in Southeast Asian and Indonesian waters, and the combination of a dark red bill and legs confirmed its identity.

Many of the gulls that have been recorded in Southeast Asian and Indonesian waters have a yellow bill and legs, or black bill and legs. These include the Heuglin's Gull *Larus heuglini*, Black-tailed Gull *Larus crassirostris*, Laughing Gull *Larus atricilla*, Mew Gull *Larus canus*, Mongolian Gull *Larus mongolicus*, Lesser Black-backed Gull *Larus fuscus*, Pallas Gull *Larus ichthyæus*, Saunder's Gull *Larus saundersii*, and Little Gull *Larus minutus* (Robson 2011, Pratt & Beehler 2015, Eaton *et al.* 2016, Gregory 2017). The dark red bill and legs of the bird observed on 20 December 2018 was similar to that of the Relict Gull *Larus relictus*, Brown-headed Gull *Larus brunnicapilla*, Slender-billed Gull *Larus genei*, and Bonaparte's Gull *Chroicocephalus philadelphia*; however, the pale eyelids and pale eyes contrasted the dark eyes of a Slender-billed Gull. Based on these features, we identified this bird as a non-breeding Black-headed Gull. Following Olsen & Larsson (2003), adult non-breeding Black-headed Gulls found in South Kalimantan are in winter plumage. Adult winter and second winter Black-headed Gulls are mostly indistinguishable at this stage, but a small minority of second

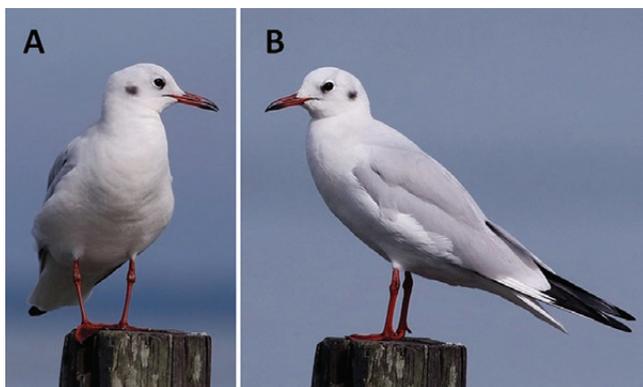


Fig. 1. First Black-headed Gull recorded in Indonesian Borneo, Semayap Beach, Kotabaru, South Kalimantan, 20 December 2018. (A) View showing combination of dark red bill and legs, white head with dark ear spot, and pale grey around eyes; (B) View showing whitish overall body with pale grey above, and the absence of a dark pattern in the tertials and covert markings (all photos: Ahyadi Hasyim).

winter individuals show traces of immature plumage such as dark-patterned tertials and covert markings (especially on the upper primary coverts). Individuals seen in South Kalimantan have been pale grey overall in the tertials, having covert markings without a dark-pattern, indicating an adult in winter plumage.

On the island of Borneo, the Black-headed Gull has been reported in the East Malaysian states of Sarawak, Sabah, and Brunei Darussalam (Smythies 1999, Mann 2008, Myers 2016, Phillipps & Phillipps 2016). In the past, this species has been a very scarce winter visitor to the coast of northern Borneo, with one inland record of its presence (Mann 2008); however, more recently, observation of this species has become increasingly regular, especially in winter around ports such as Sandakan and Kota Kinabalu in north Borneo (Phillipps & Phillipps 2016). The current record of a Black-headed Gull in South Kalimantan is the second for this species in Indonesian Borneo. The Black-headed Gull was reported for the first time in Indonesian Borneo with an observation of three birds perched on wooden pillars in the port area of Nyamuk on the Sungai Kakap in the northern Sungai Nyamuk Delta, West Kalimantan, on 15 January 2011; two birds were still present on 23 January 2011 (van Balen *et al.* 2013). Eaton *et al.* (2016) show a distribution map for the Black-headed Gull in West Kalimantan, indicating that this species occurs there; however, their mention of Black-headed Gulls in northern Borneo is limited to the distribution of this species. Phillipps & Phillipps (2016) state that the Black-headed Gull is the only gull recorded in Borneo, but they do not indicate whether its range extends into Indonesian Borneo. Another Black-tailed Gull was observed in Sabah and is supported by a photographic record from Kota Kinabalu; however, the source of this record is unclear (Eaton *et al.* 2016; J. Eaton pers. comm.). Myers (2016) listed the Black-headed Gull and Black-tailed Gull as recorded in Borneo, but neither species has been recorded in Indonesian Borneo.

Phillipps & Phillipps (2016) present three theories as to why larids and other seabirds are rare in Borneo: first, the shallow seas around Borneo do not encourage the upwelling of nutrients, which are the food source of the fish upon which seabirds feed; second, Borneo's warm, relatively calm seas are not as rich in fish as the colder waters to the north and south; third, there are very few secure nesting sites for seabirds around the coast of Borneo. In addition, other than the record in January 2013 of the first Heuglin's Gull in West Kalimantan, Indonesian Borneo (Eaton *et al.* 2016), we surmise that the lack of information on gulls and other seabirds may be the result of a lack of observer effort.

In the last decade, a rapidly increasing interest amongst local Indonesian researchers and birdwatchers in Kalimantan, as well as easier access to binoculars and cameras, has led to an increase in observations of vagrant and migratory birds in Indonesia (Iqbal *et al.* 2009, Iqbal *et al.* 2010, Imansyah & Iqbal 2015, Iqbal & Albayquni 2016, Putra *et al.* 2018). In the future, further monitoring is needed to establish the status of Black-headed Gulls and other seabirds in Indonesian Borneo.

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LONGEVITY IN THE RHINOCEROS AUKLET *CERORHINCA MONOCERATA* AND A COMPARISON WITH OTHER SPECIES OF ALCIDAE

J. MARK HIPFNER^{1*}, DANIEL SHERVILL², ALICE D. DOMALIK³,
DOUGLAS F. BERTRAM⁴, MOIRA J.F. LEMON², MICHAEL S. RODWAY⁵,
CONSTANCE SMITH³ & SARAH A. HUDSON (TREFRY)¹

¹*Environment and Climate Change Canada, Wildlife Research Division,
5421 Robertson Rd., Delta, BC V4K 3N2, Canada *(Mark.Hipfner@canada.ca)*

²*Environment and Climate Change Canada, Canadian Wildlife Service, 5421 Robertson Rd., Delta, BC V4K 3N2, Canada*

³*Simon Fraser University, Centre for Wildlife Ecology, Department of Biological Sciences,
8888 University Dr., Burnaby, BC V5A 1S6, Canada*

⁴*Environment and Climate Change Canada, Wildlife Research Division, Institute of Ocean Sciences,
9860 West Saanich Rd., PO Box 6000, Sidney, BC V8L 4B2, Canada*

⁵*Wildwing Environmental Research, Box 47, Gold Bridge, BC V0K 1P0, Canada*

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ABSTRACT

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The Rhinoceros Auklet *Cerorhinca monocerata* is an abundant and widely distributed North Pacific seabird. We describe noteworthy longevity records derived from banding operations (1984–1985 and 2008–2018) on several large breeding colonies in British Columbia, Canada. Of note was an individual banded as a nestling on the Lucy Islands in 1985 and recaptured as a breeding adult in 2016, 31 years later. Several other individuals banded in the mid 1980s survived into at least their late 20s. These longevity records for the Rhinoceros Auklet are close to the value predicted by the linear relationship between longevity and log body mass for the 15 species of Alcidae for which data are available.

Key words: banding, body mass, burrow nests, North Pacific, recapture, seabirds, survival

INTRODUCTION

The Rhinoceros Auklet *Cerorhinca monocerata* is an abundant, widely distributed seabird of the temperate North Pacific Ocean. It is misnamed, in that the species does not belong to the auklet clade (Aethiini). Rather, the genus *Cerorhinca* either is basal within the puffin clade (Fratereculini) or it forms a sister clade with *Fraterecula* (Smith & Clarke 2015). About 50 % of the global population of Rhinoceros Auklets (~750 000 pairs) breeds at colonies in British Columbia (BC), Canada (Gaston & Dechesne 1996), although that estimate may be closer to ~30 % if populations on Russia's Kuril Islands are as large as newer surveys indicate (375 000 pairs; Ushakova 2007). Birds breeding in the eastern Pacific Ocean average 475–525 g in mass, with little evidence of geographic variation, and only slight sexual dimorphism has been observed (males tend to be larger than females; Addison *et al.* 2008).

Rhinoceros Auklet nests are situated in cavities or, more often, earthen burrows that the birds excavate themselves and reuse from year to year (Richardson 1961). Adult birds are active on the colony mainly at night, and evolutionary consequences of their nocturnal habits include relatively slow offspring development and long breeding seasons (Hipfner *et al.* 2010): the single egg is incubated for ~45 days until hatch, and the nestling is provisioned for ~50–55 days until fledging (Summers & Drent 1979, Harfenist 1995). A generalist feeder (Bédard 1969), provisioning adults deliver bill-loads of small forage fish that are caught mainly in continental shelf waters within ~40–75 km of the breeding colony

(Domalik 2018, Wilkinson *et al.* 2018). The growth rates and survival of offspring vary markedly from year to year, in response to oceanographic conditions that affect the birds' prey base (Hedd *et al.* 2006, Thayer & Sydeman 2007, Borstad *et al.* 2011). Adult survival rates measured on Triangle Island, BC (UTM 09N 494480 5634395) averaged ~87 % per year with no detectable difference between males and females and no detectable effect of oceanographic variation (Morrison *et al.* 2011).

RESULTS AND DISCUSSION

On 10 July 2016, while working on the Lucy Islands, BC (UTM 09N 394673 6017550), we caught in a purse net a Rhinoceros Auklet that had been banded as a nestling by DFB on 15 July 1985 (band number 846-57235). When recaptured 31 years later, this bird was raising its own nestling in a burrow located ~225 m from its natal burrow on the largest island of the colony. The recaptured bird was most likely a female, given its bill depth of 15.9 mm. (For 17 females sexed using molecular methods, mean bill depth = 16.1 mm ± 0.5 [SD] and range = 14.7–17.0 mm. For 16 males, mean bill depth = 17.2 mm ± 0.7 [SD] and range = 16.1–18.5 mm (JMh unpubl. data).)

Nestling growth rate may be indicative of post-fledgling survival in some seabirds. In a close relative, the Tufted Puffin *Fraterecula cirrhata*, rapid growth to large size at fledging is associated with a higher probability of surviving to return to the colony in later years (Morrison *et al.* 2009). During 1985, a year in which growth

rates were generally fast owing to a strong year-class of Pacific sand lance *Ammodytes personatus* (Bertram *et al.* 1991, Bertram & Kaiser 1993), the rate at which the recaptured Rhinoceros Auklet gained mass as a nestling (8.2 g/d from 10 days old to 40 days old) was above the colony-wide average (7.1 g/d \pm 2.5 [SD]). We handled a total of 916 adults on the Lucy Islands from 2008 to 2018, and of the 166 hatch-year (HY) auklets banded in 1984 and 1985, this is the only one recaptured thus far. An additional 203 after-hatch-year (AHY) Rhinoceros Auklets were banded there in 1984 and 1985, but none has been recaptured in the recent program. The breeding population on the Lucy Islands was estimated at ~25 000 pairs in the 1980s (Rodway & Lemon 1991a) and there has been no overt change in population size since (Rodway & Lemon 2011, L. Wilson unpubl. data).

There are three other noteworthy records of Rhinoceros Auklets banded on BC colonies in the 1980s and encountered in recent years. In the first instance, a probable female (bill depth = 16.2 mm) banded as an AHY (846-57168) on Pine Island (UTM 09N 589302 5647888) in July 1985 was recaptured there in 2009, 24 years later. In 1985, 82 Rhinoceros Auklets (27 AHY and 55 HY) were banded on Pine Island. In the second instance, a near-certain female (bill depth = 14.4 mm) banded as an AHY (785-61002) on Pine Island in July 1986 was recaptured there in 2008, 22 years later. In 1986, 100 birds (25 AHY and 75 HY) were banded on Pine Island, which supported ~89 000 pairs in the 1980s (Rodway & Lemon 1991b). We handled 1097 adults on Pine Island from 2008 to 2018. In the third instance, a bird of unknown sex that was banded as an AHY (785-57806) on Triangle Island in July 1984 was found dead on a beach in Oregon, USA, in September 2010, 26 years later. In 1984, 117 Rhinoceros Auklets (49 AHY and 68 HY) were banded on Triangle Island, which supported ~41 000 pairs in the 1980s (Rodway *et al.* 1990). If we assume that these three birds were breeding when banded (they were carrying bill-loads of fish, presumably destined for nestlings) and that the minimum age at first breeding in the Rhinoceros Auklet is four or five years old (similar to the Atlantic Puffin *Fratercula arctica*, a close relative of similar size; Petersen 1976, Harris 1981), then the three were at least 26–30 years old when re-encountered. While this is mathematically improbable for a species with an annual adult survival rate of ~87 % (Morrison *et al.* 2011), it appears that it is not uncommon for some individuals of this species to survive into their late 20s and 30s.

To put these observations in perspective, we compiled longevity records for species belonging to the family Alcidae from the EURING (Fransson *et al.* 2017) and North American Bird Banding Laboratory (BBL; USGS 2017) databases. We obtained data for 15 of the 23 species in the family, and we excluded the BBL longevity record of just six years for the Tufted Puffin, a large auk (~725 g) with an adult survival rate more than 90 % (Morrison *et al.* 2011) that has not been the subject of large banding programs. For all 15 species, the maximum (oldest) longevity records were derived from individuals banded as AHYs (thus, of unknown age). We replaced the BBL records with recently published records for two species, the Ancient Murrelet *Synthliboramphus antiquus* (Shoji & Gaston 2008) and Cassin's Auklet *Ptychoramphus aleuticus* (Johns *et al.* 2017). We also substituted an unpublished record for the Thick-billed Murre *Uria lomvia*, based on an individual banded as a HY on Coats Island, Nunavut, Canada, in 1981 and encountered in 2018, alive and breeding (K. Elliott pers. comm.). Based on these records, our longevity record of 31 years for the Rhinoceros Auklet is very close to the value predicted from the

linear relationship between longevity and log body mass for other species of Alcidae (Fig. 1). Positive relationships of a similar nature have been reported in other seabird taxa, such as the procellariiforms (Ainley *et al.* 2001).

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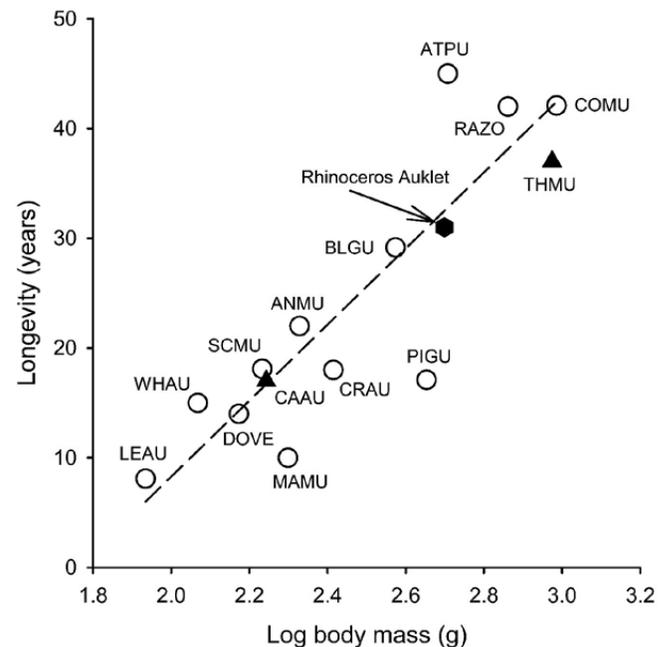


Fig. 1. Maximum longevity records in relation to body mass in the Alcidae. See text for sources for longevity records. Note that there is much interspecific variability in the quality of the data, largely related to abundance and the number of birds banded (e.g., both high in Atlantic Puffin, both much lower in Marbled Murrelet *Brachyramphus marmoratus*). Body masses are from Gaston & Jones (1998), using values for birds of unknown/combined sexes and the largest sample size reported. Filled symbols indicate known-age birds banded as HYs; open symbols indicate birds banded as AHYs. The formula for the linear relationship is $y = -56.9 + 32.9x$ ($R^2 = 0.76$, $F_{1,12} = 37.83$, $P < 0.001$). Species codes: COMU = Common Murre *Uria aalge*; THMU = Thick-billed Murre; RAZO = Razorbill *Alca torda*; DOVE = Dovekie (Little Auk) *Alle alle*; BLGU = Black Guillemot *Cephus grille*; PIGU = Pigeon Guillemot *Cephus columba*; MAMU = Marbled Murrelet; SCMU = Scripp's Murrelet *Synthliboramphus scrippsi*; ANMU = Ancient Murrelet; CAAU = Cassin's Auklet; CRAU = Crested Auklet *Aethia cristatella*; LEAU = Least Auklet *Aethia pusilla*; WHAU = Whiskered Auklet *Aethia pygmaea*; ATPU = Atlantic Puffin.

transport to field sites. We worked under Animal Care, Banding, and Migratory Birds permits from ECCC, and under permits from BC Parks and the Metlakatla, Tlatlasikwala, and Quatsino First Nations to work on the Lucy Islands, Pine Island, and Triangle Island. Alan Burger and an anonymous reviewer provided valuable suggestions to improve our paper.

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POTENTIAL NORTHWARD EXPANSION OF THE BREEDING RANGE OF RED-LEGGED KITTIWAKE *RISSA BREVIROSTRIS*

BRYCE W. ROBINSON¹, ANDREW S. JOHNSON², IRBY J. LOVETTE² & MARC D. ROMANO³

¹*Ornithologi, 615 E. Krall St., Boise, ID 83712, USA (bryce@ornithologi.com)*

²*Cornell Lab of Ornithology, Ithaca, NY 14850, USA*

³*US Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge, Homer, AK 99603, USA*

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ABSTRACT

ROBINSON, B.W., JOHNSON, A.S., LOVETTE, I.J. & ROMANO, M.D. 2019. Potential northward expansion of the breeding range of Red-legged Kittiwake *Rissa brevirostris*. *Marine Ornithology*: 47: 229–234.

We report observations of *ca.* 200 Red-legged Kittiwakes *Rissa brevirostris* occupying cliff habitat on northern St. Matthew Island, and behaviors that indicate the kittiwakes were attempting to breed. This is the first documentation of Red-legged Kittiwake breeding activity on St. Matthew Island, which represents a potential northward expansion of this species' breeding range by nearly 400 km. During a month-long expedition to St. Matthew and Hall islands in June–July 2018, we observed Red-legged Kittiwakes conducting courtship behaviors, nest building and stamping, and sitting on nests at two locations on the northwest side of St. Matthew Island. We discuss our observations with respect to past observations of the species at this location, and with respect to breeding activities at the nearest known breeding locations on St. Paul and St. George islands.

Key words: Red-legged Kittiwake, distribution, Bering Sea, St. Matthew Island

INTRODUCTION

Shifting distributions of higher trophic level consumers, such as birds, provide some of the most obvious evidence of the effects of global climate change on the biota, and serve as signals for impacts across trophic levels (Valiela & Bowen 2003, Illán *et al.* 2014, Paprocki *et al.* 2014, Billerman *et al.* 2016). The Bering Sea represents an ecotone between Arctic and Subarctic marine ecosystems that is largely governed by sea-ice extent, an environmental factor that varies among years (Stabeno *et al.* 2001, Ohashi *et al.* 2013, Wu & Chen 2016). Currently, sea-ice is experiencing a substantial overall reduction in distribution and thickness related to climate change (Wang & Overland 2009, Comiso 2012, Mueller *et al.* 2018). Because this region faces a range of climate change impacts, an overall northward shift in the biogeographic distribution of the region's fauna has followed these decreases in sea-ice distribution and the concomitant northward shift in the ecotone between Arctic and Subarctic biomes (Mueter & Litzow 2008). These changes are likely to influence distributions and population dynamics of taxa at all trophic levels (Hunt *et al.* 2002, Hunt *et al.* 2011, Ohashi *et al.* 2013), but they may be most conspicuous when they result in changes to ecosystem members at high trophic levels—such as seabirds (Springer *et al.* 2007, Renner *et al.* 2016, Hunt *et al.* 2018).

Birds are distributed throughout the Bering Sea along gradients of sea surface temperature, salinity, ocean depths, and currents (Iverson *et al.* 1979, Hunt *et al.* 2014, Santora *et al.* 2018). Because of their association with sea ice, these gradients are likely to change as the extent of sea ice changes (Hunt *et al.* 2018). The Red-legged Kittiwake *Rissa brevirostris* is a Beringean endemic that remains in the Bering Sea during winter and feeds at the margins of sea-ice (Orben *et al.* 2015, 2018). Although sea-ice coverage is correlated

with higher stress levels and may limit the ability of kittiwakes to obtain food (Will *et al.* 2018), Red-legged Kittiwake presence at the ice-edge likely reflects the presence of good foraging conditions and the opportunity to employ energy conservative techniques such as perching and foraging. Because fluctuations in sea-ice distribution in the Bering Sea influence reproductive success and productivity for surface feeding consumers such as kittiwakes (including the Black-legged Kittiwake *R. tridactyla*; Byrd *et al.* 2008, Zador *et al.* 2013), recent trends and projections of future sea-ice distributions may impact kittiwake populations.

The Red-legged Kittiwake is thought to feed on a low diversity of prey and possesses physical characteristics such as relatively large eyes and a short bill, indicating the importance of low-light foraging on a specific resource as a life-history strategy (Storer 1987). During the breeding season, Red-legged Kittiwakes feed on a range of prey types (Sinclair *et al.* 2008). In many years, myctophids (Family: Myctophidae), a diel species that is available to surface feeding kittiwakes at night, are the primary prey (Kokubun *et al.* 2015, Guitart *et al.* 2018). This narrow diet niche seems to be maintained throughout their annual cycle (Orben *et al.* 2015). Although geolocator data from the non-breeding season indicate higher diurnal activity levels, with low activity during darkness (Orben *et al.* 2015), this does not necessarily indicate a lack of nocturnal foraging. Rather, it may suggest a more energetically conservative nocturnal winter foraging strategy (Jodice *et al.* 2003) that highlights the importance of prey landscapes in this region during the winter months.

The Red-legged Kittiwake has a breeding distribution restricted to four major breeding locations, all within the Bering Sea (Fig. 1): the Pribilof Islands (St. George, St. Paul, and Otter: 235 624 individuals; Thomson *et al.* 2014, Goyert *et al.* 2017), the Bogoslof Islands

(Bogoslof and Fire: 918 individuals; Byrd *et al.* 2002), the Buldir Islands (Buldir, Outer Rock, Middle Rock: 9350 individuals; Byrd *et al.* 1997), and the Commander Islands, Russia (Bering, Toporkov, Mednyi, Arij Kamen: 32344 individuals; Byrd & Williams 1993, Vyatkin & Artukhin 1994, Byrd *et al.* 1997). Smaller breeding colonies are located on Amak and Chagulak Islands (16 and 18 individuals, respectively; Byrd *et al.* 2001, 2004) and Koniuji and Unalga Islands (eight and nine individuals, respectively; J. Williams unpubl. data), in the Aleutian Archipelago. Historically, the Red-legged Kittiwake was thought to be more widespread in the Aleutian Archipelago and elsewhere in the Bering Sea region (Byrd & Williams 1993); however, there is no existing historical evidence of breeding north of their present, northernmost breeding location on St. Paul Island (57°N). Although some Red-legged Kittiwakes winter in the northern Bering Sea (i.e., in waters off mainland Alaska and near St. Lawrence and St. Matthew islands, and Cape Navarin, Russia; Orben *et al.* 2018), they are rarely observed in this region during the breeding season (Swarth 1934, Faye & Cade 1959, Sealy *et al.* 1971, Winker *et al.* 2002); however, in recent years, they have been observed in low densities in waters around St. Matthew and St. Lawrence islands (Kuletz & Labunski 2017).

Here, we provide the first documentation of a Red-legged Kittiwake colony on St. Matthew Island. We report unprecedented numbers and behaviors of Red-legged Kittiwakes for this location, and provide evidence that these birds are likely breeding, which would represent a northern extension of the breeding distribution of this species by *ca.* 400 km. We discuss the status of colonies on St. George and St. Paul islands, and how breeding trends at these locations and other factors may relate to the discovery of the St. Matthew Island colony.

METHODS

The St. Matthew Island archipelago is part of the Bering Sea Unit of the Alaska Maritime National Wildlife Refuge, administered by

the US Fish and Wildlife Service. The archipelago consists of three main islands: St. Matthew (60°24'N, 172°42'W), Hall (60°39'N, 173°05'W), and Pinnacle (60°12'N, 172°45'W). All three islands are uninhabited by humans and designated as Federal Wilderness. These islands are volcanic in origin and located on the Bering Sea Shelf, *ca.* 230 km east of the shelf break in a roughly central position between the coasts of Russia and Alaska. Because of their position in the Bering Sea, the islands support a mixture of northern Palearctic and Nearctic avifaunas.

During a 31-d visit, from 06 June–07 July 2018, we conducted population counts and productivity monitoring for McKay's Bunting *Plectrophenax hyperboreus* and Pribilof Rock Sandpiper *Calidris ptilocnemis ptilocnemis* on St. Matthew Island. During our fieldwork, we collected data on all noteworthy bird and mammal sightings.

We conducted observations by land-based and boat-based methods. On 19 June, 01 July, and 04 July, we conducted land-based observations above a known seabird colony at cliffs on the northwest side of the island (Location A [60°29'N, 173°3'W], Fig. 2). We checked all visible cliff faces for the presence of Red-legged Kittiwakes, and noted locations where birds were sitting on nests. During land-based observations on 01 and 04 July, conditions were foggy with marginal visibility; however, the fog cleared intermittently on these dates, and we were able to make limited observations. On 06 July, we conducted a boat-based survey along the north and northwest sides of St. Matthew Island, looking for kittiwake breeding habitat and additional Red-legged Kittiwakes. We conducted boat-based observations starting north from camp and continuing around the north end of the island and south towards location A. Our survey platform was a 4.5 m-long inflatable skiff employed by a three-person crew (two observers and one skiff operator). During boat-based observations, we maintained a maximum distance of 100 m from the shoreline to best observe potential Red-legged Kittiwake nesting habitat that we could not see from land-based observation points.

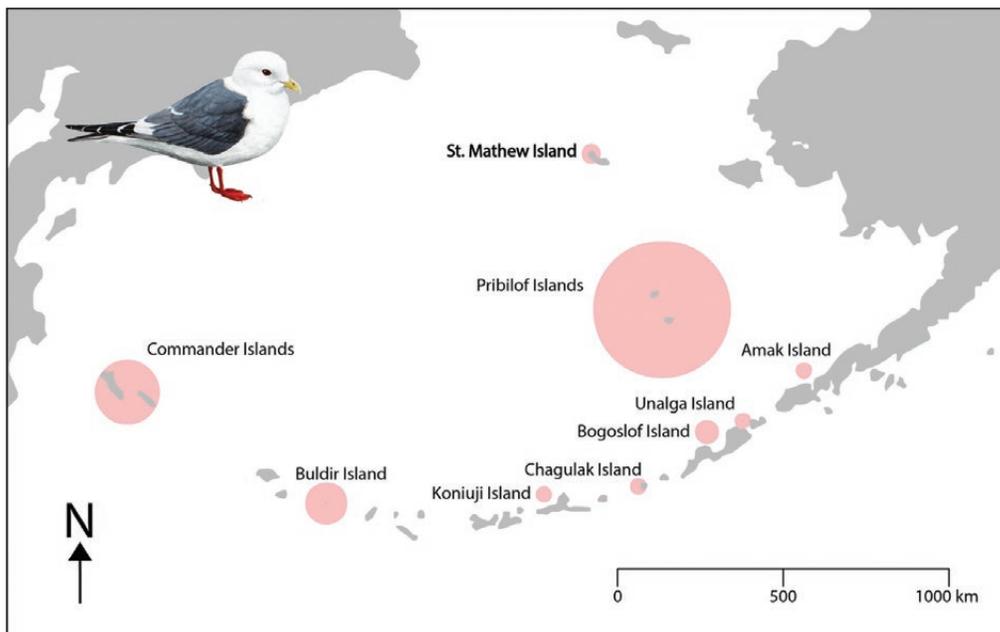


Fig. 1. Red-legged Kittiwake breeding distribution. Colonies are indicated by red circles representing relative colony size (range: 235 624 individuals on the Pribilof Islands to eight individuals on Koniuji Island). St. Matthew Island is located *ca.* 400 km north of St. Paul Island.

OBSERVATIONS

During land-based observations on 19 June, we noted two Red-legged Kittiwakes on the water in mixed flocks with *ca.* 18 Black-legged Kittiwakes (Location A, Fig. 2). In the same vicinity, we observed Red-legged Kittiwakes both in flight and perched on sea cliffs (*ca.* 130 individuals) amidst Black-legged Kittiwakes and Common Murres *Uria aalge*. Our count for this day reached *ca.* 150 Red-legged Kittiwakes across the 1.5 km sea-cliff colony. At this time, we did not observe behaviors that indicated breeding, apart from pairs perched together on the cliffs.

On 01 July, we visited the sea-cliff colony (Location A, Fig. 2) and observed *ca.* 100 Red-legged Kittiwakes. Of these birds, we observed individuals conducting courtship behaviors, carrying nest material, and building and stamping nests. Unfortunately, visibility on this date was restricted by dense fog and we were unable to fully count birds attending ledges throughout the sea-cliff colony. However, we intermittently obtained views and were able to photograph the kittiwakes on the cliff (e.g., Fig. 3). When conditions permitted, we observed *ca.* 10 Red-legged Kittiwakes sitting on nests. On one occasion, we observed two individuals for *ca.* 30 min until they stood and revealed empty nests.

On 06 July, we successfully surveyed the north end of the island, where we found only Black-legged Kittiwakes on the cliffs; however, we found *ca.* 30 Red-legged Kittiwakes on the west side

at a cliff face where they had not been seen previously (Location B [60°32'N, 173°03'W], Fig. 2), *ca.* 5.8 km north of Location A. At Location B, we observed pairs nest stamping, as well as standing and sitting on nests (Fig. 4). Unfortunately, owing to rough seas, we were unable to reach Location A to survey, from the water, the *ca.* 3 km of cliff habitat that was mostly not visible from our land-based observations.

Based on our combined high counts at Locations A and B, we conservatively estimate that there are *ca.* 200 adult Red-legged Kittiwakes present at the locations we visited (representing only *ca.* 12 % of potential kittiwake nesting habitat on St. Matthew, Hall, and Pinnacle islands; World Seabird Union 2019). At the time of our departure from St. Matthew Island on 07 July, we were unable to confirm Red-legged Kittiwake egg-laying.

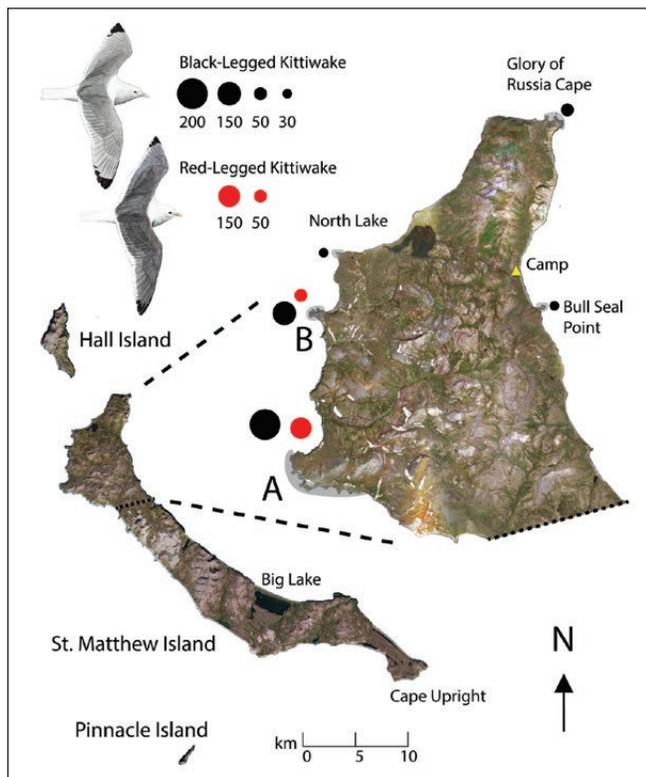


Fig. 2. The St. Matthew Islands including St. Matthew, Hall, and Pinnacle islands, along with an inset of the north end of the island where our observations were focused. Black circles indicate locations and approximate numbers of Black-legged Kittiwake, and red circles indicate location and approximate numbers of Red-legged Kittiwake.

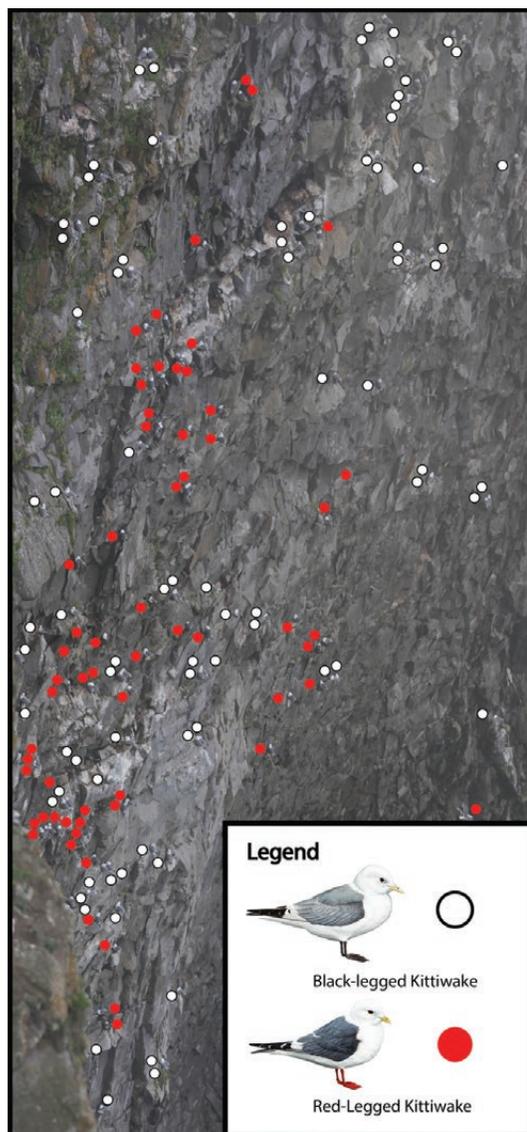


Fig. 3. Kittiwake cliff nesting habitat at a portion of the cliff faces at Location A (Fig. 1). Dots illustrate the abundance and distribution of Red-legged Kittiwake from this observation point. Other habitat where kittiwakes could be heard at Location A were out of view from land-based observers.

DISCUSSION

We document substantial numbers (*ca.* 200) of Red-legged Kittiwakes on St. Matthew Island, along with observations of copulation and nest building that likely indicate that this species is breeding there. Although we provide the first documentation for this species occupying cliffs on St. Matthew Island, it is possible that the birds have been present on the island for some time and have gone unnoticed. Previously, the species' status at St. Matthew has been considered casual or accidental in summer, with the earliest known record of one adult observed in August 1985 (Winker *et al.* 2002). The species has since been observed near the island on a few other occasions, including an eBird report listing two individuals seen in waters south of the island on 01 October 2006 (ML S9104078, www.ebird.org) and a single individual sighted in 2012 near Cape Upright, on the southern tip of St. Matthew Island (T. DeGange *in litt.*). More recently, one individual was observed at Pinnacle Island and two individuals were observed at Hall Island on 18 August 2018 by a tour group (Scott Schuette pers. comm; ML S47934195, S47921944; www.ebird.org). In the broader region of the north Bering Sea, Red-legged Kittiwakes have been documented in low numbers during the breeding season since 2006 (Kuletz & Labunski 2017).

Because of its remote location and challenging weather, very few targeted avian studies have been conducted on St. Matthew Island (Winker *et al.* 2002). Despite this, several notable previous expeditions to the area failed to document Red-legged Kittiwake (Hanna 1917, Gabrielson 1944, Goetzman & Sloan 1982). The failure to record the species was not due to lack of observer effort, as the topic is explicitly addressed in Gabrielson (1944, pg. 130): "We also looked carefully over the kittiwakes on St. Matthew and Hall islands for [Red-legged Kittiwake] but found none." More recently, several expert research teams have visited the islands to conduct standardized seabird monitoring, and none recorded the species (DeGange & Sowls 1978, Byrd & Early 1985, Murphy *et al.* 1987, Mendenhall 1994, Renner & Sowls 2005, Romano & Renner 2012). The absence of previous observations of Red-legged Kittiwakes by so many different teams of trained observers who were familiar with this species supports the scenario that it has only recently begun to occupy

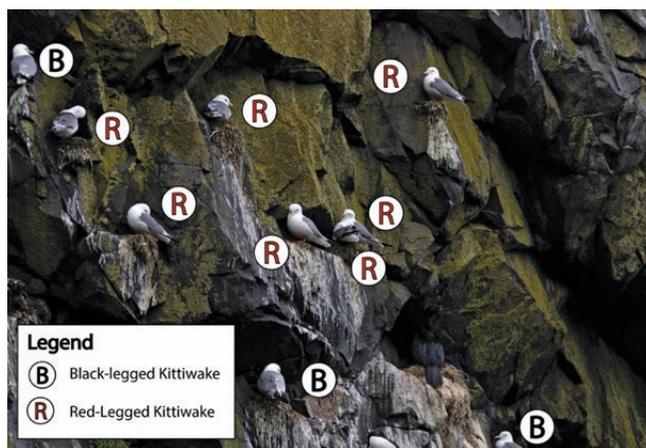


Fig. 4. Example of distribution of kittiwakes on nests at Location B (Fig. 1) as seen from boat-based observations on 06 July 2018. At this location, *ca.* 30 Red-legged and *ca.* 150 Black-legged Kittiwakes were mixed in appropriate habitat, with pairs and single birds perched at nest locations.

St. Matthew Island. However, our land-based observations were made in a very remote part of the island, well away from the usual camp locations of previous expeditions. It is unclear whether previous observers visited Locations A and B, or looked closely over the cliffs for Red-legged Kittiwake. Additionally, most previous observers were conducting their work from land-based sites. The boat-based aspect of our survey helped confirm our land-based observations and allowed us to survey areas inaccessible to land-based crews, which increased our estimate for the number of Red-legged Kittiwakes conducting nesting activities on the island.

Although our survey occurred during the early part of the seabird nesting cycle and we did not observe eggs or young, our observations of nest building and breeding behavior (courtship behavior, birds in incubation posture) provide strong evidence that Red-legged Kittiwakes attempted to breed on St. Matthew Island. The closest Red-legged Kittiwake colony with breeding phenology data for 2018 is located on St. George Island, *ca.* 470 km south of St. Matthew Island. During 2018, laying success of Red-legged Kittiwakes at St. George was very low, and breeding was delayed (Guitart *et al.* 2018). Mean hatch of Red-legged Kittiwakes there occurred on 16 August ($n = 2$), 32 d later than the long-term mean from 1975–2017. Assuming a *ca.* 30-d incubation period (Byrd & Williams 1993), mean laying on St. George occurred on 17 July (Guitart *et al.* 2018). Given the late breeding on St. George in 2018, it is possible that the Red-legged Kittiwakes that we observed on St. Matthew Island may have initiated clutches following our departure from the island on 07 July. This possibility is further supported by our lack of observations of eggs or young of Black-legged Kittiwakes, which we also observed conducting courtship behaviors and nest building. Black-legged Kittiwake is a locally abundant species with a mean laying date that occurs later at higher latitudes (Dragoo *et al.* 2018) and has very similar breeding phenology to Red-legged Kittiwakes when in sympatry (Guitart *et al.* 2018).

Our observations suggest a substantial extension of the Red-legged Kittiwake breeding distribution during a time of great change in the Bering Sea. If their presence at this location continues, it provides an opportunity to understand mechanisms involved in the capacity of this regional endemic to shift its breeding range northward. For instance, it is possible that Red-legged Kittiwake presence at St. Matthew Island was facilitated through prospecting movements, much like those documented in Black-legged Kittiwake (Ponchon *et al.* 2015). Methods such as satellite telemetry on St. Paul and St. George islands may reveal the role of such mechanisms in shifting breeding distribution in response to climatic changes in the Bering Sea region (Ponchon *et al.* 2012).

In some ways, St. Matthew is a surprising location for Red-legged Kittiwakes to colonize. This species is thought to specialize on food resources such as *Stenobranchius leucopsarus* (Family: Myctophidae), which are generally found in waters deeper than 200 m (Beamish *et al.* 1999). St. Matthew Island is located on the Bering Sea Shelf in an area where ocean depth is generally less than 200 m; therefore, deep-water myctophids may not be available as food resources to Red-legged Kittiwakes in close proximity to this breeding location. However, deep water at the shelf break may be within foraging range, although trips to obtain such food resources would be longer than those at breeding locations such as at the Pribilof Islands (*ca.* 230 km from St. Matthew Island compared to *ca.* 100 km from St. Paul). For instance, Black-legged Kittiwakes have been documented making extended foraging trips to access

resources during the brood-rearing period, across distances as large as 201.4 ± 6.9 km ($n = 18$; Paredes *et al.* 2014). Further focus on the breeding status, movements, and diet of St. Matthew Island Red-legged Kittiwakes may provide insight into the species' capacity to shift its range northward through their ability to utilize alternate food resources, or to extend foraging trips to deep water where resources are available.

The Red-legged Kittiwake is listed as vulnerable by the IUCN, a cautionary designation owing to its restricted breeding range and past population decrease (IUCN 2017). Given this status, our finding of Kittiwakes on St. Matthew Island may provide some clarity around downward trends in population and productivity on the Pribilof Islands (Guitart *et al.* 2018). Throughout their annual cycle, continued changes to the oceanographic regime in this region will likely have important implications for Red-legged Kittiwake distribution and population status (Orben *et al.* 2015). Thus, our observations underscore the need for continued focus on Red-legged Kittiwake occupancy at St. Matthew Island, as well as the multitude of other seabirds that breed at this remote Bering Sea location.

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A REVIEW OF RECORDS OF THE BLACK-CAPPED PETREL *PTERODROMA HASITATA* IN THE CARIBBEAN SEA

MARDIK F. LEOPOLD^{1*}, STEVE C.V. GEELHOED¹, MEIKE SCHEIDAT¹, JENNY CREMER¹,
ADOLPHE O. DEBROT¹ & RUUD VAN HALEWIJN²

¹ Wageningen Marine Research, PO Box 57, NL 1780 AB Den Helder, The Netherlands *(mardik.leopold@wur.nl)

² Adelaarhof 14, NL 3514 TZ Utrecht, The Netherlands

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ABSTRACT

LEOPOLD, M.F., GEELHOED, S.C.V., SCHEIDAT, M., CREMER, J., DEBROT, A.O. & VAN HALEWIJN, R. 2019. A review of records of the Black-capped Petrel *Pterodroma hasitata* in the Caribbean Sea. *Marine Ornithology* 47: 235–241.

The Black-capped Petrel *Pterodroma hasitata* is a pelagic seabird with a dangerously small population size. Remaining breeding sites are threatened by habitat loss, introduced predators, and direct harvesting. The species likely also faces several threats at sea, but because knowledge of its distribution range and ecology is meagre at best, it is challenging to take concerted action to improve its conservation status. The species is currently known to breed only on Hispaniola (in the northern Caribbean Sea), but most at-sea observations are from the Florida Current and the Gulf Stream off the southeastern coast of the USA. Within the Caribbean Sea, observations are scarce. We compiled a database of at-sea sightings of Black-capped Petrels in the Caribbean Sea from 1953 to 2018 by thoroughly reviewing published and unpublished records (Appendix 1); here, we add to the literature 12 new records from a research cruise conducted in February 2018 across the Caribbean Sea. Our database was augmented with recently published information from three birds that were fitted with tracking devices. Based on the collected information, we argue that the existing distribution maps of Black-capped Petrels need adjustments. We show that Black-capped Petrels have been recorded throughout the central parts of the Caribbean, from the known breeding sites in the north down to coastal waters off Panama, Colombia, and Venezuela. However, the birds probably forage only in small parts of the Caribbean Sea (i.e., the coastal upwelling zones off Hispaniola and Cuba in the north and off the South American mainland in the south). The waters in between (i.e., in the central Caribbean Sea) appear to be mainly used as a corridor, while the eastern and western parts are unimportant. This indicates that certain hotspots within the Caribbean Sea may be more important to this endangered species than previously thought.

Key words: Black-capped Petrel, diabolite, at-sea distribution, Caribbean Sea

INTRODUCTION

The Black-capped Petrel *Pterodroma hasitata* is an Endangered pelagic seabird (BirdLife International 2018) whose breeding distribution is not well known. The species is endemic to at least one island in the northern Caribbean Sea. Historically, it bred on several islands from Hispaniola to Martinique (Goetz *et al.* 2012) and possibly in Cuba (Ruíz 1998), but it has suffered from human exploitation since pre-Columbian times (van Halewijn & Norton 1984). It was thought to be on the brink of extinction in the early 20th century (Bent 1922, Murphy 1936), but several breeding colonies were discovered in steep, mountainous terrain in Haiti in the early 1960s (Wingate 1964). Confirmed breeding is restricted to Hispaniola, in both Haiti and the Dominican Republic (four known colonies; USFWS 2018). However, the species may also breed in Dominica, where a grounded bird with a brood patch was found in 2007 (Scofield *et al.* 2010). Brown (2015) mentions two different adults that were found in the Roseau Valley below Morne Micotrin, “indicating the potential presence of a nesting population”. Radar surveys yielded 968 Black-capped Petrel-like “targets” (i.e., petrel-like birds) flying over the island in January (breeding season) 2015, and eight birds were visually observed flying over Dominica (Brown 2015). Furthermore, the combination of nearshore sightings at sea, observations of birds flying over land, and the presence of potentially suitable breeding habitat in inaccessible mountain peaks

indicates that the species might also breed in Cuba. However, the possibility that these birds are, in fact, breeding in Hispaniola cannot be excluded yet (USFWS 2018). Congregations of birds have been recorded in the breeding season feeding just off the southern coastline of Cuba, in an area of upwelling (Lee & Vina 1993, Goetz *et al.* 2012). Both in Cuba and Dominica, active nests have yet to be found, but searching for nests is extremely difficult in the remote, inaccessible, steep, mountainous breeding habitat of this species. It seems unlikely that Black-capped Petrels are still breeding in Guadeloupe and Martinique, where birds have been over-harvested (Bent 1922) and remaining breeding colonies were destroyed by various geological events (earthquakes, landslides, volcanic eruptions; USFWS 2018). Former breeding habitats are now degraded by deforestation and birds have not been found breeding for more than 100 years on either island (USFWS 2018). However, the species still frequents the waters around these presumed former breeding sites (van Halewijn & Norton 1984, Levesque & Yésou 2005, Goetz *et al.* 2012, Simons *et al.* 2013, BirdLife International 2018) and searches for nesting birds are ongoing (e.g., Wheeler 2018).

Black-capped Petrels have only rarely been sighted in the Caribbean Sea. They are predominantly seen further north: in the Florida Current and the Gulf Stream off the southeastern USA, with stragglers reaching Canada, northwestern Africa, and southwestern

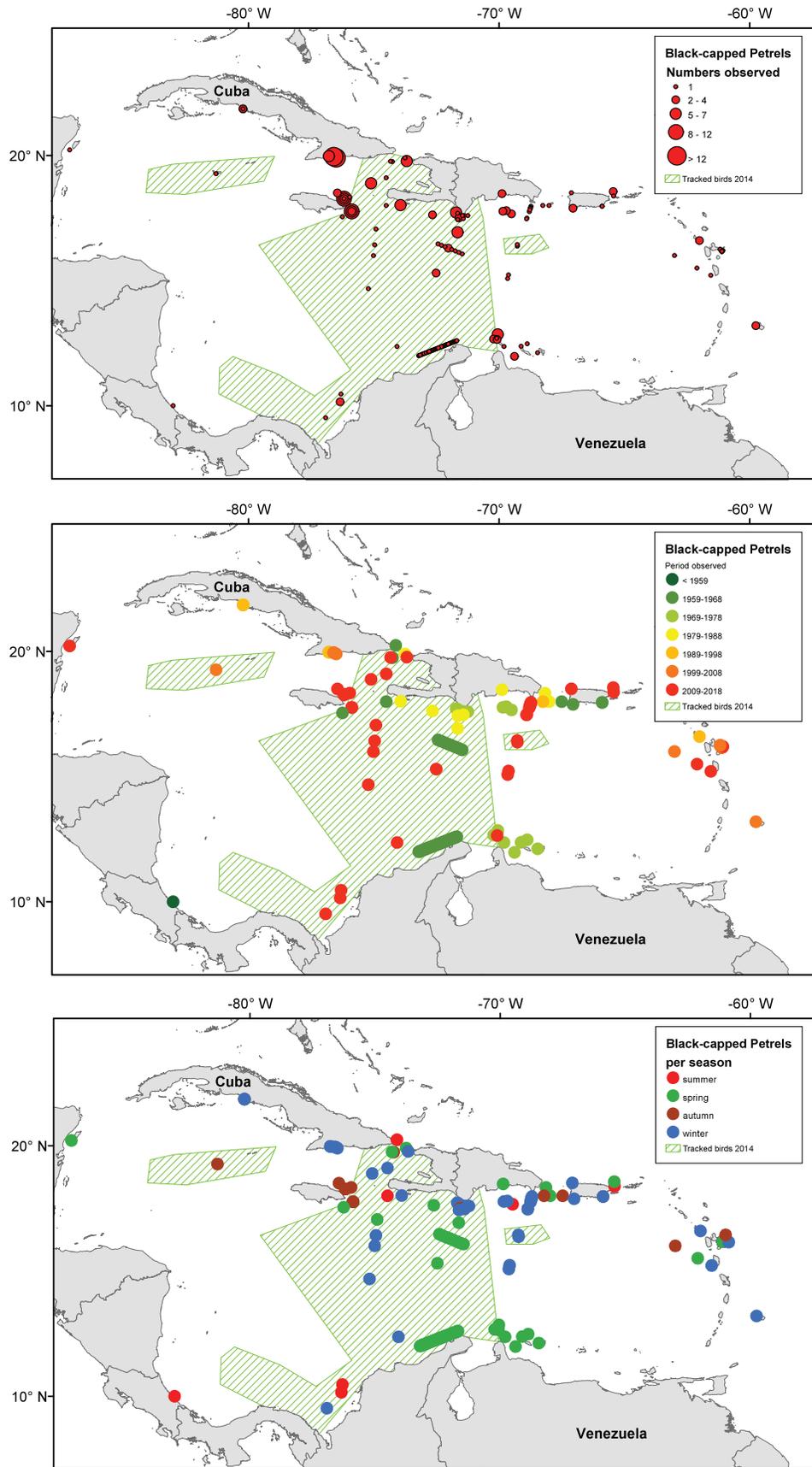


Fig. 1. Plots of all records found of Black-capped Petrels in the Caribbean Sea by numbers per sighting (top), by decade (middle), and by season (bottom). Summer: June–August, autumn: September–November, winter: December–February, spring: March–May. See Appendix 1 for further details.

Europe (Brooke 2004, Simons *et al.* 2013, Flood & Williams 2018). Their at-sea distribution range, the relationship between distribution and oceanography, the timing of occurrence, and the plumage variation of Black-capped Petrels off the east coast of the USA are documented from at-sea surveys and pelagic trips for birders (Haney 1987, Howell & Patteson 2008, Simons *et al.* 2013). General distribution maps appear to rely heavily on the data collected off the east coast of the USA and on the present and historical breeding ranges.

Knowledge of the at-sea distribution within the Caribbean Sea is scant and based on few published records. Distribution maps in standard reference works vary considerably (e.g., compare Harrison 1983, del Hoyo *et al.* 1992, Raffaele *et al.* 1998, Brooke 2004, Farnsworth 2010, Simons *et al.* 2013, BirdLife International 2018, USFWS 2018). However, most sources agree that the distribution is mainly confined to waters east of 80°W and that the species is rare or absent in the southernmost parts of the Caribbean. Recent data from three satellite-tracked breeding birds showed regular commuting between Hispaniola and waters off Venezuela and Colombia (Jodice *et al.* 2015).

Following a research cruise across the Caribbean Sea in February 2018, during which we recorded 12 Black-capped Petrels, we compiled all earlier records that we could trace to provide an updated distribution map of the species in the Caribbean Sea. This review was prompted by the poor conservation status of the Black-capped Petrel and the relative lack of knowledge on the distribution of the species in the Caribbean Sea.

STUDY AREA AND METHODS

We searched for records of Black-capped Petrels in the Caribbean Sea in the literature and via the internet. Our main sources were *Sea Swallow* (the journal of the Royal Naval Birdwatching Society), the eBird database (eBird 2017), and unpublished reports that were sent

to us by other observers, including student reports and field notes. For mapping purposes, descriptions of positions such as “just out of sight of Dominican Republic when leaving the Mona Passage to the south” were translated to latitude/longitude positions using Google Earth. Duplicates were removed and bulk records (e.g., 40 birds seen between two latitude/longitude positions in one day while on transit from Curaçao to the Panama Canal (Mörzer Bruyns 1967)) were placed equidistantly between the beginning and end of such transects.

Our own cruise track ran from Aruba across the Caribbean Sea to the coastal waters off the southeastern tip of the Dominican Republic, then on to St. Maarten (04–11 February 2018). Seabirds and other megafauna were recorded within a 300 m wide strip on the side of the vessel that offered the best viewing conditions. In addition to these strip counts, all birds seen within a 180° scan ahead (port to starboard) were recorded (see Tasker *et al.* 1984). The observation platform was situated along the ship’s centerline on the top of the bridge, nine metres above sea level; this offered an unobstructed view forward and to both sides. Counts were conducted during daylight hours when the ship was steaming at speeds of 5.6 ± 1.2 knots (10.3 ± 2.3 km/h). The total distance covered was 293 nautical miles (542 km) over 52.7 hours. Birds were not actively attracted to the vessel (e.g., by chumming), and the ship did not deviate from its track to approach birds that were sighted.

RESULTS

The first record of a Black-capped Petrel in the Caribbean Sea concerned a bird that was presumably blown off course towards the coast of Costa Rica in the southwestern Caribbean by a hurricane on 14 August 1953 (Stiles & Skutch 1989). From the 1960s to the 1980s, birds were reported by naval and merchant ships’ officers to the *Sea Swallow* administrator, starting with 40 birds seen on 01 May 1962 in the south-central Caribbean Sea by Capt. Mörzer Bruyns (1967) while in transit from Curaçao to the Panama Canal (Fig. 1, Appendix 1). Additional sightings in the southern Caribbean

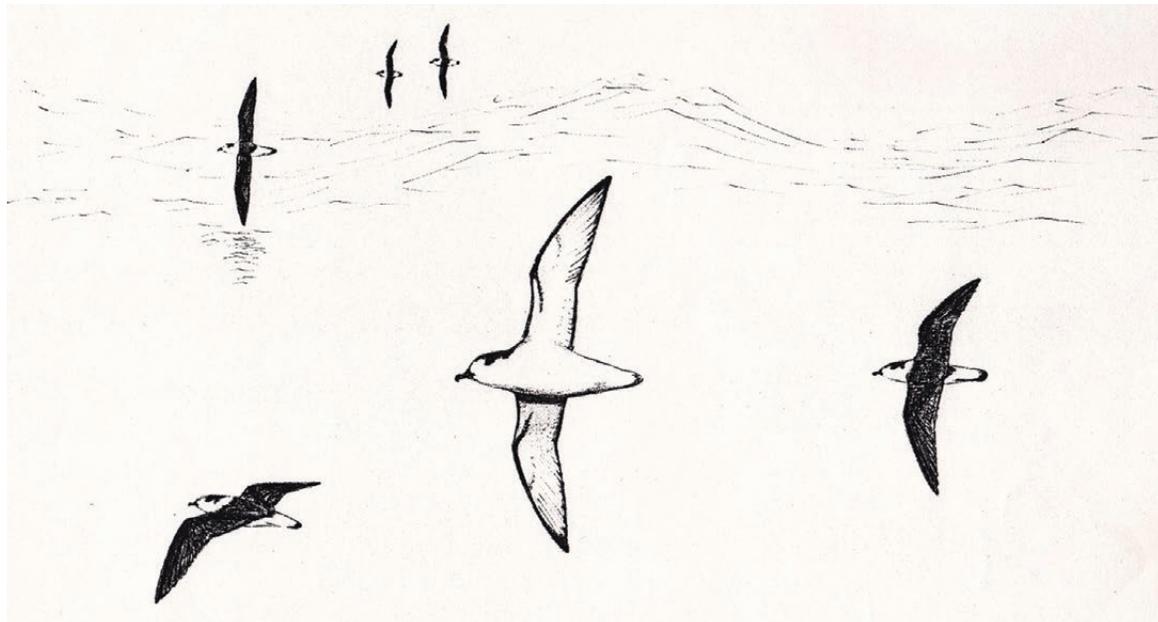


Fig. 2. A field sketch of Black-capped Petrels in the northern Caribbean Sea off Hispaniola, drawn by Käthy Meeth-Kühr, 03 December 1977. Käthy was married to Piet Meeth, director of the Nedlloyd shipping company in Rotterdam. Both were avid birdwatchers with a special interest in (rare) seabirds, and as pensioners, the couple made several long sea voyages (Voous 1995).

were made in April–May 1970 by van Halewijn (1972), who sighted 15 birds near Aruba, Curaçao, and Bonaire on seven occasions (see Appendix 1 for details on dates and positions of sightings).

Most records come from the northern and central Caribbean (Figs. 1, 2), rather close to known and possible breeding colonies. Relatively large numbers of birds were recorded in Windward Passage (between Cuba and Haiti) and Mona Passage (between the Dominican Republic and Puerto Rico), both of which are frequently used by ships heading to or from the Panama Canal. Six birds were collected at sea on 28 January 1977 in waters with coastal upwelling off (Punta) La Bruja, Sierra Maestra in southeastern Cuba (~76.5°W). According to local fishermen interviewed in January 1992, “the sounds [of birds calling] occurred [here] every night during the winter”. Fifteen years later, “hundreds” of birds (based on vocalisations at night) were present in the same waters on 20 and 21 January 1992 (Lee & Vina 1993). On 23 February 2004, 40 birds were noted vocalising on the water in the same area (Goetz *et al.* 2012). Slightly farther west, off Uvero (~76.6°W), Norton *et al.* (2004) reported similar observations of 25 birds on 09 February 2004 and 46 birds on 24 February 2004. Still further west along the coast of southern Cuba (~80.2°W), Ruíz (1998) reported vocalising birds in nearshore waters at the mouth of the River Yaguanabo in November 1976, February 1982, and January 1990. On this last occasion, one bird was shot from a small boat but was lost at sea; however, a rather freshly dead but scavenged corpse of a female Black-capped Petrel was found on the beach the next morning.

In November 2009, between one and twelve birds were attracted to a small vessel during nine successful chumming sessions off eastern Jamaica (Shirihai *et al.* 2010). This confirmed the only previous record of a Black-capped Petrel in this area (in December 1979; Douglas & Zonfrillo 1997). In January and February 2004, three Black-capped Petrels (and another four unidentified *Pterodroma* from the January–March period that were “most likely this species”) were seen passing by eastern Guadeloupe during 380 hours of year-round land-based seawatching (2001–2004; Levesque 2005, Levesque & Yesou 2005). Continued seawatching from Guadeloupe produced 10 more Black-capped Petrel sightings between 2005 and 2008: six between October and January and four between March and May (eBird 2017; Levesque & Yésou 2018). This contrasts with results of aerial surveys from 04 February to 05 March 2008 around St. Maarten/St. Martin, St. Barthélémy, Guadeloupe, and Martinique, which produced no sightings of Black-capped Petrels (Van Canneyt *et al.* 2009).

Recent records of Black-capped Petrels in the southern and central Caribbean Sea are restricted to three birds seen in association with killer whales *Orcinus orca* near Aruba on 14 April 2011 (Luksenburg & Sangster 2013) and seven birds seen in nearshore Colombian waters (five birds in June 2014 and two birds in January 2015; Digby *et al.* 2015). In addition, our own sightings comprise 12 single birds, seen 06–08 February 2018, between 15°N and 18°N and between 68°W and 70°W. Only one of these birds observed in 2018 was seen swimming; all others were flying, without any indication of foraging behaviour. All collected data are summarised in Appendix 1.

Jodice *et al.* (2015) satellite-tagged three Black-capped Petrels that were breeding on the Sierra de Bahoruco in the Dominican Republic. These birds were found to commute between their

breeding colony and continental shelf waters off northern South America during the chick-rearing period (April–July 2014). These coastal waters off Venezuela, Colombia, and Panama are known for regional seasonal upwelling, which results in enhanced productivity from January to June (Castellanos *et al.* 2002; Paramo *et al.* 2003, 2011; Rueda-Roa & Muller-Karger 2013; Villamizar & Cervigón 2017). The tracking data corroborated the earlier records of birds seen across the Caribbean by Mörzer Bruyns (1967), van Halewijn (1972), Luksenburg & Sangster (2013), and Digby *et al.* (2015). One of the tagged birds flew further west than any visually recorded bird in the Caribbean Sea, except for one seen off Costa Rica in August 1953 and one observed in nearshore Mexican waters in April 2011 (Simons *et al.* 2013). These two apparent outliers (Fig. 1) would now seem more fitting in the light of the tagging results of Jodice *et al.* (2015) and recent sightings in the Gulf of Mexico (Gleason 2017, USFWS 2018, Wheeler 2019).

Seasonality

In coastal waters within the northern Caribbean Sea, Black-capped Petrels have been observed in all four seasons (Fig. 1). No observations are known from the northeastern Caribbean in summer, though there are records from these parts in all other seasons. In the southern Caribbean, Black-capped Petrels have not been recorded in autumn, when coastal upwelling and biological productivity are at an annual minimum (Rueda-Roa & Muller-Karger 2013), but they have been observed in this region during all three other seasons, when coastal upwelling is prominent. Black-capped Petrels have been recorded in the southern Caribbean both in the breeding season (see Jodice *et al.* 2015) and at other times of the year, but only when upwelling occurs.

Negative records

Negative records (i.e., seabird watches during which no Black-capped Petrels are seen) that have been reported to eBird are depicted at <https://ebird.org/map/bkcpet?neg=true> (accessed 29 May 2019). Considerable effort with only negative records is shown for both the western and eastern Caribbean Sea, indicating that the positive records (Fig. 1) in the central Caribbean Sea are not just due to lack of effort in other parts. Negative records for the northeastern Caribbean Sea can be found in Postma & Nijkamp (1996), Keith & Ward (1997), Keith & Keith (2005), and Van Canneyt *et al.* (2009); records for the southwest in Naranjo (1979), Hilty & Brown (1986), and Ridgely & Gwynne (1989); and records for the central and southeastern parts of the Caribbean Sea in Poppe (1974), Murphy (2002), Buckley *et al.* (2009, excepting one record near Barbados), French (2012), and Geelhoed *et al.* (2014).

Adjacent waters

Black-capped Petrels are mostly seen in Atlantic Gulf Stream waters north of the Caribbean Sea, particularly off the southeastern USA (Haney 1987, White 2004, Howell & Patteson 2008, Simons *et al.* 2013). Anywhere else, the species is rare or absent. In the Gulf of Mexico, the species was considered very rare (eBird 2017), but recent surveys for the Gulf of Mexico Marine Assessment Program for Protected Species (GoMMAPPS) revealed a more prominent presence than previously known (Gleason 2017, Wheeler 2019). In the Atlantic Ocean east of the West Indies, only one credible record exists: two birds were seen just southwest of Barbados in early 2003 (Norton *et al.* 2003). Despite at-sea surveys, the species

is unrecorded in waters off Trinidad & Tobago, Guyana, Suriname, French Guiana, and northeastern Brazil (F. Hayes pers. comm.; de Boer *et al.* 2014; eBird 2017; Willems *et al.* 2017; Lepage 2018a, 2018b, 2018c). Though records are often claimed (and copied from earlier claims) from northeastern Brazilian waters, these are questionable (Piacentini *et al.* 2015). In the Atlantic at large, only a few stragglers have been reported (Brooke 2004, Simons *et al.* 2013, Flood & Williams 2018).

DISCUSSION

Our overview shows that birds have been recorded over the central parts of the Caribbean Sea, from coastal waters off southeastern Cuba and Hispaniola south to Panama, Colombia, and Venezuela. In the northeastern part of the Caribbean Sea, the distribution continues from Hispaniola along the chain of islands down to Dominica and possibly further, given the single observation just southwest of Barbados in early 2003. However, there are few records from the western and the eastern Caribbean Sea. In particular, the waters east of Curaçao, including the upwelling areas off Isla Margarita, northeastern Venezuela, and Trinidad and Tobago, have been relatively well surveyed (van Halewijn 1972, Poppe 1974, Murphy 2002), but Black-capped Petrels were never seen. Claims of birds seen even further southeast are doubtful at best (Piacentini *et al.* 2015). We therefore conclude that, given the amount of effort and only negative results in the eastern and western Caribbean Sea, the range of Black-capped Petrels appears to be confined to the central third of the Caribbean Sea.

The collected sightings and tagging data show that the existing distribution maps of Black-capped Petrels need adjustments. Published maps either show no Black-capped Petrels in the entire southern half of the Caribbean Sea (e.g., Harrison 1983, del Hoyo *et al.* 1992, Farnsworth 2010), or they miss the coastal upwelling waters off the South American mainland (Brooke 2004, Simons *et al.* 2013, BirdLife International 2018). The most recent distribution map published by the US Fish and Wildlife Service (USFWS 2018) incorporates the new insights from the tracking data. However, it still leaves the nearshore waters off Venezuela, Colombia, and Panama blank while showing the entire eastern Caribbean Sea and parts of the Atlantic Ocean east of the southeastern Caribbean islands as regular Black-capped Petrel range. More emphasis is needed on the coastal upwelling zone in the southern Caribbean Sea, while the central Caribbean Sea should be shown as merely a commuting lane for Black-capped Petrels.

Most at-sea sight records of Black-capped Petrels in the Caribbean Sea appear to be of birds passing through. Except for the Luksenburg & Sangster (2013) record of three individuals associated with killer whales hunting near Aruba, at-sea observers (including ourselves) never reported feeding behaviour. Recent work with satellite-tracked breeding birds (Jodice *et al.* 2015) indicated that Black-capped Petrels cross the Caribbean Sea swiftly, heading for presumed feeding areas in the seasonally highly productive coastal waters off western Venezuela, Colombia, and Panama. However, exactly how the birds exploit these coastal waters and which prey they target remains unknown. Dedicated vessel-based surveys of these presumed foraging areas that cover the prey and the feeding behaviour of Black-capped Petrels synoptically, would be the next logical step to get a complete picture of the conservation value of the upwelling zone in the southern Caribbean Sea for Black-capped Petrels. Additionally,

more birds should be satellite tagged, to provide a better picture of the full range of the species in the Caribbean Sea and to find any ecological hotspots worthy of special protection (see Soanes *et al.* 2016, American Bird Conservancy 2019).

The poor conservation status of the Black-capped Petrel should be an incentive for such studies: the species has a small and declining population size, and it is threatened at its remaining breeding sites by habitat loss, introduced predators, direct harvesting, collisions with man-made structures, and light pollution (DeNovelis 2011, Goetz *et al.* 2012, Simons *et al.* 2013, BirdLife International 2018, USFWS 2018). The species is at risk while at sea as well, through the increasing incidence of hurricanes and the weakening of upwelling systems due to climate change (Hass *et al.* 2012, Villamizar & Cervigón 2017); poor supervision of offshore mining and shipping operations that results in frequent oil spills; other pollutants, such as mercury or plastics (USFWS 2018); and competition for resources from fisheries (Lindop *et al.* 2015). Identifying key at-sea feeding areas, understanding how Black-capped Petrels exploit the resources within these sites, and protecting these areas are of fundamental importance to save the species from extinction.

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MAXIMUM OBSERVED AGES OF GALÁPAGOS PENGUINS

GUSTAVO JIMÉNEZ-UZCÁTEGUI¹ & F. HERNÁN VARGAS²

¹Charles Darwin Research Station, Charles Darwin Foundation, Puerto Ayora, Galápagos, Ecuador (gustavo.jimenez@fcdarwin.org.ec)

²The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, ID 83709, USA

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ABSTRACT

JIMÉNEZ-UZCÁTEGUI, G. & VARGAS, F.H. 2019. Maximum observed ages of Galápagos Penguins. *Marine Ornithology* 47: 243–246.

A maximum age of at least 17.7 years was recorded for a Galápagos Penguin *Spheniscus mendiculus* on Isabela Island during studies up until 2018. This individual was first captured as an adult of at least two years of age, as indicated by its plumage. In addition, we present records of other penguins, not quite as old, that were first captured as chicks. Longevity is affected by many different factors, making it useful in the design of conservation strategies.

Key words: longevity, Galápagos Islands, penguins

INTRODUCTION

The Galápagos Penguin *Spheniscus mendiculus* (GAPE) is endemic to the Galápagos Islands (Harris 1973), breeding on Fernandina, Isabela, Floreana, and Santiago islands, and Marielas and Lougie islets (Vargas 2006). With restricted geographic distribution and a small, fluctuating population size, this species is listed as Endangered (IUCN 2018). The latest survey estimates the population at 1900 individuals (Jiménez-Uzcátegui 2018), although the population fluctuates greatly with El Niño Southern Oscillation (ENSO) events (Vargas *et al.* 2006, 2007; Valle & Coulter 1987, Valle *et al.* 1987). The species faces several threats: introduced species such as cats *Felis catus* and rats *Rattus* spp. prey on chicks and eggs (Boersma 1977), and artisanal fishing causes mortality by entanglement (Crawford *et al.* 2017). Pollution (Jiménez-Uzcátegui *et al.* 2017), pathogens, and parasites put further pressure on its population (Merkel *et al.* 2007, Deem *et al.* 2010, Levin *et al.* 2013, Carrera *et al.* 2014).

The average life expectancy of the GAPE was estimated at 11 years (Boersma *et al.* 2013). Of the 17 species of penguins (Sphenisciformes) worldwide, the oldest recorded individual in the wild belongs to the Magellanic Penguin *Spheniscus magellanicus* species at 30 years old (Scolaro 1990), followed by the African Penguin *Spheniscus demersus* species at 27 years old (Whittington *et al.* 2000), the King Penguin *Aptenodytes patagonica* species at 26 years old (Flower 1938), and the Little Penguin *Eudyptula minor* species at 25.8 years old (Dann *et al.* 2005). For comparison, the longevity records of other Galápagos seabirds range from 40.8 years for the Waved Albatross (WAAL) *Phoebastria irrorata* to 17.2 years for the Flightless Cormorant (FLCO) *Phalacrocorax harrisi* (Jiménez-Uzcátegui *et al.* 2012, 2016).

METHODS

As part of the ecological monitoring program carried out from 2001 to 2018 by the Charles Darwin Foundation (CDF) with the Galápagos National Park Directorate (GNPD), a total of 1822 penguins were marked with Passive Integrated Transponder (PIT) tags at the following locations: Caleta Iguana (0.97668°S,

91.44682°W), Puerto Pajas (0.75480°S, 91.37505°W), El Muñeco on Isabela Island (0.03058°N, 91.54682°W), and the Marielas Islets (0.59570°S, 91.08750°W).

Over the last eight years (2010–2018), 1011 tagged penguins were recaptured. Data from 2015 to 2018 were used to estimate their maximum ages. Median and maximum ages were established for penguins tagged when they were chicks or adults. Median age was estimated with non-parametric statistics. The maximum age of penguins tagged as chicks was calculated as the time elapsed in years since the bird was tagged until the latest recapture. The maximum age of penguins tagged as adults was calculated as the time elapsed in years from when the bird was tagged to the time of the latest recapture, plus two years to account for the transition time from juvenile to adult plumage (Boersma 1977).

RESULTS

Median and maximum ages of penguins tagged as chicks

The oldest penguin that was tagged as a chick and recaptured was 14.2 years old (Table 1). The last recapture of this penguin was on 24 July 2018 at Caleta Iguana. This male was marked with PIT-tag 053-770-030 as a chick on 15 May 2004 by HV and was recaptured in 2010, 2012, 2013, 2015, 2016, 2017, and 2018 by GJU at the same location. The next oldest penguin was 13.11 years old (Table 1). It was last recaptured on 27 July 2018 at El Muñeco (Isabela Island) by GJU. This male was tagged by HV as a chick on 09 August 2004 with PIT-tag 053-260-894 and was recaptured in 2005 and 2018 at the same location. The maximum age of penguins tagged as chicks in 2015, 2016, and 2017 was 12 years old (Fig. 1). In 2018, 17 penguins were recaptured and 142 individuals captured for first time. The median age of these 17 birds was 2.7 years old (SE ± 1.14).

Median and maximum ages of penguins tagged as adults

The oldest GAPE was recaptured on 08 November 2016 on Caleta Iguana (Isabela Island). It was a female penguin tagged as an adult by HV on 01 April 2001, a capture-recapture interval of 15.7 years.

At the time of tagging, with PIT-tag 041-858-870, this bird had adult plumage, suggesting that the penguin was at least two years of age. Therefore, the individual was estimated to be 17.7 years of age in November 2016, the oldest age recorded for GAPE (Table 1, Fig. 2). This individual was recaptured in the same colony at Caleta Iguana in 2004, 2005 (when it was recorded breeding), 2015, and 2016 by GJU. The maximum age of penguins tagged as adults in 2015, 2017, and 2018 was 17, 13, and 12 years, respectively (Fig. 1). In 2016, a total of 68 GAPE were recaptured, and 45 were captured for first time. The median age of these 68 individuals tagged as adults was 5.4 years (SE \pm 0.4; Fig. 2).

DISCUSSION

It is known that animal longevity is related to genetic, environmental, evolutionary, and physiological factors (Harvey & Purvis 1999). The three oldest penguins, listed in Table 1, were born after the last strong ENSO event of 1997–1998. Warm-ENSO events are known

to cause population crashes of penguins (Vargas *et al.* 2007), which might affect their age structure. Over the past 20 years, warm-ENSO events in the Galápagos Islands have been weak, but were associated with reduced breeding success (Jiménez-Uzcátegui *et al.* 2019). Introduced species in the study area, such as cats and rats, could also affect age structure because they prey on chicks and eggs. Interestingly, the highest survival rates of penguins occur in areas where the Galápagos National Park controls these exotic predators. Penguins are subject to additional threats, but these threats have minimal effects on penguin mortality. Regardless, it is important to study and control these factors (Jiménez-Uzcátegui *et al.* 2019).

Lacking large mammalian predators, Galápagos birds are expected to live longer than their counterpart mainland species. On the other hand, GAPE and other marine birds face extreme climatic variations due to El Niño (Valle *et al.* 1987, Vargas *et al.* 2006, Jiménez-Uzcátegui *et al.* 2019), which puts them under extreme stress due to food shortages. GAPE are also not the only species that

TABLE 1
Maximum observed ages of Galápagos Penguins, Galápagos Archipelago

| Identification | | Tagging | | | Re-capture | | Age (years) | |
|----------------|------------------|-------------|------------------|---------------|-------------|---------------|-------------|---------|
| PIT-tag | Sex ^a | Date | Age ^b | Location | Date | Location | Actual | Maximum |
| 041-858-870 | F ^c | 01 Apr 2001 | A | Caleta Iguana | 08 Nov 2016 | Caleta Iguana | 15.7 | 17.7 |
| 053-770-030 | M ^c | 15 May 2004 | C | Caleta Iguana | 24 Jul 2018 | Caleta Iguana | 14.2 | - |
| 053-260-894 | M ^d | 09 Aug 2004 | C | El Muñeco | 27 Jul 2018 | El Muñeco | 13.11 | - |

^a F: Female, M: Male.

^b A: Adult, C: Chick.

^c Sexed by morphological measurements (Capello & Boersma 2018).

^d Sexed by molecular techniques.

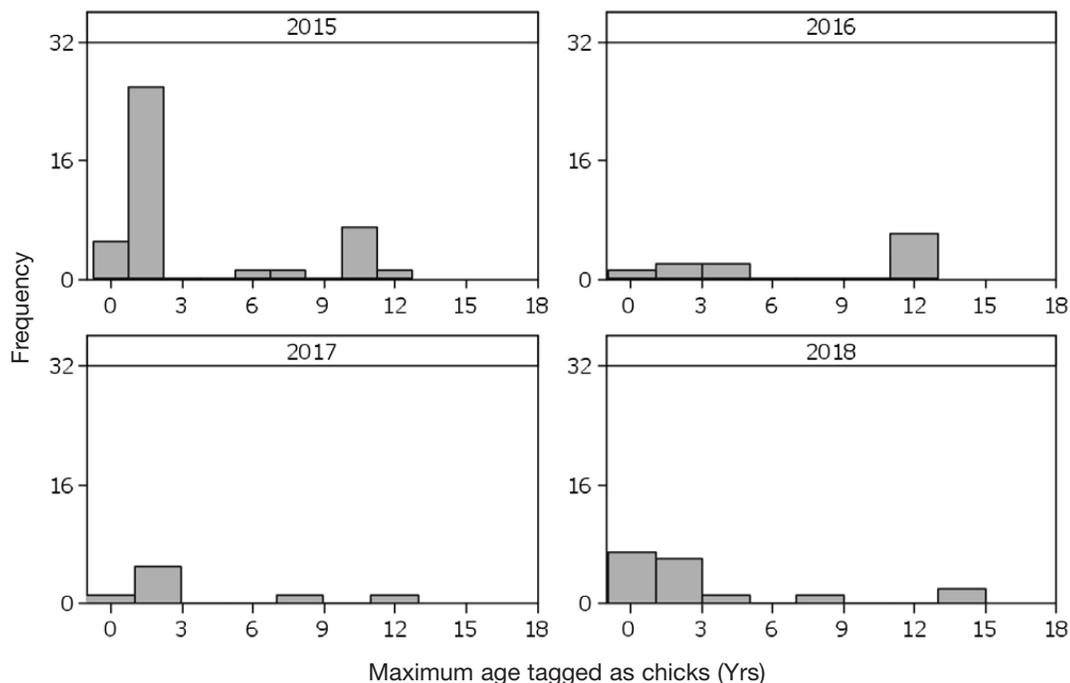


Fig. 1. Distribution of maximum ages of Galápagos Penguins that were tagged as chicks and recaptured between 2015 and 2018. The oldest penguins were recaptured in 2018.

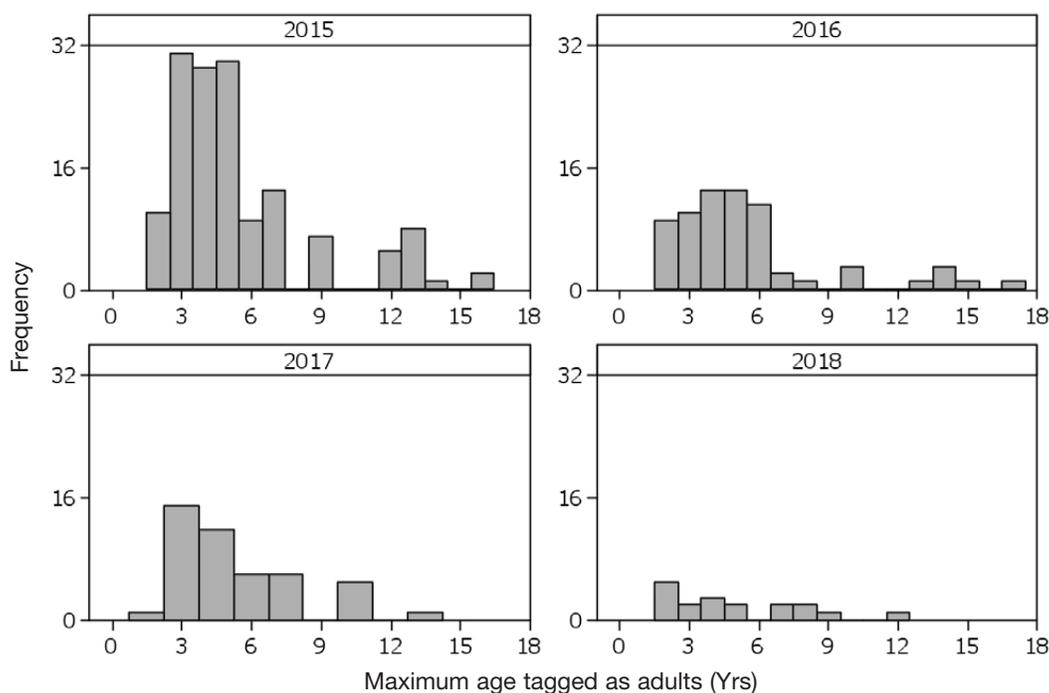


Fig. 2. Distribution of maximum observed ages of Galápagos Penguins that were tagged as adults (age at least 2 years) and recaptured between 2015 and 2018. The oldest penguin (17.7 years old) was recaptured in 2016.

deal with ENSO. Further investigation of the longevity of GAPE and other marine birds, including increased sample sizes of tagged individuals, is essential for devising conservation strategies.

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PHYSIOLOGICAL TOOLKIT TO ASSESS THE HEALTH IMPACTS ON A MAGELLANIC PENGUIN *SPHENISCUS MAGELLANICUS* COLONY IN A HIGH-USE TOURISTIC REGION OF PATAGONIA, ARGENTINA

VERÓNICA L. D'AMICO^{1*} & MARCELO BERTELLOTTI^{1,2}

¹Laboratory of Applied Ecophysiology, Centro para el Estudio de Sistemas Marinos-Centro Nacional Patagónico (CESIMAR-CCT CONICET CENPAT), Bvrd. Brown 2915 (9120), Puerto Madryn, Chubut, Argentina *(damico@cenpat-conicet.gob.ar)

²Faculty of Production, Environment and Sustainable Development, University of Chubut, Alem 1573 (9120) Puerto Madryn, Chubut, Argentina

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ABSTRACT

D'AMICO, V.L. & BERTELLOTTI, M. 2019. Physiological toolkit to assess the health impacts on a Magellanic Penguin *Spheniscus magellanicus* colony located in a high-use touristic region of Patagonia, Argentina. *Marine Ornithology* 47: 247–251.

We evaluated the health status of Magellanic Penguins *Spheniscus magellanicus* inhabiting a region on the Valdés Peninsula (Patagonia, Argentina) that is subject to extensive tourism. We compared individuals nesting along tour trails with others inhabiting non-touristic zones. Hematocrits, blood cell counts, glucose, cholesterol, total proteins, and heterophil/lymphocyte were considered as stress indices. Most parameters were not affected by tourism. Adults and chicks tested positive for bacterial pathogens in both the touristic and control areas. These data complemented a long-term database of systematic physiological monitoring on penguins and will be useful tools for future comparative analyses.

Key words: bacteria test, biochemistry, hematology, Patagonia, penguins, tourism

INTRODUCTION

Physiological parameters are very useful indicators of the health status of free-living mammals and birds. Due to the functional links between the immune system, nutrition, and metabolism, hematological studies have provided accurate assessments of the overall physical condition in several vertebrate groups (Wikelski & Cooke 2006). Consequently, hematology parameters have been recently used to assess anthropogenic effects on wildlife (Geffroy *et al.* 2017, Palacios *et al.* 2018).

Ecotourism is an activity that adversely impacts wildlife by altering the behavior of wild animals (Ellenberg 2017), along with their stress condition and/or reproduction (French *et al.* 2010). For example, it has been reported that changes in behavior alter glucocorticoid levels and immunity parameters in several penguin species (Walker *et al.* 2005, 2006; Palacios *et al.* 2018).

Penguin colonies constitute one of the most popular tourism destinations, particularly during the reproductive season, in the Southern Hemisphere (Ellenberg 2017). The Magellanic Penguin *Spheniscus magellanicus* is the most important touristic resource species inhabiting the Patagonian coast in Argentina (Bertelotti *et al.* 2015). The total penguin population is estimated to be greater than 900 000 breeding pairs (Bertelotti 2013, Pozzi *et al.* 2015). One colony that is known to be growing is in San Lorenzo, which is within the Peninsula Valdés area (42°50'S, 063°49'W); it has ~135 000 breeding pairs and a growth rate of 1.21 breeding pairs per year (Pozzi *et al.* 2015). In parallel, tourist activity in San Lorenzo has also been increasing during the last 20 years (e.g., ~10 000 tourists visited the area in 2014), according to Secretaría de Turismo y Areas Protegidas (Chubut, Argentina).

We evaluated the physiological conditions of the Magellanic Penguins at San Lorenzo using hematological parameters to compare individuals occupying tourist-accessible areas with control individuals located in a portion of the colony that never receives tourist visits. Tourist visits are restricted to a small portion of the colony by way of fenced walking trails. Thus, we would expect that penguins inhabiting these touristic areas to show depressed physiological conditions when compared to individuals in the control area. Additionally, as humans could introduce novel pathogens into the system (Barbosa & Palacios 2009), we analyzed the presence of bacterial pathogens thought to be potentially harmful. The results from this study will complement a long-term database used to address the health condition of Magellanic Penguins over time. This database was formed using results from studies on cellular immunology (D'Amico *et al.* 2014), immune responses to helminth parasites (D'Amico *et al.* 2018), physiological parameters (Palacios *et al.* 2018), and oxidative stress parameters (Carabajal 2017, Colominas-Ciuró *et al.* 2017). Therefore, the final aim of this study is to add data to build a more comprehensive database that could be used as a toolkit to address the health condition of any Magellanic Penguin colony.

METHODS

Fieldwork

Penguins were sampled in early December 2014, when adults were rearing young chicks. We randomly selected 32 adults and 22 chicks (1.5–2 months old), both in the touristic area and in the control area. The latter was comparable to the touristic area in terms of nest density, breeding phenology, and distance to the shore (Villanueva *et al.* 2014). After capture, blood samples

(0.5–1.0 mL) were extracted from the peripheral foot vein using heparinized syringes (3 mL) and heparinized capillary tubes (75 µL). Samples were kept in a cooler until laboratory processing. Thin blood smears were prepared with a drop of fresh blood, air-dried, fixed with ethanol, and stained with Tinción 15 (Biopur). Penguins were weighed with spring scales (Pesola; nearest 100 g for adults and 10 g for chicks), and bill length and depth were measured with digital calipers (Essex; nearest 0.1 mm). Adult sex was determined using a discriminant function based on morphometries (Bertellotti *et al.* 2002). Cloacal samples were obtained using swabs and placed in transport medium (Stuart's medium) for later detection of bacteria.

Laboratory analyses

Blood samples were centrifuged for 12 minutes at 12000 g. Plasma was processed by colorimetric and enzymatic methods on a spectrophotometer (Metrolab 1600 Plus, UV-Vis, Argentina) to determine levels of total protein (g·dL⁻¹), cholesterol (mg·dL⁻¹), and glucose (mg·dL⁻¹). These plasmatic biochemical parameters contribute to the assessment of body condition and nutritional status in birds (Brown 1996). We used a microhematocrit ruler to measure hematocrit, which is a physiological index of condition in birds when evaluated together with other hematological parameters (Fair *et al.* 2007).

TABLE 1
Physiological parameters measured for Magellanic penguins at San Lorenzo^a

| | Area | Adult ^b | | | | Chick | | | |
|--------------------------------------|------|--------------------|-----------------|-------|-----------|----------|------|------|----------|
| | | <i>n</i> | Mean | SE | Min–Max | <i>n</i> | Mean | SE | Min–Max |
| Weight (g) | 1 | 16 | 3781 | 95.0 | 3200–4300 | 13 | 846 | 62.9 | 600–1400 |
| | 2 | 16 | 3813 | 129.7 | 3000–4800 | 9 | 694 | 17.6 | 600–750 |
| Glucose (mg·dL ⁻¹) | 1 | 16 | 142 | 3.5 | 111–164 | 13 | 175 | 4.8 | 143–206 |
| | 2 | 16 | 145 | 3.4 | 119–166 | 9 | 187 | 1.6 | 153–207 |
| Cholesterol (mg·dL ⁻¹) | 1 | 16 | 195 | 5.8 | 148–246 | 13 | 244 | 4.8 | 147–308 |
| | 2 | 16 | 204 | 9.3 | 149–298 | 9 | 241 | 6.1 | 162–314 |
| Total proteins (g·dL ⁻¹) | 1 | 16 | 7 | 0.1 | 6–8 | 13 | 5 | 17.9 | 5–6 |
| | 2 | 16 | 7 | 0.1 | 6–8 | 9 | 5 | 18.9 | 5–6 |
| Hematocrit | 1 | 16 | 37 ^c | 1.9 | 21–50 | 13 | 23 | 0.1 | 15–58 |
| | 2 | 16 | 45 ^c | 1.6 | 25–53 | 9 | 20 | 0.1 | 15–26 |
| RBCi (%) | 1 | 16 | 2 | 0.8 | 0–8 | 13 | 45 | 3.3 | 20–75 |
| | 2 | 16 | 2 | 0.9 | 0–12 | 9 | 61 | 6.2 | 20–90 |
| tWBC | 1 | 16 | 61 | 5.0 | 25–105 | 13 | 26 | 3.1 | 11–51 |
| | 2 | 16 | 58 | 3.9 | 38–95 | 9 | 28 | 1.3 | 10–72 |
| H/L | 1 | 16 | 1 | 0.1 | 1–2 | 13 | 1 | 4.0 | 1–2 |
| | 2 | 16 | 1 | 0.2 | 0–2 | 9 | 1 | 8.6 | 0–2 |
| Basophils (%) | 1 | 16 | 0 | 0.1 | 0–1 | 13 | 0 | 0.1 | 0–1 |
| | 2 | 16 | 0 | 0.2 | 0–2 | 9 | 0 | 0.2 | 0–0 |
| Eosinophils (%) | 1 | 16 | 14 | 1.7 | 6–33 | 13 | 3 | 0.1 | 0–9 |
| | 2 | 16 | 12 | 1.1 | 7–19 | 9 | 4 | 0.0 | 1–8 |
| Heterophils (%) | 1 | 16 | 43 | 2.0 | 28–55 | 13 | 43 | 0.6 | 30–64 |
| | 2 | 16 | 42 | 3.1 | 18–58 | 9 | 37 | 0.7 | 11–56 |
| Lymphocytes (%) | 1 | 16 | 36 | 1.5 | 23–45 | 13 | 49 | 2.8 | 30–64 |
| | 2 | 16 | 39 | 2.5 | 23–58 | 9 | 56 | 4.8 | 34–87 |
| Monocytes (%) | 1 | 16 | 7 | 1.0 | 0–13 | 13 | 4 | 3.2 | 1–10 |
| | 2 | 16 | 6 | 1.1 | 1–18 | 9 | 3 | 5.3 | 0–5 |
| Thrombocytes (count) | 1 | 16 | 122 | 10.7 | 30–180 | 13 | 36 | 0.6 | 5–105 |
| | 2 | 16 | 100 | 13.5 | 25–200 | 9 | 18 | 0.6 | 0–70 |

^a 1 = touristic area, 2 = control area, *n* = sample size, SE = standard error, RBCi = red blood cells (immature), tWBC = total white blood cells, H/L = heterophil/lymphocyte index

^b Adult values were from both sexes combined. Weights and hematocrits showed statistically significant differences between sexes.

^c Statistical differences of hematocrit values in adults between areas (*P* = 0.005).

Blood smears were scanned under a light microscope to analyze erythrocytes and leukocytes. Immature erythrocytes were registered as a percentage in the total erythrocyte counts (Martinho 2012). The leukocyte profile provides valuable information on the cellular components of the immune system, and it was assessed by estimating the total white blood cell count (number of leukocytes per 10000 erythrocytes, tWBC), the five leukocyte types (heterophils, eosinophils, basophils, lymphocytes, and monocytes), and thrombocytes (Campbell 1995). The tWBC was estimated under 400× magnification, the percentage of each leukocyte type was obtained from a sample of 100 leukocytes under 1000×, and thrombocytes were estimated as a total count (Campbell 1995). The heterophil/lymphocyte (H/L) index, which is considered a reliable measure of stress in birds (Davis *et al.* 2008), was calculated from the corresponding leukocyte counts.

Bacteria with zoonotic potential were scanned through specific techniques of selective and differential culture (Ryan & Ray 2004). To test for *Salmonella* spp. and *Shigella* spp., samples were incubated for 18–24 h in selenite broth and then cultured on *Salmonella-Shigella* agar (agar SS). Tryptone-soya agar (TSA) was used to test for *Corynebacterium* spp. To test for enteropathogenic *Escherichia coli* bacteria, a differential medium agar that was cysteine-lactose deficient in electrolytes (agar BD-CLDE) was used. To test for *Staphylococcus* spp., a blood agar-enriched medium was used.

All variables were normally distributed (Kolmogorov-Smirnov test > 0.05). Statistical analyses were done using one-way ANOVA. All P values < 0.05 were termed significant. The relationships between the physiological parameters and age and sex were evaluated using a Pearson test. All statistical analyses were done using Statistica package 7.0 (StatSoft, Inc. 2007).

RESULTS AND DISCUSSION

Biochemical and hematological parameters

Values of physiological parameters obtained during the reproductive season are presented in the Table 1. Male penguins are heavier than females (Bertellotti 2013), with male mass ranging between 3500 g and 4800 g (mean = 4047 g, SD = 321 g) and female mass ranging between 3000 g and 3500 g (mean = 3318 g, SD = 172 g). No significant differences in adult mass were observed between touristic and control areas. Similar results were observed in chicks, though chicks inhabiting touristic trails tended to be heavier (Table 1). The physiological parameter results of adult females and males were pooled because no significant differences in these parameters were observed between sexes (adult females $n = 11$, adult males $n = 21$).

Plasmatic metabolites reflect the nutritional status, as they are the main source of energy during prey digestion (Brown 1996). Values obtained in this study were in the range previously reported for healthy birds (Campbell 1995), including the Magellanic Penguin (Palacios *et al.* 2018). Glucose levels in chicks in both touristic and control areas were higher than the values reported by Palacios *et al.* (2018) (175 mg·dL⁻¹ and 187 mg·dL⁻¹ here, respectively, and 137 mg·dL⁻¹ and 134 mg·dL⁻¹, respectively, in Palacios *et al.* 2018). However, no significant differences in glucose, total proteins, and cholesterol values were observed between penguins, either adults or chicks, sourced from the touristic and control areas. These parameters are directly related to diet; the main prey species for adults is the Argentine anchovy *Engraulis anchoita*, which

represents at least 90 % of their diet and is, in turn, transferred to their chicks (Wilson *et al.* 2005). Therefore, although in different proportions, both adults and chicks feed on the same prey. Other studies reported higher values of glucose and cholesterol in chicks compared to adults, suggesting that adults maximize the food quality to feed their chicks by choosing prey with higher energy content (Forero *et al.* 2002).

As expected, hematocrit values were higher in adults than chicks (ANOVA $P = 0.003$; Table 1); hematocrit values typically increase with age in birds (Fair *et al.* 2007, Smith & Barber 2012). Hematocrit values were higher in adults sourced from the control area (ANOVA $P = 0.005$), but no significant differences were observed in hematocrit values for chicks between the different areas. Considering that exposure to environmental stressors affects hematocrit values (Fair *et al.* 2007), the higher values observed in adults from the touristic area could be related to human presence during breeding. However, as birds have natural variation in hematocrit caused by age, reproductive status, geographical elevation, season, parasitism, and nutritional status (Fair *et al.* 2007), this issue needs further analysis.

The percentage of immature erythrocytes was higher in chicks than adults (Table 1). Nearly half of the erythrocytes in chicks were immature, with no differences between the touristic and the control sites. Similarly, levels of immature erythrocyte were similar in adults regardless of whether sourced from the touristic or control areas. Leukocytes constitute the primary line of defense against pathogens (Roitt *et al.* 1998). In this study, adults and chicks from touristic and control areas showed similar tWBC values (ANOVA $P > 0.05$). Lymphocytes and heterophils were the most abundant cells displayed for adults and chicks in both areas. Total counts and percentages of basophils, eosinophils, and monocytes remained low, which is expected in healthy birds (Campbell 1995; Table 1). Adults and chicks showed no statistical differences in leukocyte types between areas (ANOVA $P > 0.05$). Mean values of tWBC, H/L, and leukocyte types observed in adult penguins were similar to those previously found in the same colony five years earlier (D'Amico *et al.* 2014). When compared with values from the previous season (December 2013) at the same site, adults maintained similar values. Chicks, however, except for eosinophils and monocytes, exhibited lower values among the remaining leukocyte types, tWBC, H/L index, and thrombocytes (see Palacios *et al.* 2018). Although, leukocyte counts are influenced by several factors, such as food deprivation, parasites, severe weather changes, contamination, habitat modification, and human impacts (Davis *et al.* 2008), the main cause of leukocyte production and activation would be exposure to several pathogens (Campbell 1995).

Bacterial tests

The growing touristic activities around the penguin colony could contribute to the dissemination of diseases by incidental transport of pathogenic agents. Therefore, as already found in other colonies, penguins could be exposed to new pathogens carried by visitors. A direct relationship between human presence and an increase in the range distributions, abundance, and/or virulence of parasites and pathogens was already reported for Antarctic penguins (Barbosa & Palacios 2009). Here, 38 samples were tested for bacteria (20 adults, 18 chicks; Table 2). All samples showed positive results for all bacteria tested. *E. coli* was the most prevalent bacterium in both adults and chicks (60 % and 56 %, respectively). Adults in

touristic areas carried higher concentrations of *E. coli* than control adults (Table 2), but chicks showed equal percentage in both areas (55.5 %).

Although our study did not go deeply into the analysis of bacterial strains, there are several reported cases of transmission of *E. coli* and other bacteria from humans to animals, a process known as a reverse zoonosis. Many of these have been associated with tourism among Antarctic penguin colonies (Barbosa & Palacios 2009, Griekspoor *et al.* 2009, Hernández *et al.* 2012). In addition, thrombocytes exhibit phagocytic activity in several bird species. For instance, it has been documented in ducks as a response to *Staphylococcus aureus* (see more examples in Claver 2005). Furthermore, thrombocytes can phagocytose 1.7 times more bacteria in the blood, making it three times faster than heterophils and monocytes together (Chang & Hamilton 1979).

In our study, *Corynebacterium* spp. were present solely in adults (20 %), regardless of area. One adult tested positive for *Salmonella* spp. in the control area (5 %), as did one chick in the touristic area (5.5 %). *Staphylococcus* spp. had a prevalence of 30 % in adults and 44 % in chicks, with a similar percentage in both areas (Table 2). *E. coli* and *Staphylococcus* spp. were positively correlated to the thrombocyte counts of chicks in both touristic and control areas (Pearson $P = 0.021$). The presence of *Salmonella* spp. in the touristic area was correlated with the H/L stress index (Pearson $P = 0.022$). For adults, *E. coli* in both areas was correlated with the production of L (Pearson $P = 0.0032$), H/L index (Pearson $P = 0.024$), and E (Pearson $P = 0.047$), while *Corynebacterium* spp. was correlated to the production of tWBC (Pearson $P = 0.03$), H (Pearson $P = 0.0139$), L (Pearson $P = 0.02$), and, consequently, induced a higher H/L index (Pearson $P = 0.0028$) in both areas.

Using the physiological parameters obtained in this study (except for hematocrits in adults), we suggest that growing tourism does not impact the health condition of adults and chicks inhabiting the San Lorenzo colony. These results agree with previous work showing that penguins at San Lorenzo colony did not show alterations on their physiological parameters compared to their congeners at

Punta Tombo (Chubut, Argentina), which showed physiological indicators of chronic stress, altered immunity, and poor general health (Palacios *et al.* 2018).

One shortcoming of our work was the low sample size. However, these data complement the systematic physiological monitoring that has been carried out on penguins at San Lorenzo since 2007. Villanueva *et al.* (2012) and Walker *et al.* (2006) suggested that a continuous monitoring of touristic activity would be important, as a history of visitation disturbance seemed to have behavioral and physiological effects on how birds responded to tourists. Likewise, Villanueva *et al.* (2014) found that penguins displayed different behavioral responses depending of the proximity to touristic areas: penguins inhabiting touristic zones were more tolerant to human approach than those inhabiting non-touristic areas. Palacios *et al.* (2018) showed an integrated set of immune-state and health-state indices that could be used to evaluate the effects of ecotourism on Magellanic Penguins, and they concluded that high exposure to humans resulted in physiological stress and poor health despite a long history of exposure and behavioral habituation to human visitation. Likewise, oxidative stress is a chemical imbalance occurring when there is an excessive production of reactive oxygen species or an inefficient elimination of them. Oxidative stress is considered to be a physiological indicator of environmental stressors, including human activities such as tourism, recreation, fishing activities, burning fuels, and dumping or spilling solid and liquid human waste. Measurements in penguins at San Lorenzo showed that individuals nesting around touristic trails exhibited higher oxidative stress compared with control areas (Carabajal 2017).

Taken together, our hematological and health condition parameters can provide useful information to better understand the physiological responses of penguins to global environmental change.

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TABLE 2
Bacterial testing of Magellanic penguins at San Lorenzo colony^a

| | Area | Adults ^b | | | Chicks | | |
|-----------------------------|----------------|---------------------|----------------|-------|--------|----------------|-------|
| | | n | Prevalence (%) | | n | Prevalence (%) | |
| | | | per site | Total | | per site | Total |
| <i>Escherichia coli</i> | Touristic area | 9 | 81.8 | 70 | 5 | 55.6 | 56 |
| | Control | 5 | 62.5 | | 5 | 55.6 | |
| <i>Salmonella</i> spp. | Touristic area | 0 | 0 | 5 | 1 | 11.1 | 6 |
| | Control | 1 | 12.5 | | 0 | 0 | |
| <i>Corynebacterium</i> spp. | Touristic area | 2 | 18.2 | 20 | 0 | 0 | 0 |
| | Control | 2 | 25 | | 0 | 0 | |
| <i>Staphylococcus</i> spp. | Touristic area | 3 | 27.3 | 30 | 4 | 44.4 | 44 |
| | Control | 3 | 37.5 | | 4 | 44.4 | |

^a Adults: Touristic area = 11 samples analyzed; Adult control = 8 samples analyzed. Chicks: Touristic area = 9 samples analyzed; Chick control = 9 samples analyzed.

^b Adult values were from both sexes combined because they did not show statistically significant differences.

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3D MODELING REVEALS FUNCTIONALITY OF A HEALED BUT MALALIGNED LEG FRACTURE IN A WHITE-FACED STORM PETREL *PELAGODROMA MARINA*

JESSICA REICHERT¹, GERALD MAYR², THOMAS WILKE¹ & WINFRIED S. PETERS³

¹Department of Animal Ecology and Systematics, Justus Liebig University, Heinrich-Buff-Ring 26-32 (IFZ), 35392 Gießen, Germany

²Ornithological Section, Senckenberg Research Institute and Natural History Museum Frankfurt, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

³School of Biological Science, Washington State University, Pullman, WA 99164, USA (petersw@pfw.edu)

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ABSTRACT

REICHERT, J., MAYR, G., WILKE, T. & PETERS, W.S. 2019. 3D modeling reveals functionality of a healed but malaligned leg fracture in a White-faced Storm Petrel *Pelagodroma marina*. *Marine Ornithology* 47: 253–256.

We describe a deformed tibiotarsus in a museum skeleton of a White-faced Storm Petrel *Pelagodroma marina* (Oceanitidae), probably resulting from a healed but malaligned fracture. Digital 3D modeling of intertarsal joint kinematics suggested that the affected leg could support neither terrestrial walking locomotion nor the usual foraging activities on open water. Nonetheless, the bird survived, presumably because it employed alternative feeding strategies. Considering this case in the context of previous studies on hindlimb injuries in other storm petrels, we conclude that these birds experience high frequencies of leg injuries but low frequencies of leg fractures.

Key words: bone fracture healing, long bone malalignment, 3D modeling, White-faced Storm Petrel, *Pelagodroma marina*, Ilhas Selvagens

INTRODUCTION

Birds often survive long bone fractures in the wild, but frequencies of healed fractures reported for various taxa vary considerably (Lidauer 1983, Brandwood *et al.* 1986, Goodman & Glynn 1988, Houston 1993). Segments of broken long bones may become oriented abnormally during the healing process (Tiemeier 1941, Atherton *et al.* 2012, Reichert *et al.* 2017b). The biomechanical and behavioural effects of such malalignments can be observed in live animals or deduced from geometrical analyses of bones and joints in skeletons (Reichert *et al.* 2017b). Because the affected birds survived the fracture event at least long enough for the bone to heal, each healed but malaligned fracture represents a natural experiment testing how far the biomechanical apparatus may deviate from the norm without fatal consequences.

Storm petrels, formerly considered a single family (Hydrobatidae, Procellariiformes), appear to represent two phylogenetically distinct taxa, Oceanitidae and Hydrobatidae. Both taxa are ecologically similar and are characterized by a pelagic lifestyle, except for their breeding season (Warham 1990, del Hoyo *et al.* 1992). The efficiency of their bipedal locomotion on land is notoriously poor (Warham 1996). However, when flying just above the water surface, especially the Oceanitidae use their feet to perform unique locomotory techniques (Withers 1979, Sugimoto 1998) that have been described as ‘pattering’, ‘walking’, or ‘standing’ on the water (del Hoyo *et al.* 1992; for videos, consult the Internet Bird Collection, www.hbw.com/ibc). One species, the White-faced Storm Petrel *Pelagodroma marina*, inhabits the Atlantic, Pacific, and Indian Oceans (del Hoyo *et al.* 1992). The North Atlantic subspecies, *P. m. hypoleuca*, breeds almost exclusively on the Ilhas Selvagens, a small archipelago

between Madeira and the Islas Canarias (Campos & Granadeiro 1999). Here, we report a strongly deformed tibiotarsus in a White-faced Storm Petrel skeleton from this location and analyze the biomechanical consequences by optical 3D scanning and modeling.

METHODS

The bird skeleton collection of the Senckenberg Research Institute (Frankfurt am Main, Germany) includes 33 White-faced Storm Petrels. Here, we describe a skeleton with the catalogue number SMF 17899, which belongs to the subspecies *hypoleuca* and had been collected as a mummified cadaver on 06 October 2013 on Selvagem Grande (30°09'N, 015°52'W), Ilhas Selvagens, Portugal.

Tibiotarsi (one deformed) and tarsometatarsi were scanned using the 3D optical scanner Artec Spider controlled with the Artec Studio v9.2.3.15 software (Artec Group, Luxemburg) as described by Reichert *et al.* (2017a, 2017b). In short, each bone was scanned from two opposite sides, and pairs of scans were aligned using the software’s Rigid Alignment tool. 3D models were computed by Fine Serial Registration, Global Registration (min. distance 10, 40 000 iterations), and Sharp Fusion (resolution 0.2; fill holes by radius, max. radius 5). Models were exported as OBJ-files and visualized in Blender v2.6 (www.blender.org/features/2-73/). To directly compare the injured and healthy legs, bones of the healthy right leg were mirrored. Flexion of the intertarsal joints was modeled using single bone armatures. Images of the models for publication were designed with the free MeshLab software (www.meshlab.net). Planes in which tarsometatarsi rotated due to flexion of the intertarsal joints were calculated from the 3D coordinates of the distal ends of the tarsometatarsi at different flexion angles.

RESULTS

The skeleton of the White-faced Storm Petrel, SMF 17899, is complete and without apparent abnormalities, except for the left tibiotarsus (Fig. 1). The distal 7 mm of the bone with the articular surface are displaced from their normal position and are attached to the bone's shaft more proximally through a subtriangular mass of bone material (Fig. 1A). The long axis of the displaced distal bone portion forms an angle of $\sim 53^\circ$ with the shaft axis (Fig. 1B) and protrudes caudally. The straight distance from the proximal end of the tibiotarsus to the distal end of the tarsometatarsus at fully extended intertarsal joint is 16 mm shorter in the deformed leg than in the healthy leg. Thus, the functional length of the deformed leg (straight distance from the hip joint to the tip of the longest toe at full extension of all joints) was reduced compared to the healthy leg. The distal end of the deformed tibiotarsus is developed normally, including lateral and medial condyles and the supratendinal bridge over the extensor canal, but is axially rotated (Fig. 1B, C). As a result, the left foot moved at an angle with respect to the sagittal plane when it rotated around the intertarsal joint.

To obtain a clearer picture of the geometrical effects of the deformation, we generated 3D models from optical scans of the tibiotarsi and tarsometatarsi (Fig. 2). Mirroring the bones of the healthy right leg into their left counterparts enabled direct visual comparison of the deformed and the healthy legs. In the standing posture (20° flexion of the intertarsal joints; Fig. 2A-C), the foot of the deformed leg pointed backwards with the distal end of the tarsometatarsus some 25 mm higher above ground than that of the healthy leg (Fig. 2B). At increasing flexion of the intertarsal joints (70° in Fig. 2D-F), the foot of the deformed leg rotated upwards and outwards on a plane that obliquely intersected the parasagittal plane, in which the healthy foot would have moved, at an angle of about 75° (Fig. 2G).

DISCUSSION

The most plausible explanation for the deformation of the left tibiotarsus described herein (Fig. 1) is that the bone broke 7 mm from its distal end in an accident or predatory attack that the bird survived. The foot distal to the fracture was bent backwards, perhaps when the animal attempted to swim or crawl on land, and became fixed in this orientation when the fracture healed by periosteal callus formation and subsequent ossification. The duration of the healing process in the wild is hard to estimate, but based on general experience from veterinary practice it must have been four to eight weeks at least, and probably more (Doneley 2016). Alternatively, pathological conditions such as calcium deficiency disorders may cause bone deformations; however, these conditions would be expected to affect more than a single bone in one leg only. The normal morphology of the distal end of the deformed tibiotarsus (Fig. 1B, C) further supports the idea that the intertarsal joint had functioned normally before the deformation occurred.

Storm petrels can perform a digitigrade gait (i.e., walk on their toes) but rarely do. Rather, they shuffle forward on their tarsi when moving on land. A plantigrade posture also is their preferred resting stance (Warham 1996). The backward-pointing left tarsus (Fig. 2) certainly made digitigrade walking impossible for SMF 17899, but plantigrade resting and even movement may have been feasible if the bird could stand on the distal end of its deformed left tibiotarsus.

Pattering White-faced Storm Petrels touch the water with both feet simultaneously as if jumping, or alternately as if walking, while the intertarsal joints flex and extend (del Hoyo 2013, de Groot Boersma 2016). In SMF 17899, the functional length of the deformed leg was reduced and the intertarsal joint did not operate in a sagittal plane (Fig. 2). Thus, if the bird was pattering at all, it must have done so in an asymmetric manner, maybe using only its healthy leg to interact with the water. The pattering bird may have counteracted the asymmetric foot movements by appropriate modifications of its wing action.

Tube-noses use their feet alternately when surface-swimming. The main action occurs at the intertarsal joints, while the tibiotarsi and femora hardly move (Warham 1996). Even under the doubtful assumption that the left intertarsal joint was fully functional in SMF 17899, alternating strokes of the legs would not have produced a simple forward-directed force. The left foot's oblique movement (Fig. 2G) would have rotated the swimming body's long axis to the right with every stroke, and the required compensatory actions would have decreased the efficiency of swimming locomotion.

Members of the Hydrobatidae appear capable of compensating for impediments that result from leg injuries, as such injuries hardly affect body mass (in Leach's Storm Petrel *Oceanodroma leucorhoa*, European Storm Petrel *Hydrobates pelagicus*; Love 1984) and breeding success (in the Band-rumped Storm Petrel *Oceanodroma castro*; Allan 1962, Harris 1969). The case of SMF 17899 suggests that this conclusion holds true for Oceanitidae as well. Sparsely available data on incubation spans in breeding White-faced Storm Petrels

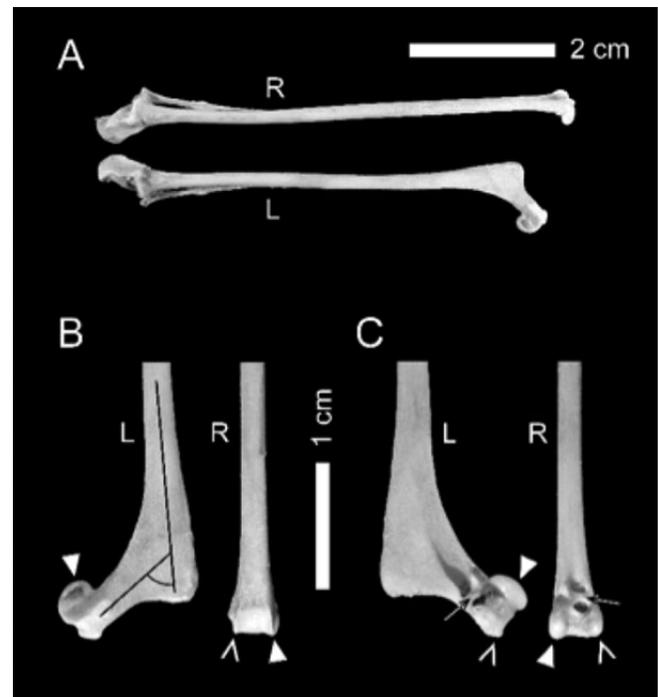


Fig. 1. Photographs of the tibiotarsi of the White-faced Storm Petrel, SMF 17899. A) The deformed left (L) and the healthy right (R) tibiotarsi, with the distal ends of the two bones also shown at higher magnification in caudal (B) and cranial (C) view. The angular malalignment of $\sim 53^\circ$ is highlighted in (B). Filled arrowheads, lateral condyles; open arrowheads, medial condyles; arrows, supratendinal bridges over the extensor canals.

indicate that well-fed birds can easily fast for five days (Richdale 1965), but this is only a fraction of the estimated duration of the healing process in SMF 17899. Therefore, the bird must have been foraging successfully while its leg fracture healed. Storm petrels are known to be pelagic surface feeders, but they readily exploit alternative sources, such as intertidal benthos (European Storm Petrel; d'Elbee & Hemery 1998, Thomas *et al.* 2006) and the beached remains of whales and fish (Fork-tailed Storm Petrel *Oceanodroma furcata*; Gill 1977, Robinson *et al.* 2018). Similar stationary food sources on solid ground may have enabled the survival of SMF 17899 on Selvagem Grande.

We are aware of only one census of leg injuries in Oceanitidae: Furness (1984) reported no injuries in a small sample ($n = 35$) of White-faced Storm Petrels from Gough Island. In contrast, significant proportions of larger samples had parts of their legs missing in several Hydrobatidae, including Band-rumped Storm Petrels (5.3 % of the combined sample of $n = 414$; Allan 1962, Harris 1969), Leach's Storm Petrels; (3.4 %, $n = 5396$; Waters 1964, Threlfall 1974, Morse & Buchheister 1977, Love 1984, Kirkham *et al.* 1987), and European Storm Petrels (1.5 %, $n = 4789$; Waters 1964, Love 1984, Mínguez 1996, Wojczulanis-Jakubas *et al.* 2014). The cause of the injuries remains conjectural, but infectious diseases and predatory attacks by fish on swimming or pattering birds have been implicated (Love 1984, Kirkham *et al.* 1987, Wojczulanis-Jakubas *et al.* 2014). The cited reports list >280 injured individuals but mention only two healed longbone fractures (Love 1984) and four 'deformed'

feet (Threlfall 1974, Love 1984) without further details. Because pronounced deformations probably would not have passed unnoticed, cases like White-faced Storm Petrel SMF 17899 appear rare among Hydrobatidae. Notably, the leg bones of tubenoses are non-pneumatic and, thus, particularly strong (Warham 1996). In combination, these lines of evidence indicate high frequencies of leg injuries but low frequencies of leg fractures in storm petrels.

The legs protrude beyond the tail in flying Oceanitidae (except for White-bellied Storm Petrels *Fregetta grallaria*), but not Hydrobatidae (comprehensively documented by Brooke 2004, who did not formally separate the two taxa). Proportionally longer legs seem to facilitate pattering (Sausner *et al.* 2016), which appears to be more regularly observed in the Oceanitidae (Brooke 2004). Therefore, if hindlimb injuries are caused by attacks of predatory fishes on pattering birds, they may be expected to be more common in Oceanitidae than Hydrobatidae. Because the sample of procellariiform skeletons available to us is small, this hypothesis will have to be addressed in future surveys of larger museum collections and by field observations.

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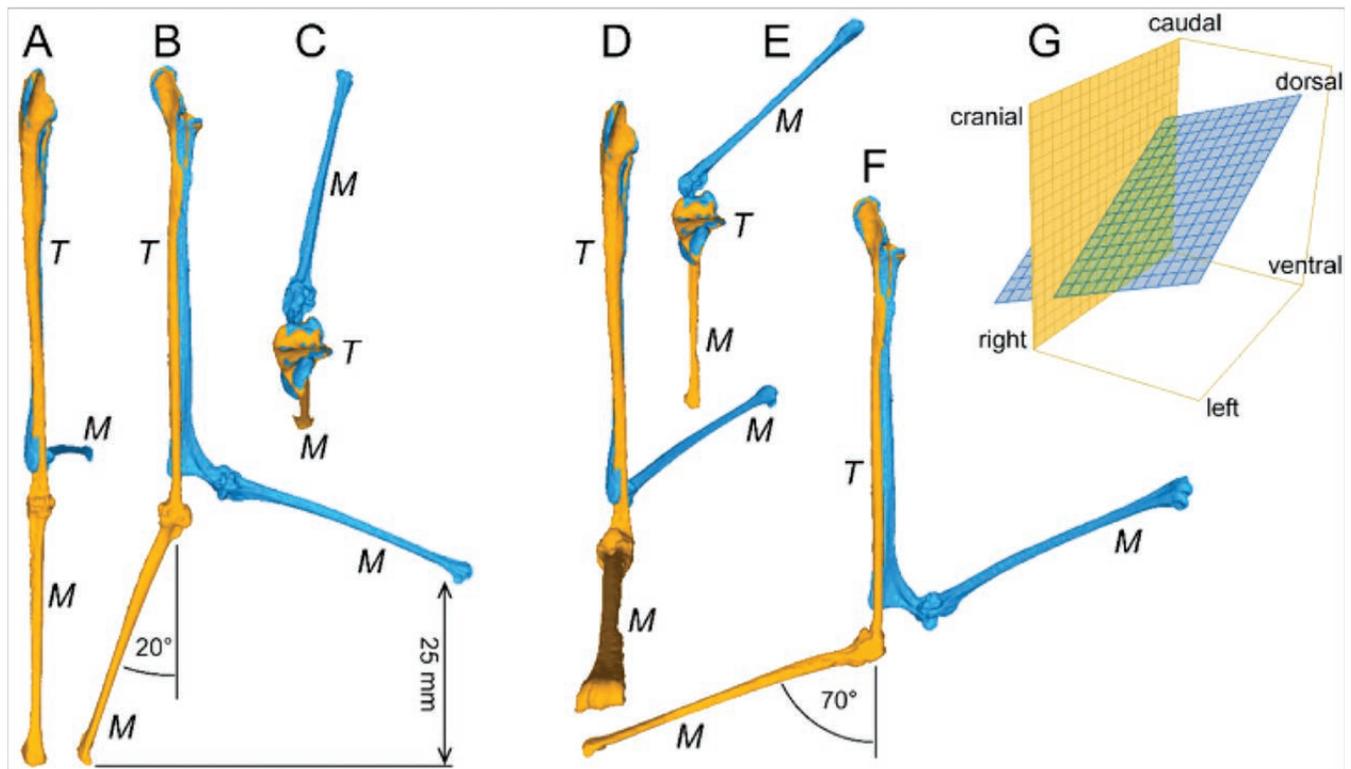


Fig. 2. Effects of the tibiotarsus deformation in the White-faced Storm Petrel, SMF 17899, on limb geometry and the kinematics of the intertarsal joint. Digital 3D models of the left and right tibiotarsi (*T*) and tarsometatarsi (*M*) are shown for flexions of the intertarsal joint of 20° (A, B, C) and 70° (D, E, F). The bones of the healthy right leg were mirrored, and the proximal ends of the tibiotarsi overlain, for direct visual comparison between the healthy (orange) and the deformed (blue) leg. Each combined model is shown in a frontal view in the caudal direction (A, D), in a lateral view (B, F; cranial is to the left), and in a view onto the proximal end of the tibiotarsus with the line of view along this bone's long axis (C, E; cranial is toward the bottom). (G) Comparison of the plane in which the left tarsometatarsus moved when the intertarsal joint was flexed in the deformed leg (blue) and the parasagittal plane in which this bone moves in a healthy leg (orange).

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POPULATION TRENDS OF SPECTACLED PETRELS *PROCELLARIA CONSPICILLATA* AND OTHER SEABIRDS AT INACCESSIBLE ISLAND

PETER G. RYAN^{1*}, BEN J. DILLEY¹ & ROBERT A. RONCONI²

¹FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa
*(pryan31@gmail.com)

²Canadian Wildlife Service, Environment and Climate Change Canada, 45 Alderney Dr., Dartmouth, NS B2Y 2N6, Canada

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ABSTRACT

RYAN, P.G., DILLEY, B.J. & RONCONI, R.A. 2019. Population trends of Spectacled Petrels *Procellaria conspicillata* and other seabirds at Inaccessible Island. *Marine Ornithology* 47: 257–265.

Inaccessible Island, in the Tristan da Cunha archipelago, is the sole breeding site of the Spectacled Petrel *Procellaria conspicillata*. The island also supports globally important populations of four threatened seabirds, as well as populations of other seabird species. A seabird monitoring protocol was established in 2004, following baseline surveys of most surface-breeding species in 1999. For the species monitored, we report population trends that are based on visits in 2009 and 2018. Populations of most monitored species appear to be stable or increasing, including three albatross species currently listed as Endangered or Critically Endangered. However, numbers of Northern Rockhopper Penguin *Eudyptes moseleyi* may have decreased slightly since 1999, and numbers of Antarctic Tern *Sterna vittata* have decreased since 1982. The population of Spectacled Petrels is estimated to be at least 30000 pairs and continues to increase since feral pigs *Sus scrofa* died out on the island in the early 20th century. We describe a new monitoring protocol for Spectacled Petrels that will be easier to repeat and implement and that should provide a more sensitive measure of future population changes.

Key words: Inaccessible Island, Tristan da Cunha, Spectacled Petrels, seabird population trends, feral pigs

INTRODUCTION

Inaccessible Island is a 14 km² uninhabited island in the Tristan da Cunha archipelago. It was declared a nature reserve in 1997, a natural World Heritage Site (as part of the Gough and Inaccessible Islands World Heritage Site) in 2004, and as a Ramsar wetland in 2008. The island is the only known breeding site of the Spectacled Petrel *Procellaria conspicillata* (listed as globally Vulnerable; BirdLife International 2018a) and is home to other globally important seabird populations, including three albatross species listed under the Agreement on the Conservation of Albatrosses and Petrels (www.acap.org). The island supports a remnant population of Tristan Albatross *Diomedea dabbenena* (Critically Endangered), the last population remaining in the Tristan archipelago (Ryan *et al.* 2001), and it is the only breeding site for this species that is free from introduced mammalian predators (Cuthbert *et al.* 2004). Inaccessible Island is also one of only four breeding locations for Atlantic Yellow-nosed Albatross *Thalassarche chlororhynchos* (Endangered), and it has a significant population of Sooty Albatross *Phoebastria fusca* (Endangered). Northern Rockhopper Penguins *Eudyptes moseleyi* (Endangered) breed at nine sites on the island (Ryan & Moloney 2000), which supports roughly 22 % of the world population for this species (Robson *et al.* 2011, BirdLife International 2018b).

The status of seabirds at Inaccessible Island was reviewed by Fraser *et al.* (1988) and updated by Ryan *et al.* (1990). Ryan & Moloney (2000) published the most recent overview of the island's seabird populations, based on a three-month visit in 1999/2000. This visit also resulted, in part, in the development of a Seabird Monitoring Manual for the island (Ryan 2005). This manual acknowledged the

difficulty of access to the island and provided a set of pragmatic approaches to estimate the status of the island's surface-nesting seabird populations, assuming a visit of several weeks in November (early summer) to Blenden Hall, on the island's west coast. Blenden Hall offers the only ready access to the island plateau, which is where Spectacled Petrels and most albatrosses breed. These monitoring protocols were field tested in November 2004 (Ryan 2005) and resulted in an updated estimate of the Spectacled Petrel population (Ryan *et al.* 2006). Since then, PGR visited the island twice in November during which he monitored and updated the ongoing growth of the Spectacled Petrel population: in 2009 (Ryan & Ronconi 2011) and in 2018 (this paper). Based on these surveys, we report trends in most of the island's surface-nesting seabird populations over the last two decades. We also suggest a revised monitoring approach for Spectacled Petrels that will be easier to implement and that will provide a more sensitive indicator of population change.

METHODS

We visited Inaccessible Island from 13 September to 26 November 2018, working from the field hut at Blenden Hall or from a camp established on the island plateau near Denstone Hill. Details of visits in 2004 and 2009 are presented in Ryan *et al.* (2006) and Ryan & Ronconi (2011), respectively. During each of these visits, we implemented the count methods outlined in the *Inaccessible Island Seabird Monitoring Manual* (see Ryan 2005 for details), although we revised the count approach for Spectacled Petrels in 2018. An additional visit took place from 15 September to 06 October 2011; this was too early to census Spectacled Petrels or summer-breeding albatrosses, but it was well-timed to census incubating Northern Rockhopper Penguins.

Spectacled Petrels

Previous counts of Spectacled Petrels (Rowan *et al.* 1951, Hagen 1952, Fraser *et al.* 1988, Ryan & Moloney 2000, Ryan *et al.* 2006, Ryan & Ronconi 2011) attempted to estimate the entire island population. This was feasible when the population was smaller, given the strongly clustered distribution of burrows, with most pairs breeding in conspicuous terraces created by the petrels in bogfern *Blechnum palmiforme* heath. This latter habitat dominates most of the western plateau of Inaccessible Island (Ryan 2007). However, the continued growth of the population was making a complete count increasingly arduous, and the approach was not sensitive to subtle changes in the species' range or burrow densities because counts were simply reported per catchment area (Ryan *et al.* 2006, Ryan & Ronconi 2011). In 2018, we adopted a more repeatable, transect-based approach that sampled the entire range of the species. We counted all burrows within five metres of either side of a series of north-south transect lines running through the species' known breeding range (Ryan & Ronconi 2011). That is, we conducted a strip survey, where burrow density was the number of burrows found in the sampled area (transect length \times 10 m). This method was preferred to a distance-based line transect approach because of the great difference in detection distance between isolated burrows and petrel terraces. We walked transects every 0.1 minutes of longitude (which equates to 147 m between transects) throughout the species' main breeding range, covering 14 lines from 012°40.6'W to 012°41.9'W. We walked transects every 0.05 minutes of longitude (i.e., 73.5 m apart) through the smaller outlying colonies on Denstone Hill (five lines from 012°40.05'W to 012°40.25'W) and Round Hill (six lines from 012°39.75'W to 012°40.0'W; Fig. 1). At these outlying colonies,

we worked from a central line outwards, and we considered the first outer transect with zero burrows to be the colony boundary. All transects were counted between 29 October and 15 November 2018.

Most lines were walked by two observers walking roughly five metres apart and guided by a handheld GPS (Garmin 60 and 64s) to remain on the desired track. We recorded the habitat (three main habitats based on the dominant vegetation, see below) along each transect, noting where each habitat type started and ended; this was subjectively determined in the field as a point where the dominant vegetation type changed. We counted the number of burrows in each habitat block, recording the locations of the first and last burrows. For the purposes of mapping the species' range, we combined habitat blocks if they were separated by less than 50 m of unoccupied habitat. Spectacled Petrel burrows are, for the most part, large and fairly easy to detect. However, in some dense tussock slopes, burrows that were difficult to locate were found using playback of a repertoire of Spectacled Petrel groans and rattles (the petrels are very responsive to playback during late October and early November; Ryan *et al.* 2006).

Burrow detection rate and occupancy were checked by assessing the status of 20 burrows at each of five locations during the census period: two in Ringeye Valley, one on Cairn Peak, one at Molly Bog, and one on Round Hill (Fig.1). These checks determined the likelihood that a burrow was indeed a burrow, ensured that no burrows were missed, and determined the occupancy rate of burrows by response to playback. The repertoire described above was played directly into the burrow entrance for 15 seconds using a JBL IPX7 Bluetooth speaker at medium volume. If this failed to elicit a response, the burrow contents were checked by probing

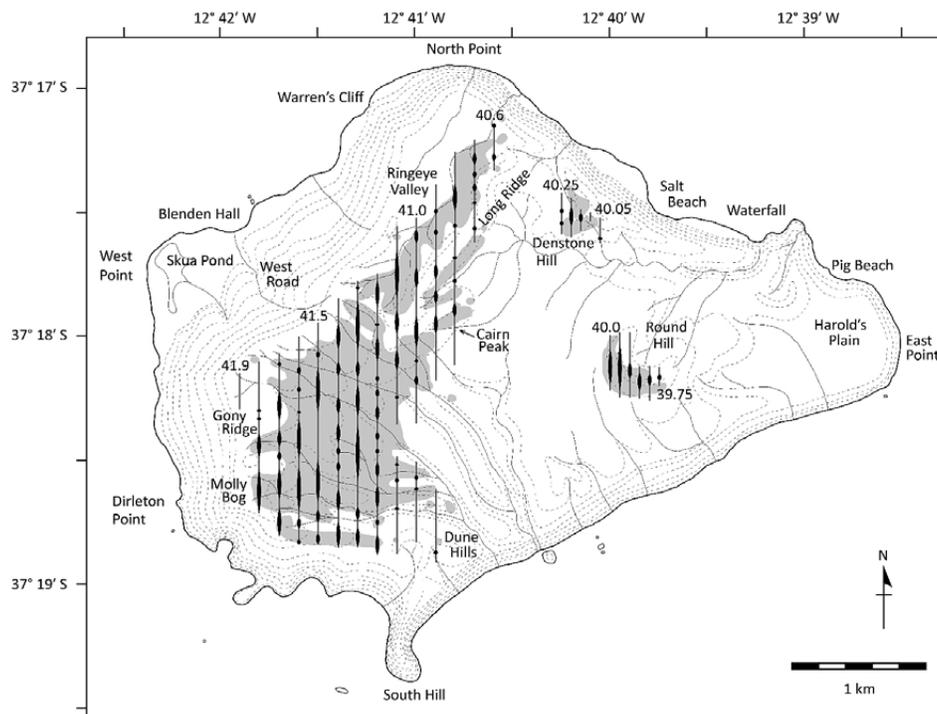


Fig. 1. The distribution of Spectacled Petrel nests counted during transects at Inaccessible Island, superimposed on the range estimated in 2009 (grey shaded area from Ryan & Ronconi 2011). Fine lines indicate transect areas sampled; black bulges indicate occupied patches (i.e., pooling areas with gaps smaller than 50 m between occupied patches).

with a stick or by using a burrowscope. We also counted all burrows within the upper section of Ringeye Valley, as recommended in the monitoring manual (Ryan 2005).

We used two approaches to estimate the total population of Spectacled Petrels: 1) simple extrapolations based on the area sampled, which consisted of 7 % of the main range and 14 % of the peripheral populations on Denstone Hill and Round Hill, and 2) extrapolations based on the average density in the different habitats sampled (i.e., stratified by habitat). The petrels breed in three main types of habitat: *Scirpus* terraces created by the petrels' burrowing activities, bogfern heath, and slopes covered in tussock grass *Spartina arundinacea*. Few birds breed on slopes dominated by ferns other than bogferns or in island tree *Phyllica arborea* woodland. Because these habitats support less than 0.5 % of the population (see Results), they were ignored for this exercise. We used Google Earth Pro to estimate the areas of each of the three main habitat types available within the breeding range. However, the Google Earth image was from 2005 and thus didn't reflect the current extent of terraces, which have increased with the petrel population. It was also difficult to identify smaller terraces among bogfern heath in the image. Therefore, we made two extrapolations: one based on three habitat types and one pooling both terraces and bogfern heath (because all terraces were within this habitat type). Populations were extrapolated based on the average \pm standard error (SE) of burrow density (burrows per 100 m²) recorded per habitat type. Burrow counts and extrapolated counts were converted into occupied burrows, which we defined as the best estimate of the number of breeding pairs, based on the burrow detection and occupancy tests described above.

Other seabird species

Northern Rockhopper Penguin populations were crudely estimated in 2009 and 2018 from counts of beach parties at each of the breeding colonies, a procedure that provides a rough proxy of colony size (Ryan *et al.* 1990, Ryan & Moloney 2000, Ryan 2005). Shore-based counts ($n = 5-8$) were made throughout November for colonies accessible from Blenden Hall, with the remaining colonies counted from images taken from a small boat (03 November) or ship (26 November, 30 November, and 01 December) that passed close to shore around the island's coast. We obtained a correction factor for the vessel-based counts on 01 December, when beach parties at three colonies on the east coast (Waterfall Slump, Salt Beach main, and Salt Beach north; Fig. 1) were photographed from a ship between 12h30 and 13h00, then counted during shoreline walks between 14h30 and 16h00. The beach party at the South Hill Beach also was counted from the cliffs above the beach on 11 November.

Estimates of the number of penguins breeding in each of the two colonies accessible from Blenden Hall were made in 2009 (Robson *et al.* 2011) and were repeated in September 2011. Colony areas were estimated by walking the perimeter with a handheld GPS. Penguin density was then estimated within each colony by counting the number of nests in 25 randomly selected 2x2 m quadrats. Incubation counts were not undertaken in 2018 because many birds abandoned their nests when we tried to map the edge of the colony, and several eggs were lost to predation by Tristan Thrushes *Turdus eremita* (Ryan & Ronconi 2010).

The tiny population of Tristan Albatrosses have large chicks in the

austral spring, and we counted all chicks. Atlantic Yellow-nosed Albatross nests containing eggs (or broken eggshells at newly refurbished nests) were counted in eight count areas, mostly centred around the top of the West Road. Together these areas accounted for around 20 % of the island's population (Ryan 2005). Sooty Albatrosses were harder to count, as most breed on the island's sheer cliffs, where their dark plumage makes them hard to detect. We counted incubating birds in the small colonies on the island plateau and thus accounted for perhaps 10 % of the island population (Ryan 2005). All albatross counts were conducted from late October to early November. Brown Skuas *Stercorarius antarcticus* breed throughout the island, with a major concentration around Skua Pond at West Point (Ryan & Moloney 2000). We recorded the locations of all nests encountered during October and November with a handheld GPS; given similar coverage of the island plateau, the counts in 1999, 2009, and 2018 are roughly comparable. Brown Noddies *Anous stolidus* and Antarctic Terns *Sterna vittata* were counted along the west coast from Warren's Cliff to Dirleton Point, with only incidental observations at the Waterfall during brief visits on 03 November and 01 December 2018. In addition, images were taken from a ship-based circumnavigation of the island on 01 December 2018. The east coast was not surveyed in 2009.

RESULTS

Spectacled Petrels

The burrow count in the top end of Ringeye Valley in 2018 (1 135) was down slightly from 2009 (1 210, compared to 970 in 2004 and 380 in 1999); some habitat was lost in this area due to the slumping and stripping of streambanks during a severe storm in winter 2017. During the systematic survey in 2018, we counted 2 922 Spectacled Petrel burrows in 25 transects (Fig. 1). The total length of transects sampled was 24.2 km, but the occupied range along transects (i.e., the distance from the first to the last burrow on each transect) was 18.7 km. Our counts were 2 449 burrows in 17.2 km in the main breeding range (21.2 km sampled), 75 burrows in 0.4 km at Denstone Hill (1.0 km sampled), and 398 burrows in 1.1 km at Round Hill (2.0 km sampled; Fig. 1). Average nest density in occupied habitat patches was 3.1 burrows per 100 m², but the density varied with habitat type. *Scirpus* terraces in bogfern heath supported a greater density of burrows (4.7 burrows per 100 m²) than other habitats (Table 1). *Scirpus* terraces supported 62 % of burrows in 40 % of the occupied area, with most of the remaining burrows in bogfern heath (31 % of burrows in 43 % of the area) and *Spartina* tussock grassland (5 % of burrows in 12 % of the area, Table 1).

Assuming the five-metre limit on either side of the transect line was strictly followed, the number of burrows counted crudely extrapolated to some 39 200 burrows (Table 2). Based on the area of suitable habitat within the breeding range (bogfern heath 104 ha (1.04 km²), *Scirpus* terraces 17 ha (0.17 km²), and tussock grasslands 19 ha (0.19 km²)), the extrapolated number of burrows is 47 316 (95 % confidence interval (CI) = 43 505–51 127); pooling bogfern heath and tussock grasslands gave a total of 58 471 burrows (49 453–67 490; Table 2). Burrow occupancy checks found that 8 % of perceived burrows were collapsed; in these cases, burrow entrances or fresh diggings did not lead to a nest chamber. However, five 'extra' burrows were found that were not detected in test areas, either through birds calling from hidden burrows or two burrows sharing a common entrance. Together, we suggest that some 97 % of counted

burrows were potential breeding sites. Of these, 90 % contained petrels (range 84 % to 100 % at the five test areas), with petrels responding to playback in 91 % of occupied burrows. This gave an overall correction factor from burrow counts to occupied burrows of 87 %, which translated to a crude population estimate of 34 000 to 50 000 pairs (31 000 to 46 000 pairs in the main breeding range, 2 500 to 3 100 at Round Hill, and 500 to 950 at Denstone Hill), based on the three different extrapolation methods. The total population of Spectacled Petrels has increased by ~12 % per year since 1999, faster than the ~7 % per year growth rate estimated up to 1999 (Fig. 2). There is less confidence in the population estimates prior to 1999.

Northern Rockhopper Penguins

At a decadal scale, counts of penguins in beach parties at colonies have decreased on average by 1 % to 2 % per year since 1999 (Table 3). However, numbers were much lower in 2004 than in any other year (Table 3), despite similar numbers of birds breeding in both colonies accessible from Blenden Hall (Ryan 2005). This emphasises the crude nature of these counts as a tool to monitor

population trends. Beach party counts also vary considerably both within days and seasonally through the breeding season (Ryan 2005). Counts from offshore tend to underestimate numbers of birds, even when using photographs; direct comparisons of beach parties at the three colonies around Salt Beach on 01 December gave ship-based counts of 975 birds (195, 560, and 220 for the Waterfall Slump, Salt Beach main, and Salt Beach north colonies, respectively), whereas shore-based counts made 2–3 h later averaged 50 % higher (285, 805, and 380 for the three colonies).

At a colony level, numbers of penguins at Where-the-Pig-Fell-Off decreased dramatically following a landslide that inundated part of the colony area between 2000 and 2004. A slip also covered much of the South Hill colony between 2011 and 2018. It is not known whether these slips happened during the breeding season. The decrease at South Hill has been offset to some extent by the formation of a new satellite colony west of the beach at Blenden Hall, some 160 m away from the main colony.

Estimates of nest densities at Warren's Cliff and Blenden Hall

TABLE 1
Numbers of Spectacled Petrel burrows counted and estimated densities (per 100 m²) by habitat type, based on fixed line transects (10 m width) at Inaccessible Island, October–November 2018

| Habitat | Patches | Length (m) | Burrows | Density | % Distance | % Burrows |
|-------------------------|---------|------------|---------|---------|------------|-----------|
| <i>Scirpus</i> terraces | 103 | 3 813 | 1 802 | 4.73 | 40.4 | 61.7 |
| Bogfern | 102 | 4 071 | 918 | 2.26 | 43.2 | 31.4 |
| <i>Spartina</i> tussock | 25 | 1 161 | 153 | 1.32 | 12.3 | 5.2 |
| Riverbank | 5 | 146 | 36 | 2.46 | 1.6 | 1.2 |
| Ferns | 3 | 109 | 7 | 0.64 | 1.2 | 0.2 |
| Woodland | 2 | 131 | 6 | 0.46 | 1.4 | 0.2 |
| Totals | 240 | 9 431 | 2 922 | | | |

TABLE 2
Estimates of the number of Spectacled Petrel burrows based on different extrapolation approaches using up to three habitat types: Bogfern heath (B), *Scirpus* terraces (T), and *Spartina* tussock grasslands (S)

| Area | Extrapolation | Burrows (95 % CI) | Bogfern | Terrace | <i>Spartina</i> |
|---------------|-------------------------|------------------------|---------------------|---------|-----------------|
| Main range | crude area | 35 755 | | | |
| | B/T + S | 53 679 (45 959–61 398) | 49 502 ^a | | 4 177 |
| | B + T + S | 42 576 (39 992–45 160) | 29 640 | 8 760 | 4 177 |
| Denstone Hill | crude area ^b | 548 | | | |
| | B/T + S | 1 134 (869–1 398) | 1 134 ^a | | 0 |
| | B + T + S | 992 (701–1 282) | 485 | 507 | 0 |
| Round Hill | crude area ^b | 2 905 | | | |
| | B/T + S | 3 659 (2 625–4 693) | 3 659 ^a | | 27 |
| | B + T + S | 3 748 (2 812–4 685) | 2 821 | 927 | 27 |
| Totals | crude area ^b | 39 208 | | | |
| | B/T + S | 58 471 (49 453–67 490) | 54 295 ^a | | 4 177 |
| | B + T + S | 47 316 (43 505–51 127) | 32 946 | 10 194 | 4 177 |

^a Extrapolation for bogfern and *Scirpus* terraces combined

^b The crude estimate simply corrects for the proportion of area not searched and so has no error term; habitat extrapolations use the standard error of the mean density estimate per habitat type to estimate the 95 % confidence intervals (CI) of the population per habitat.

did not differ significantly between 2009 and 2011, or between colonies (average overall was 1.48 nests per m², 95 % CI of the mean = 1.39–1.58, $n = 82$ quadrats). Colony areas decreased by ~10 % from 2009 to 2011 at both Warren’s Cliff (3 395 to 3 060 m²) and Blenden Hall (2 040 to 1 870 m²).

Albatrosses

Tristan Albatrosses are biennial breeders and seldom, if ever, attempt to breed in successive years if they raise a chick (Ryan *et al.* 2001). As a result, the number of large chicks we counted in November reflects only a subset of the population and does not account for early nest failures. Since 1990, at most one chick has been counted each spring, and even visits in late summer (when adults are incubating) recorded only one incubating pair (Herian & Malan 2011, 2012). However, at least two pairs were present in 1999/2000, when there was one chick in late 1999 and another pair incubating in early 2000 (Ryan & Moloney 2000). In November 2018, two large chicks were present on the island: one on Gony Ridge at 37°18.357’S, 012°41.635’W and one on the ridge north of Gony Ridge at 37°18.226’S, 012°41.885’W. Numbers of Atlantic Yellow-nosed and Sooty Albatrosses were roughly constant from 2004 to 2009, then increased slightly from 2009 to 2018 (Tables 4 and 5).

Skuas, noddies, and terns

Reasonably comprehensive counts of Brown Skua pairs were obtained in 2009 and 2018 (Fig. 3). In 2004 there was little chance to explore the eastern plateau and only 66 pairs were counted (59 nests and 7 pairs holding territory). The northeastern coast between the Waterfall and Salt Beach was not visited in 2009 (two nests and one pair holding territory in 1999, one nest in 2018), and the southeastern coast from Pig Beach to Twin Falls was visited in 1999 only (one nest and one pair holding territory). However, there was better coverage on Harold’s Plain in 2009 (nine nests) compared to 1999 (three nests and two pairs holding territory) or

2018 (two nests and two pairs holding territories). Despite these differences in coverage, there has been a steady increase in the number of pairs recorded either breeding or holding territory, from 18 in 1982 (Fraser *et al.* 1988) to 90 in 1999 (Ryan & Moloney 2000) to 107 in 2009 to 118 in 2018. This increase is also reflected in the well-studied Blenden Hall–West Point area (including Skua Pond), which supported 9 pairs in 1982, 10 in 1989, 21 in 1999, 22 in 2004, 28 in 2009, and 33 in 2018. Numbers of non-breeding birds attending the skua ‘club’ between Blenden Hall and West Point have remained roughly constant over this period (usually 50 to 90 birds).

Numbers of Brown Noddies nesting in trees in the vicinity of Blenden Hall also have increased steadily, from 4 pairs in the 1980s to 7 in 1999, 11 in 2004, 14 in 2009, and 19 in 2018 (Table 6). However, numbers breeding at the Waterfall appear to have decreased; we saw only a few pairs on the cliff here during a brief visit on 01 December 2018 (with none in the pine trees), compared to ~20 pairs in 1999 (Ryan & Moloney 2000) and perhaps 30 pairs in 1982 (Fraser *et al.* 1988). Noddy nests also were observed in rock crevices on the east side of South Hill as well as in *Phylica* trees along the river in middle Waterfall Valley and on the eastern slopes of Round Hill on the island plateau at around 300 m elevation.

Only two or three pairs of Antarctic Terns bred along the section of coast accessible from Blenden Hall (Warren’s Cliff to Dirleton Point) in 2009 and 2018, with all nests at Warren’s Cliff. Birds apparently no longer breed on the large rock exposure south of Skua Pond or at Dirleton Point (see Fraser *et al.* 1988). Elsewhere, they still breed on the low cliff behind the pine trees at the Waterfall (up to 10 pairs in 2018) and in rock crevices on the east side of South Hill (up to 20 pairs in 2018).

DISCUSSION

The populations of most monitored seabird species appear to be

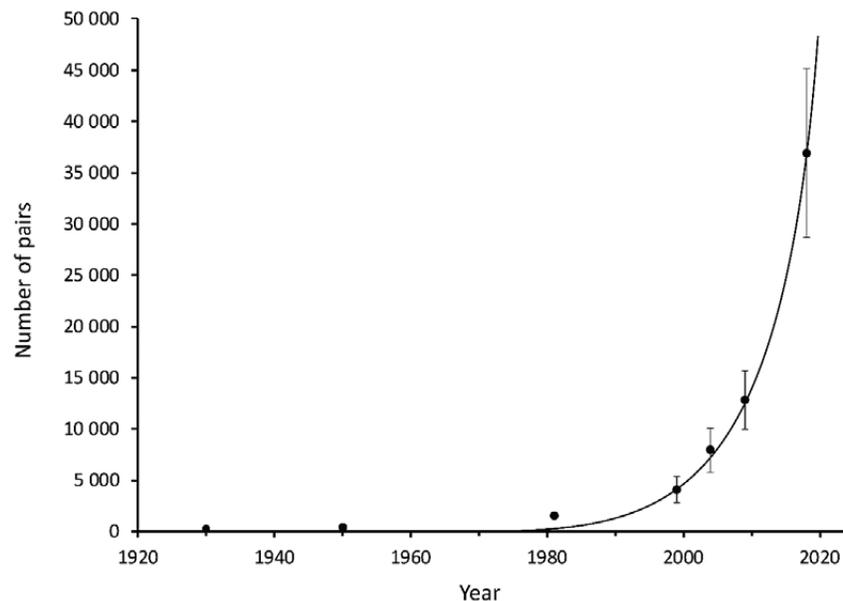


Fig. 2. Growth in the number of breeding pairs of Spectacled Petrels at Inaccessible Island. Error bars indicate standard error (no data for estimates made before 1999); the curve shows the best exponential growth model for surveys from 1999 to 2018 with an average annual growth rate of 11.4 % ($R^2 = 0.997$).

stable or increasing at Inaccessible Island, based on the most recent surveys in 2009 and 2018. The number of Northern Rockhopper Penguin may have decreased but counts of penguin beach parties give only a crude index of population size, and the apparent change in numbers was probably within the range of variance among and within years (considering the very low counts in 2004). Size estimates for the two colonies accessible from Blenden Hall decreased ~10 % from 2009 to 2011, but this might reflect inter-year variation rather than any long-term trend in the population. The fact that a new satellite colony has formed at Blenden Hall suggests that number of penguins is not decreasing dramatically, although it might include birds displaced by the landslip at the South Hill colony. More dedicated surveys of breeding colonies (e.g., Robson *et al.* 2011) are needed to assess whether the population is stable or decreasing. Considerable caution is needed to minimize disturbances (which potentially result in breeding failures) during such surveys.

The number of albatrosses has remained stable or perhaps

increased slightly, despite all three species being listed as Endangered or Critically Endangered. The breeding population of Tristan Albatross at Inaccessible Island appears to be stable at around 2–3 pairs, with no indication of the population recovering to previous levels of several hundred pairs in the late 1870s (Fraser *et al.* 1988). The stable population indicates a low recruitment rate; juveniles may die at sea, recruit elsewhere, or perhaps die if they land among dense vegetation on the plateau of Inaccessible Island (Ryan *et al.* 1990). The only other breeding location is Gough Island, where depredation by introduced house mice *Mus musculus* is a major threat (Davies *et al.* 2015). A mouse eradication is planned for 2020.

Atlantic Yellow-nosed and Sooty Albatrosses breed on all three islands in the Tristan group and on Gough Island. Recent population trends on Tristan and Nightingale islands are not known, but at Gough Island, a small study colony of Atlantic Yellow-nosed Albatross has remained stable over a 30-year period (1982–2011) and a larger population that has been monitored since 2000 has also been stable (Cuthbert *et al.* 2014). The pattern is similar to the stable trend observed on Inaccessible Island since 2004. Similarly, monitored colonies of Sooty Albatrosses at Gough Island have been stable since 2000 (Cuthbert *et al.* 2014), as has been also true for Inaccessible Island (this paper). These encouraging findings could warrant a review of these species' global status, especially for Sooty Albatrosses, given their ongoing increase at Marion Island (Schoombie *et al.* 2016). However, climate change and the risk of introduced diseases are potential threats to the Tristan populations (see below).

Although numbers of Brown Noddies breeding on the west coast of Inaccessible Island have increased since the 1980s, there have been decreases of roughly the same order at other sites on the island. Antarctic Tern numbers appear to have decreased since the 1980s. The best data are for the west coast, where only 2–3 pairs bred at one site in 2018 compared to 16 pairs at three sites in 1982 (Fraser *et al.* 1988). There were also an estimated 70 pairs on the east coast in 1982, compared to about 10 pairs in 2018. The reason for this decrease is unclear, but it may be a consequence of climate warming, as Tristan is the northernmost breeding site for the species. By comparison, there has been a clear increase in the number of skuas breeding at Inaccessible Island. The counts from the Blenden Hall area are particularly telling, because this

TABLE 3
Trends in the numbers of Northern Rockhopper Penguins counted in beach parties during November at Inaccessible Island

| Colony | 1989 ^a | 1999 ^b | 2004 | 2009 | 2018 |
|-------------------------|-------------------|-------------------|-----------------|------|------|
| Blenden Hall | 100 | 180 | 60 | 120 | 205 |
| Blenden Hall new colony | | | | | 55 |
| Warren's Cliff | 500 | 380 | 130 | 500 | 340 |
| Where-the-Pig-Fell-Off | 500 | 700 | 155 | 280 | 280 |
| Salt Beach north | 250 | 350 | 135 | 620 | 380 |
| Salt Beach main | 700 | 900 | 550 | 1200 | 990 |
| Waterfall Slump | 150 | 180 | 65 | 85 | 215 |
| Pig Beach | 100 | 300 | 115 | 76 | 115 |
| East Point | 80 | 220 | 105 | 54 | 75 |
| South Hill | nc ^c | 130 | nc ^c | 100 | 25 |
| Total | 2380 | 3340 | 1315 | 3035 | 2680 |

^a Data from Ryan *et al.* 1990

^b Data from Ryan & Moloney 2000

^c nc = not counted

TABLE 4
Trends in the numbers of Atlantic Yellow-nosed Albatrosses in eight count zones on the plateau of Inaccessible Island

| Count area | 2004 | 2009 | 2018 |
|------------------|------|------|------|
| Ringeye Valley | 160 | 125 | 146 |
| Slump | 27 | 24 | 30 |
| West Road valley | 42 | 44 | 43 |
| Cairn Peak South | 28 | 29 | 32 |
| Joe's River | 43 | 44 | 42 |
| Denstone River | 56 | 58 | 78 |
| Molly Bog | 39 | 29 | 42 |
| Total | 359 | 353 | 413 |

TABLE 5
Trends in the numbers of Sooty Albatrosses in eight count zones on of Inaccessible Island

| Count area | 2004 | 2009 | 2018 |
|--------------------|------|------|------|
| West Road gully | 4 | 3 | 7 |
| Slump scarp | 6 | 6 | 8 |
| Long Ridge South | 14 | 11 | 12 |
| Denstone Crag | 5 | 9 | 6 |
| 2nd River West | 2 | 10 | 8 |
| Boulder Hill River | 3 | 3 | 7 |
| Gony Ridge | 11 | 5 | 5 |
| Dune Hills falls | 6 | 1 | 8 |
| Total | 51 | 48 | 61 |

area is the best monitored and here the population has more than tripled since the 1980s. Skuas were killed and their nests destroyed on Tristan due to the perceived threat they pose to livestock, and similar persecution presumably occurred on Inaccessible Island up to the 1950s, when sheep were grazed on the island (Elliott 1957, Wace & Holdgate 1976). However, Tristan islanders seldom visited Inaccessible Island after the 1950s, allowing plenty of time for skua numbers to recover before the first population estimate in 1982 (Fraser *et al.* 1988). Skuas breeding at Inaccessible Island prey mainly on burrowing petrels (Ryan & Moloney 1991), and the distribution of nests has remained largely the same since 1999 (Fig. 3; Ryan & Moloney 2000). This suggests that petrel populations have remained relatively constant or possibly increased over the last 20 years.

Among monitored seabird species, the endemic Spectacled Petrel showed the greatest increase, continuing the species' long-term recovery following its near extinction due to depredation by introduced pigs *Sus scrofa* (Ryan 1998, Ryan & Moloney 2000, Ryan *et al.* 2006, Ryan & Ronconi 2011). The increase over the last few decades has been most obvious in peripheral breeding areas. For example, Spectacled Petrels apparently did not breed on Round Hill in the 1980s (Fraser *et al.* 1988), but there were

some 120 burrows in 1999 (Ryan & Moloney 2000), 690 in 2009 (Ryan & Ronconi 2011), and by 2018 we counted 398 burrows by sampling along transects that covered ~1/7th of the available habitat. The total estimate was close to 3000 burrows (Table 2). Range expansion was also detected on Denstone Hill, where isolated burrows were found on a ridge 180 m southwest of the 2009 range (transect 40.05; Fig. 1). Spectacled Petrels were found breeding for the first time in 2018 in mature *Phylica* woodland on the northern slopes of Denstone Hill. The ongoing range expansion presumably indicates a limited availability of favourable breeding sites within the core range, causing pairs to search for less crowded breeding sites elsewhere. This inference is supported by the high burrow-occupancy rates detected in all recent surveys (Ryan *et al.* 2006, Ryan & Ronconi 2011, this study). The population estimate from the new count technique has broader confidence intervals due to extrapolation from sampling less than 10 % of the species' range. However, by documenting exact ranges and burrow numbers per patch along repeatable transects, it will be easier to accurately detect future changes in both the density and distribution of Spectacled Petrel burrows. The latter procedure also reduces the amount of time necessary to conduct the survey.

Despite changing the count technique in 2018, the population growth of Spectacled Petrels has been consistently growing at ~12 % per year since the first systematic survey in 1999 (Fig. 2). This is faster than the annual growth rate up to 1998 of ~7 % per year, assuming that the estimates of ~50 pairs in 1937 (Hagen 1952), 200 in 1950 (Rowan *et al.* 1951), and 1000 in 1982 (Fraser *et al.* 1988) are reasonably accurate. An increased growth rate over the last two decades might reflect reductions in the impact of fisheries bycatch on the species. The foraging ranges of Spectacled Petrels overlap substantially with long-line fisheries off Brazil and Uruguay (Bugoni *et al.* 2009, Reid *et al.* 2014), resulting in hundreds of Spectacled Petrels being killed in the 1980s and 1990s (Ryan *et al.* 2006 and references therein). Seabird bycatch rates in these fisheries have declined substantially thanks to the implementation of various mitigation methods (e.g. bird-scaring lines, branch line weighting, and night-time setting of hooks; Bugoni *et al.* 2008b, Jiménez *et al.* 2010, Melvin *et al.* 2013, Jiménez *et al.* 2019, Santos *et al.* 2019), with decreases in incidental capture detected from around the time of the first systematic census in 1999 (Ryan *et al.* 2006 and references therein). It is particularly encouraging that the number of seabirds killed has decreased while the population of Spectacled Petrels has increased, suggesting that the benefits

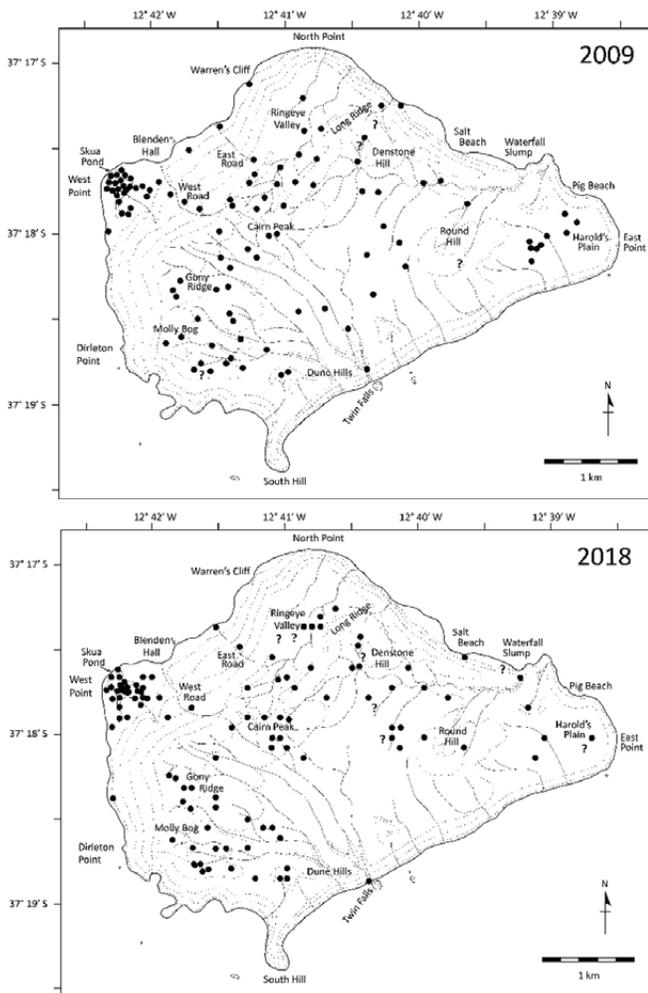


Fig. 3. The distribution of skua nests at Inaccessible Island in 2009 ($n = 107$) and 2018 ($n = 118$); “?” denotes pairs holding a territory but breeding was not confirmed.

TABLE 6
Long-term trends in the numbers of Brown Noddy nests in trees around Blenden Hall, Inaccessible Island

| Count area | 1980s ^a | 1999 ^b | 2004 | 2009 | 2018 |
|--------------------|--------------------|-------------------|------|------|------|
| Hut/Nelson’s Gulch | 2 | 0 | 0 | 2 | 3 |
| First Apples | 1 | 4 | 5 | 5 | 4 |
| Second Apples | 0 | 2 | 2 | 3 | 3 |
| Wilkins’ Copse | 1 | 0 | 4 | 4 | 7 |
| East Road | nc ^c | 1 | 0 | 1 | 2 |
| Total | 4 | 7 | 11 | 15 | 19 |

^a Data from Fraser *et al.* 1988 & Ryan *et al.* 1990

^b Data from Ryan & Moloney 2000

^c nc = not counted

of these mitigation measures are even greater for this species than is apparent from the changes in bycatch rate alone. Fortunately, Spectacled Petrels appear to be less susceptible to capture on long-lines than their close relative, the White-chinned Petrel *Procellaria aequinoctialis*, which is the species most often killed on long-lines in the Southern Ocean (Bugoni *et al.* 2008a, Jiménez *et al.* 2009, Rollinson *et al.* 2017, Jiménez *et al.* 2019).

The Spectacled Petrel provides an excellent example of how a petrel population can recover following near extinction due to depredation by an introduced mammal. Such success stories are important for promoting further restoration programmes that involve removing introduced predators from seabird breeding islands (Brooke *et al.* 2018). The IUCN down-listed the Spectacled Petrel from Critically Endangered to Vulnerable in 2007, and, although its breeding population continues to increase, it still qualifies as globally Vulnerable under criterion D2 (“population very small or restricted”) since the entire breeding population is confined to a single 14 km² island and has a total breeding range of less than 5 km². It remains susceptible to fishery impacts, given that Spectacled Petrels probably are killed by high-seas tuna fisheries, for which there are scant data on seabird bycatch rates (Reid *et al.* 2014). However, threats at the colony pose the greatest concern, despite Inaccessible Island’s status as a nature reserve and World Heritage Site.

Seabirds are at risk from peat slips, which kill breeding birds (e.g., Ryan 1993) and reduce suitable habitat for burrow-nesting birds (e.g., loss of deep soils on favourable slopes), penguins (e.g., when coastal breeding sites are destroyed by a deluge of debris from slips), and albatrosses (e.g., nest mounds and surrounding substrate washed away). The severe winter storm that washed away roads and buried pastures on Tristan in 2017 also caused extensive peat slips on Nightingale Island (BJD pers. obs.) and was probably responsible for the many recent slips observed on the plateau of Inaccessible Island in 2018. These slips contributed to the apparent slight decrease in Spectacled Petrels breeding in the top of Ringeve Valley. Ongoing climate change is likely to increase the frequency and intensity of severe weather events, with possibly adverse impacts for Spectacled Petrels and other seabirds breeding on Inaccessible Island. However, introduced diseases from domestic poultry pose perhaps the most serious threat. Jaeger *et al.* (2018) document the severe demographic impact of avian cholera on albatrosses and penguins breeding on Amsterdam Island. The disease apparently was introduced from poultry kept on the island (Jaeger *et al.* 2018). Skuas provide a potential vector for transferring poultry diseases from the main island of Tristan da Cunha to Inaccessible Island (Jaeger *et al.* 2018, Cerdà-Cuéllar *et al.* 2019). Tristan’s biosecurity measures need to be particularly stringent on any poultry imports to reduce the risk of diseases such as avian cholera, avian influenza, or Newcastle disease from reaching Tristan.

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POPULATION ESTIMATES OF BURROW-NESTING PETRELS BREEDING AT THE NIGHTINGALE ISLAND GROUP, TRISTAN DA CUNHA ARCHIPELAGO

BEN J. DILLEY^{1,2*}, DELIA DAVIES^{1,2}, ALEX MITHAM^{2,3}, TREVOR GLASS²,
JULIAN REPETTO², GEORGE SWAIN² & PETER G. RYAN¹

¹*FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa*
**(dilleyben@gmail.com)*

²*Conservation Department, Government of Tristan da Cunha, Edinburgh of the Seven Seas,
Tristan da Cunha TDCU IZZ, UK (South Atlantic Ocean)*

³*Current address: Government House, Stanley, Falklands, FIQQ IZZ, UK (South Atlantic Ocean)*

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ABSTRACT

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Nightingale is a group of three small, uninhabited islands in the central South Atlantic Ocean. The islands are free of introduced mammals and are largely pristine, supporting two endemic land birds as well as globally important populations of several species of seabirds. Seven species of burrow-nesting petrels are known to breed on the islands, including roughly 40 % of the world's population of Great Shearwaters *Ardenna gravis*. We estimated burrow densities by systematically searching for their burrows in 5×5-m quadrats across the main island in the austral summer of 2015. A total of 1 789 petrel burrows fell within the 75 sample quadrats with an average density of 0.95 burrows-m⁻², suggesting that upwards of four million petrels breed on the main island. Burrow densities and occupancy rates were extrapolated by species for each habitat type to generate population estimates: Great Shearwaters 2.34 million burrows (1.82 million pairs, 95 % CI 1.67–1.97 million); Broad-billed Prions *Pachyptila vittata* a minimum of 83 000 burrows (with many more pairs breeding in rock crevices, total estimate 100 000–500 000 pairs), White-faced Storm Petrels *Pelagodroma marina* 17 800 burrows (11 700 pairs, 95 % CI 4 700–16 600), Soft-plumaged Petrels *Pterodroma mollis* 12 100 burrows (estimated 8 000–10 000 pairs), Fregetta Storm Petrels *F. grallaria/tropica* 6 600 burrows (estimated 5 000 pairs), Common Diving Petrels *Pelecanoides urinatrix* 3 900 burrows (estimated 5 000 pairs), and Subantarctic Shearwaters *Puffinus elegans* an estimated 1 000 pairs. Although Great Shearwater burrow densities and occupancies were lowest in the areas historically used for exploitation of chicks and eggs (ongoing, but now monitored), these results suggest the great shearwater population on Nightingale Island has remained relatively stable since the first estimates in the 1950s.

Key words: Great Shearwaters *Ardenna gravis*, burrow densities, petrel survey, seabird exploitation

INTRODUCTION

Nightingale Island and its two offshore islets, Middle and Stoltenhoff Islands, are located at 37°25'S, 012°28'W and are the smallest of a group of mountainous islands that comprise the Tristan da Cunha Archipelago in the central South Atlantic Ocean. The main island of Tristan (96 km²) is inhabited by approximately 260 people, whereas neighbouring Inaccessible (14 km², 32 km to the southwest of Tristan) and Nightingale (2.6 km², 32 km to the south by southwest) Islands are uninhabited and largely pristine, supporting endemic land birds (e.g., *Nesospiza* finches) as well as globally important populations of seabirds (Ryan 2007). Despite its small size, Nightingale Island supports at least 40 % of the world's population of Great Shearwaters *Ardenna gravis* (BirdLife International 2018), and Middle Island, a small 10-ha (0.1 km²) islet off the north coast of Nightingale, supports an estimated 36 % of the world's population of Northern Rockhopper Penguins *Eudyptes moseleyi* (Robson *et al.* 2011). The archipelago's birds have been documented in some detail following surveys in the 1930s (Hagen 1952), 1950s (Rowan 1952, Elliot 1957, Rowan 1965), 1970s (Wace & Holdgate 1976, Richardson 1984), 1980s (Fraser *et al.* 1998, Ryan & Moloney 1991), and more recently (e.g., Ryan & Moloney 2000, Robson *et al.* 2011). However, recent and accurate surveys of breeding populations of burrow-nesting petrels on the Nightingale group of islands are lacking.

Historic island estimates of the Great Shearwater population of Nightingale Island range from two to three million pairs (Rowan 1952, Richardson 1984, Ryan *et al.* 1990). Globally, the breeding population estimate is ~five million pairs (BirdLife International 2018), with an estimated ~two million pairs breeding on Inaccessible Island (Ryan 2007) and ~one million pairs breeding on Gough Island (situated 400 km southeast of the Tristan islands; Cuthbert 2004). Islanders collected tens of thousands of Great Shearwater eggs, chicks, and adults from Nightingale and Inaccessible Islands from the 1930s to the early 1950s, when up to 15 000 eggs and 20 000 chicks were collected annually (Hagen 1952, Rowan 1952). In the early 1970s, an estimated 40 000–70 000 adult Great Shearwaters were taken annually from Nightingale Island (Richardson 1984), but, in 1976, exploitation was restricted to the collection of eggs and chicks (prohibited elsewhere in the archipelago; Wace & Holdgate 1976). Currently, the Tristan da Cunha Conservation Ordinance of 2006 (St. Helena 2006) protects Great Shearwaters at all islands except Nightingale, where exploitation is still restricted to the collection of eggs and chicks. Tristan's Conservation Department now roughly monitors the numbers of Great Shearwater chicks and eggs that are taken, which in recent years has varied from zero (2008–2010) to ~5 000 (2012) to a few hundred annually (2015–2019). Here, we present observations and population estimates of burrow-nesting petrels breeding on Nightingale Island recorded over the austral summers of 2015, 2016, and 2017.

STUDY AREA AND METHODS

The geography, vegetation, and history of the Tristan group of islands are described in detail by Wace and Holdgate (1976) and more recently in Ryan (2007). Nightingale's landscape is dominated by the 350–450-m high elongated ridge which rises steeply in the east. The central plateau (~250 m) is broken up into small hills and valleys, with four boggy ponds that have developed in shallow depressions on the western plateau, dominated by the sedge *Scirpus sulcatus*. Most of the island is covered with tussocks of *Spartina arundinacea* grass, which form dense, almost uniform stands that are 2–3 m high, broken only by copses of island trees *Phylica arborea* and small meadows of hummock-forming *Scirpus bicolor* that together cover ~5 % of the island (Fig. 1). Nightingale Island has two large, offshore islets: Middle Island (10 ha; 0.1 km²), which is a relatively low-lying island dominated by tussock vegetation and rocky outcrops; and Stoltenhoff Island (8 ha; 0.08 km²), a taller island with 70-m cliffs around much of its coastline and two rock stacks at its eastern end. Stoltenhoff is also dominated by tussock vegetation, but has a small copse of island trees at the highest point of the main islet (Ryan *et al.* 2011; Fig. 1). Nightingale and its islets are free of introduced mammals (e.g., house mice *Mus musculus* and ship rats *Rattus rattus*, which both occur on neighbouring Tristan da Cunha) and support millions of nesting seabirds (Rowan 1952, Ryan 2007). Nightingale has ~20 huts (each ~10 m²) and a large Conservation hut (~150 m², Fig. 1), both of which are occasionally used by islanders for holidays and work.

Fieldwork

DD and BD stayed on Nightingale Island for >10 mo over three successive summers: 46 d between 16 September 2015 and 11 January 2016; and continuously from 07 October 2016–25 January 2017 and 15 September 2017–22 January 2018. The bulk of the dedicated survey fieldwork was completed in 2015, but in 2016 and 2017 we collected additional data and recorded ad hoc observations while in the field studying Nightingale's endemic finches.

Burrow survey

To estimate burrow-nesting petrel breeding densities, BD and DD systematically searched for burrows in 75 5x5-m quadrats across Nightingale Island (Fig. 1). The two islets, Middle and Stoltenhoff Islands, were not sampled. Burrows were sampled at eight sites (altitudes 20–350 m), where quadrats were arranged approximately 25 m apart in lines of five. These sites covered the three main habitat types: (1) *Spartina* tussock grass, which covers most of the island; (2) *Scirpus* meadows, known locally as 'lamb houses,' which are small clearings around the ponds and on gentle slopes on the central plateau; and (3) forests of *Phylica* trees with an understory of ferns (mainly *Asplenium* spp. and bracken *Histioglossis incisa*) and sedges (*Scirpus*, *Carex*, and *Ucinia* spp.). Because Broad-billed Prions *Pachyptila vittata* mostly breed in rock crevices found in the numerous rock stacks on Nightingale Island, only a subset of the population was sampled by the burrow survey.

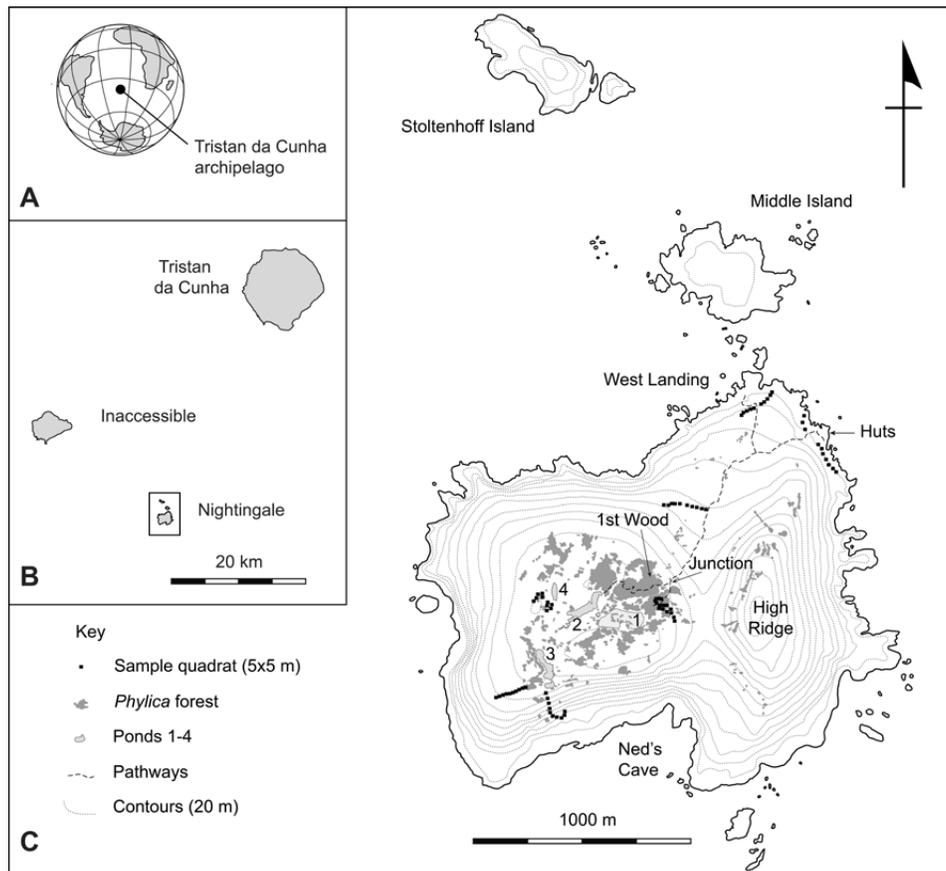


Fig. 1. (A) The location of the Tristan da Cunha Archipelago; (B) Nightingale and Inaccessible Islands relative the Tristan; (C) Nightingale Island and the outer islets, Stoltenhoff and Middle Islands, showing the locations of the 75 (5x5-m) quadrats (black squares not shown to scale) sampled in 2015.

The survey was completed from 07–29 November 2015 to coincide with the laying period of the most numerous petrel on the island, the Great Shearwater. At the time of the survey, Broad-billed Prions, White-faced Storm Petrels *Pelagodroma marina*, Subantarctic Shearwaters *Puffinus elegans*, and Common Diving Petrels *Pelecanoides urinatrix* were still breeding (see Fig. 2), but Soft-plumaged Petrels *Pterodroma mollis* and *Fregetta* Storm Petrels were not yet breeding (Fig. 2). Both Black-bellied *Fregetta tropica* and White-bellied Storm Petrels *F. grallaria* occur at Inaccessible Island (Robertson *et al.* 2016), and both have been recorded ashore on Nightingale Island (PGR unpubl. data). However, we did not extract birds from burrows to try to identify them to the species level.

All entrances to active burrows (with a bird present), and recently active burrows that fell within each 5x5-m quadrat, were identified and counted. Every burrow was inspected with a burrowscope (custom-made burrowscope with a high resolution conical pinhole camera, LED torch, and an 18x21-cm colour monitor) to determine the burrow status (empty, loafer, incubator). Large empty burrows were counted as Great Shearwater burrows because there are no other large burrow-nesting petrels on Nightingale Island. For smaller empty burrows, we used the relative shape and size of the burrow entrance

and the physical burrow characteristics (Schramm 1986, Dilley *et al.* 2017) to infer which species previously occupied the burrow.

Data analyses

Burrow occupancy was defined as the proportion of burrows that contained a bird incubating an egg, and was recorded only for Great Shearwaters and White-faced Storm Petrels (at the start of our field seasons, Broad-billed Prions were already at hatching stage). Hatching success was calculated as the proportion of eggs that hatched, and fledging success was calculated as the proportion of hatched chicks that survived to fledge (i.e., fledglings alive at the last nest check). The overall breeding success was calculated as the proportion of eggs that produced a fledgling. However, the estimates we present are maximum estimates, given that some chicks may have died after observations ceased and before fledging. For nests found at the chick stage, approximate hatch dates were deduced based on the size of the chick (relative to chicks of known age at other study nests).

We aimed to survey the density of seven species of burrow-nesting petrels; however, for three of these species we recorded too few burrows to include in the extrapolation analyses. For these species,

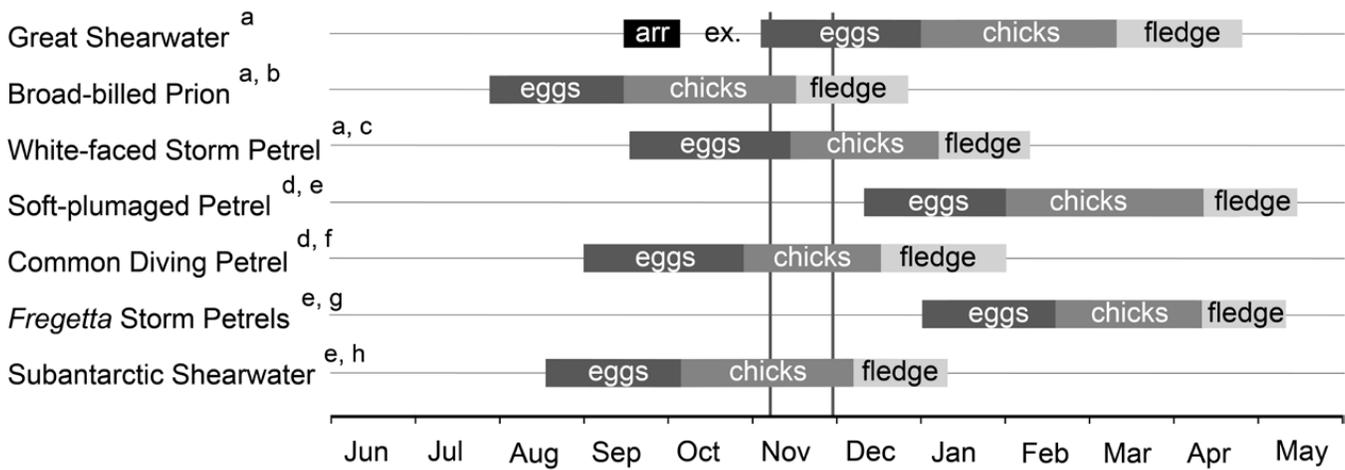


Fig. 2. Breeding months of seven species of burrow-nesting petrels at Nightingale Island. Vertical lines indicate the timing of the 2015 survey of 75 (5x5-m) quadrats. Data sources: ^a This study; ^b Berruti & Hunter 1986; ^c Campos & Granadeiro 1999; ^d FitzPatrick Institute unpubl. data; ^e Ryan 2007; ^f Payne & Prince 1979; ^g Quillfeldt & Peter 2000; ^h Booth *et al.* 2000.

TABLE 1
Population estimates of seven species of burrow-nesting seabirds breeding at Nightingale Island (excluding Middle and Stoltenhoff Islands) in 2015

| Species | Burrows (95 % CI) | Pairs (95 % CI) | Method ^a |
|--|------------------------------|------------------------------------|---------------------|
| Great Shearwater <i>Ardenna gravis</i> | 2212 000 (2034 000–2391 000) | 1716 000 (1 573 000–1 860 000) | 1 |
| Broad-billed Prion <i>Pachyptila vittata</i> | 83 600 (51 600–109 900) | <i>100 000–500 000^b</i> | 2 |
| White-faced Storm Petrel <i>Pelagodroma marina</i> | 17 800 (7 100–25 400) | 11 700 (4 700–16 600) | 1 |
| Soft-plumaged Petrel <i>Pterodroma mollis</i> | 12 100 (9 100–23 200) | <i>8 000–10 000</i> | 2 |
| Fregetta Storm Petrels <i>F. grallaria/tropica</i> | 6 600 (4 500–15 700) | <i>5 000</i> | 2 |
| Common Diving Petrel <i>Pelecanoides urinatrix</i> | 3 900 (1 100–12 500) | <i>5 000</i> | 2 |
| Subantarctic Shearwater <i>Puffinus elegans</i> | <i>1 500</i> | <i>1 000</i> | 2 |

^a Method: 1 = quadrats & density extrapolation; 2 = quadrats & *best estimate (italics)* based on field experience.

^b Total estimates, including prions that breed in rock crevices and caves.

we report a ‘best estimate’ of the island population size based on our field experience (Table 1). For the remaining four species, we calculated burrow densities ($n/25 \text{ m}^2$) for each quadrat plot. The standard errors ($SE = SD/\sqrt{n}$) and 95 % confidence intervals ($CI = \text{mean} \pm 2SE$) were calculated from the mean burrow densities of each species for the three habitat types. Where data produced a negative CI (White-faced Storm Petrels, Broad-billed Prions, Soft-plumaged Petrels, *Fregatta* Storm Petrels, and Common Diving Petrels), these data were bootstrapped using library *boot* (Canty and Ripley 2014) in R (R Core Team 2018) with 5000 iterations.

The areas occupied by the Northern Rockhopper Penguin colonies on Nightingale and Middle Islands were excluded from the analyses. Although some burrow-nesting petrels do breed in these areas, they occur at lower densities than in other areas; burrow densities were not measured to avoid disturbance to the breeding penguins. The main penguin colony areas on Nightingale and Middle Islands were calculated in 2015 by walking the perimeter with a handheld GPS set to record a waypoint every five seconds. The edge of the main *Phylica* copse ‘1st Wood’ was also calculated by walking the perimeter with a GPS. Because these areas are relatively flat, no correction for slope was needed. The remaining habitat perimeters and planar surface areas were captured remotely using Google Earth imagery and QGIS (version 2.18.11). Means are presented as mean \pm SD, unless stated otherwise. Breeding years refer to austral seasons (i.e., 2015 for the 2015/16 summer breeding season).

RESULTS

A total of 1 789 petrel burrows were found within the 75 sample quadrats (Fig. 1), suggesting upwards of four million petrels (1.95

million pairs; Table 1) breed on Nightingale Island with an average density of 0.95 burrows·m⁻².

Great Shearwater

A total of 1 551 Great Shearwater burrows occurred within the 75 sample quadrats (Table 2) at Nightingale Island, where Great Shearwater burrows were found in 100 % of the quadrats sampled. Average burrow density for tussock habitat was 1.02 ± 0.25 (SD) burrows·m⁻² and across all habitat types was 0.83 ± 0.30 burrows·m⁻². Assuming the same density occurs on the offshore islets, this suggests a total of 2.34 million burrows. Given burrow occupancies of 49 % to 78 % (by habitat, see Table 2), this equates to 1.82 million breeding pairs (95 % CI 1.67–1.97 million) of Great Shearwaters on Nightingale, Middle, and Stoltenhoff islands in 2015 (Table 2). The average density of Great Shearwater burrows sampled in tussock around the huts (5720 ± 905 burrows·ha⁻¹; 5720 ± 905 burrows·0.01 km⁻²) was nearly half the density of burrows sampled in tussock across the rest of the island (10220 ± 2517 burrows·ha⁻¹; 10220 ± 2517 burrows·0.01 km⁻²; Table 2, Fig. 1). Burrow occupancy (incubators) was also lowest around the huts (49 %) and in the *Phylica* copses (60 %), with an overall mean occupancy for all 75 quadrats of 70 % \pm 13 %.

Breeding phenology and breeding success

Great Shearwaters returned to Nightingale from mid-September to renovate their burrows and mate. By the last week in September, huge rafts of birds were offshore in the afternoons. Birds were very vocal at their burrows, especially at dusk and at night, when many birds were calling from outside their burrow entrances. In 2017, we estimated the peak return period for new birds arriving on the island

TABLE 2
The estimated number of Great Shearwater burrows and breeding pairs on Nightingale, Middle and Stoltenhoff islands

| Island Great Shearwater habitat (ha) | Number of quadrats | Total burrows | Empty burrows | Adult loafer | Adult incubator | Average burrows per ha \pm SD | Estimated number of burrows (95 % CI) | Breeding pairs (95 % CI) |
|---|--------------------|---------------|-------------------|------------------|--------------------|-----------------------------------|---------------------------------------|----------------------------------|
| Nightingale | | | | | | | | |
| Tussock around huts (1.9) | 10 | 143 | 50 (35 %) | 23 (16 %) | 70 (49 %) | 5720 \pm 905 | 10819 (9736–11902) | 5296 (4214–6378) |
| Rest of the island tussock (211.0) ^a | 40 | 1022 | 156 (15 %) | 68 (7 %) | 798 (78 %) | 10220 \pm 2517 | 2154577 (1986794–2322361) | 1682341 (1547857–1816826) |
| <i>Phylica</i> copses (12.2) | 10 | 82 | 26 (31 %) | 7 (9 %) | 49 (60 %) | 3280 \pm 1012 | 40051 (32236–47866) | 23933 (17511–30355) |
| <i>Scirpus</i> meadows & pathways (0.9) | 15 | 304 | 62 (20 %) | 20 (7 %) | 222 (73 %) | 8107 \pm 3643 | 7277 (5588–8965) | 5314 (3937–6691) |
| Middle^b | | | | | | | | |
| Tussock (5.2) ^a | - | - | - | - | - | - | 53462 (49299–57625) | 41744 (38407–45081) |
| Stoltenhoff^b | | | | | | | | |
| Tussock (7.6) | - | - | - | - | - | - | 78097 (72015–84179) | 60980 (56105–65855) |
| Total | 75 | 1551 | 294 (19 %) | 118 (8 %) | 1139 (70 %) | 8272 \pm 3518 | 2344283 (2155669–2532897) | 1819608 (1668031–1971186) |

^a Excluding the penguin colony areas (2015).

^b Islets not sampled; burrow densities assumed to be the same as on Nightingale.

to breed as 26 September (25–28 September, based on daily checks of 70 marked burrows from 19 September to 03 October; Fig. 3).

By early October, the island was noticeably quieter at night because most pairs had left on their pre-laying exodus, returning from late October to early November. The timing of laying was highly synchronous, with a peak in mid-November in all three study years (13 November \pm 2.5 d in 2015, $n = 50$ eggs; 15 November \pm 4.4 d in 2016, $n = 44$; 11 November \pm 3.1 d, $n = 47$ in 2017; Fig. 4). No birds were found incubating an egg on the surface (a common practice at Inaccessible Island, where the tussock is denser; PGR pers. obs.), although occasional eggs were found abandoned under the tussock around laying time. The incubation period averaged 53 d (range 52–55 d) at five nests where laying and hatching dates were noted accurately (daily checks) in 2017. Eggs measured an average of 78.0 ± 2.8 mm (74.0–86.4 mm) \times 49.3 ± 1.4 mm (46.9–52.1 mm, $n = 21$); mean hatching date in 2017 was 03 January \pm 3.9 d (26 December 2017 – 09 January 2018, $n = 34$ chicks). Hatching success was 72 % ($n = 50$ burrows), 64 % (44), and 74% (47) for the three consecutive study years. Survival to fledging could not be recorded because we left the island well before the chicks fledged. However, in January 2018, two of 34 chicks disappeared within a

week of hatching, but no further chick failures were seen on the final check, two weeks after peak hatching.

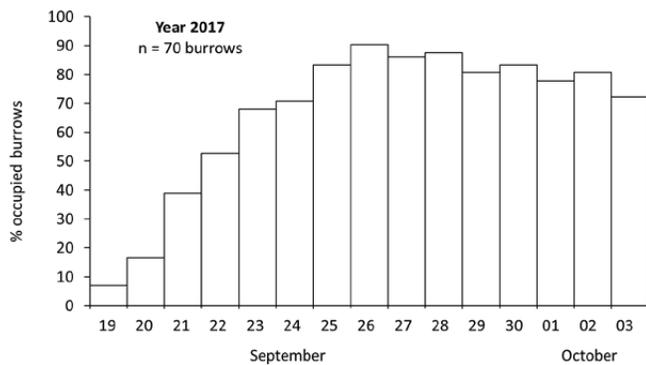


Fig. 3. The peak return period for Great Shearwaters arriving at Nightingale Island to breed in 2017.

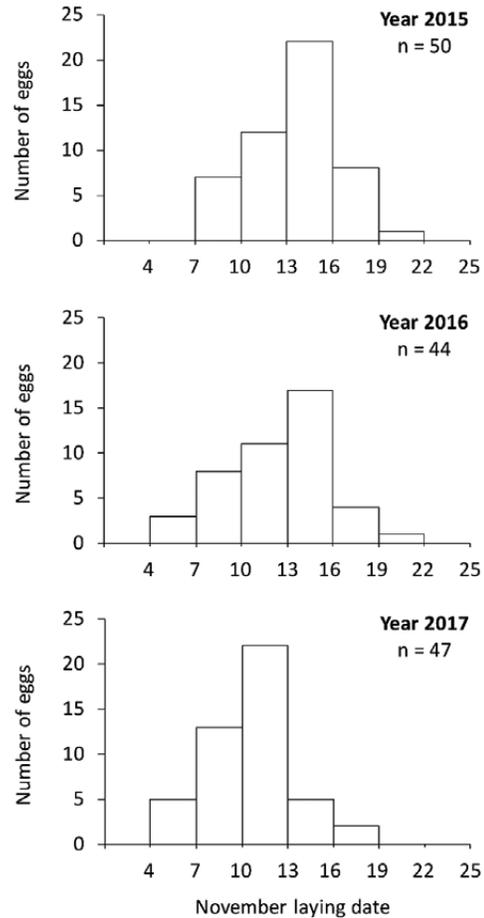


Fig. 4. Great Shearwater laying dates at Nightingale Island over three successive years.

TABLE 3
The number of petrel burrows found in 75 (5 \times 5-m) quadrats at Nightingale Island in 2015^a

| Nightingale habitat types (ha) | Number of quadrats | Great Shearwater | Broad-billed Prion | White-Faced Storm Petrel | Soft-plumaged Petrel | <i>Fregatta</i> Storm Petrels | Common Diving Petrel | Subantarctic Shearwater | Total burrows |
|---|--------------------|------------------|--------------------|--------------------------|----------------------|-------------------------------|----------------------|-------------------------|---------------|
| Tussock around huts (1.9) | 10 | 143 (100 %) | 51 (100 %) | 4 (30 %) | 8 (60 %) | 1 (10 %) | 4 (30 %) | 1 (10 %) | 212 |
| Rest of the island tussock (211.0) ^b | 40 | 1022 (100 %) | 34 (48 %) | 5 (8 %) | 2 (3 %) | 0 | 1 (3 %) | 0 | 1064 |
| <i>Phylica</i> copses (12.2) | 10 | 82 (100 %) | 16 (70 %) | 13 (70 %) | 14 (70 %) | 13 (90 %) | 3 (30 %) | 0 | 141 |
| <i>Scirpus</i> meadows & pathways (0.9) | 15 | 304 (100 %) | 10 (33 %) | 25 (67 %) | 21 (40 %) | 10 (47 %) | 2 (13 %) | 0 | 372 |
| Total | 75 | 1551 | 111 | 47 | 45 | 24 | 10 | 1 | 1789 |

^a Numbers in parenthesis indicate the percentage of quadrats which had burrows in each habitat.

^b Excluding the penguin colony areas (2015).

Broad-billed Prion

Broad-billed Prions are abundant on Nightingale Island and are the most numerous seabird after Great Shearwaters. Estimating the population size is very difficult because they nest in a wide range of habitats, often with complex twisted burrows that can have multiple nest chambers from a common entrance. They also favour rocky stacks, caves, and crevices, which are abundant on the island. We recorded 111 burrows (39 with large chicks, 3 loafers, 69 unoccupied) within the 75 quadrats, suggesting a total of 83 000 burrows (95 % CI 51 000–109 000). Broad-billed Prion burrows were most common in coastal tussock (100 % of these quadrats contained prion burrows) and *Phylica* (70 %) habitats (Table 3). However, this burrow estimate is a minimum estimate of the island population, as it excludes the estimated thousands of prions that breed in rocky stacks and caves on Nightingale, Middle, and Stoltenhoff Islands (which have very high densities of prions; PGR pers. obs. 2009). We therefore estimate that 100 000–500 000 pairs breed on the three islands.

Eggs measured 37.7 ± 1.7 mm (36.0–42.0 mm) \times 51.5 ± 1.6 mm (47.8–53.4 mm, $n = 11$). Average bill width of prions was 21.0 ± 1.0 (range 19.0–23.1, $n = 79$). On 18 September 2017, four of 11 active burrows had newly hatched chicks. Egg shells and depredated small prion chicks seen outside burrows in late September suggest that hatching time was approximately mid-late September. Small chicks (<5 d of age) were frequently killed by Tristan Thrushes *Turdus eremita*, which removed the chicks through the burrow entrance before bludgeoning their heads with their powerful bills (Ryan & Ronconi 2010). We only observed this behaviour once, but small chicks (1–2 weeks old) were found dead with head wounds on numerous occasions in early October 2016 and 2017, and it is likely that these were also killed by thrushes. Skuas *Catharacta antarctica* targeted fledglings in late November through to early December by excavating burrows or killing fledglings on the ground.

White-faced Storm Petrel

White-faced Storm Petrels were commonly encountered on Nightingale Island, and burrows were found under tufts of *Scirpus*

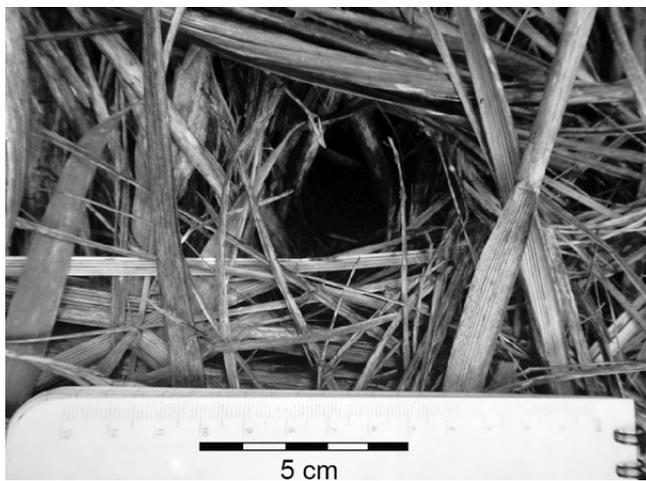


Fig. 5. Entrance of a White-faced Storm Petrel burrow in dead grass stems of *Spartina* tussock.

sedge as well as under the introduced farm grass *Holcus lanatus* in the pathways, in the understory of *Phylica* copses and to a lesser extent under tussock grass (Fig. 5, Table 3), usually close to an open area for easy access. We recorded 47 burrows (four with incubating adults, 26 with chicks, 17 unoccupied) within the 75 quadrats. Burrows had a small, neat entrance (average 70 mm wide \times 50 mm high, $n = 6$) with a narrow dry passage (mean length 500 ± 200 mm, 300–900 mm), often in an ‘S’-shape, leading to a fist-sized chamber with a sparse nest lining of *Scirpus* or *Spartina* leaves. On two occasions, we found an active burrow leading off a Great Shearwater burrow passage. Burrow densities were highest in the *Scirpus* meadows and pathways (mean density of 0.06 burrows- m^{-2} ; 25 of the 47 burrows found within the quadrats). Mean occupancy across all habitat types was 65 % \pm 22 %, with the lowest occupancy rates in the tussock around the huts (25 %) and the highest in the *Phylica* copses (77 %). Some cryptic burrows were inevitably overlooked; thus, we estimate a minimum total of 17 800 burrows (95 % CI 7 100–25 400) and 11 700 (95 % CI 4 700–16 600) breeding pairs on Nightingale.

Eggs were white with red speckles concentrated around the broad end, measuring 38.7 ± 0.5 mm (38.1–40.0 mm) \times 26.6 ± 0.4 mm (26.1–27.1 mm, $n = 16$). We marked 25 active nests during 09–13 November 2015; 15 already had small chicks when found (identified as White-faced Storm Petrels by their yellow toe webs), and those with eggs (10) were monitored every three days until hatching. Thereafter, nests were only checked once more, on 11 January 2016. Peak hatching time was approximately mid-November (average 11 November, range 29 October–24 November, $n = 6$ observed and 15 deduced); peak laying period was likely mid-late September (estimated as 05–30 September, using an incubation period of 54 d; Campos & Granadeiro 1999). Hatching success was not assessed because most nests were found at the late incubation or small chick stage. On 11 January 2015, 12 chicks had <20 % down feathers and three had up to 50 % down, suggesting a fledging period of mid-late January and a fledging success of 60 % (15/25). Chicks and adults were particularly vulnerable to predation by skuas, which excavated into burrows through the ceiling of the nest chambers. Although we did not observe any direct predation at a storm petrel burrow, a Tristan Thrush was seen killing a live ~two-day-old chick on 12 November 2015, and another was seen with a newly hatched chick in its bill on 19 November 2015.



Fig. 6. A pair of Soft-plumaged Petrels in a burrow in the 1st Wood, Nightingale Island, on 11 January 2016.

Soft-plumaged Petrel

Soft-plumaged Petrel calls (especially flight calls) were heard at night, especially from November onwards. Our quadrat survey was completed before Soft-plumaged Petrels started to lay; however, a total of 45 burrows of Soft-plumaged Petrel-size fell within the 75 sample quadrats: four contained pairs, while 41 (of which 34 were newly renovated) were unoccupied. These figures indicate a minimum of 12 100 (95 % CI 9 100–23 200) burrows and a crude estimate of 8000–10000 breeding pairs. Six of the unoccupied forest burrows were revisited after the survey on 11 January 2016, of which four contained incubating birds (Fig. 6), lending some confidence to our identification of these unoccupied burrows.

Fregatta Storm Petrels

Fregatta Storm Petrels were present on the island from September, but were more commonly seen and heard as their January breeding season approached. A total of 24 burrows was recorded as *Fregatta* Storm Petrels within the 75 sample quadrats, indicating a minimum of 6600 (95 % CI 4500–15700) burrows. Although the burrow characteristics were similar to those recorded for White-faced Storm Petrels, it seems unlikely that *Fregatta* Storm Petrels would share burrows with White-faced Storm Petrels because there is some overlap in their breeding cycles. We considered these 24 burrows to be those of *Fregatta* Storm Petrels because the burrows showed no signs of recent use (we observed thick cobwebs in the entrance and passage with no soil scrapings or signs of occupancy).

Five active nests were found in 1st Wood on 06 January 2017; eggs were white-pink in colour with a concentration of red speckles at the broad end, measuring 35.3 ± 0.4 mm (34.9–35.7 mm) \times 24.7 ± 0.2 mm (24.4–25.0 mm, $n = 5$). Based on the

quadrat burrow densities and frequency of calls, and observations at night in December/January, we crudely estimate a minimum of 5000 pairs.

Common Diving Petrel

Common Diving Petrels were often heard around the huts at night and frequently observed at sea (either singly or in groups of 5–25) when crossing by boat between Tristan and Nightingale. Diving petrels were also very abundant outside the kelp zone at Nightingale, where high densities of birds were seen on numerous occasions. A total of 10 burrows of diving petrel-size fell within the 75 sample quadrats, of which only two were active: one incubating adult (egg 39.2×29.7 mm) in a forest burrow south of Pond 4 on 11 November 2015 and one adult brood-guarding a small chick in a burrow in the steep coastal tussock slopes on 18 November 2015. This suggests a minimum of 3900 (95 % CI 1100–12500) burrows and a crude estimate of 5000 breeding pairs. On 29 December 2017, a newly fledged chick was found dead outside its earth burrow in 1st Wood, with ‘bludgeon’ head wounds similar to those inflicted by Tristan Thrushes on storm petrel chicks and adults (Ryan & Ronconi 2010).

Subantarctic Shearwater

Subantarctic Shearwaters were occasionally heard at night on the island, most commonly from the steep tussock coastal slopes. One occupied burrow was found in a quadrat in the coastal tussock slopes on 29 November 2017. The burrow was 1.2 m long, with a sharp curve ending in a small nest chamber and lined with *Spartina* leaves, where an adult was incubating an addled egg (53.3×36.2 mm). The burrow was empty one week later. JR found an incubating adult in the steep coastal tussock slopes above West

TABLE 4
The estimated number of Great Shearwater burrows and breeding pairs on Nightingale Island since the 1950s

| Nightingale Island (excl. Middle & Stoltenhoff) | Rowan (1952) | Richardson (1984) | Ryan <i>et al.</i> (1990) | This study |
|--|----------------------------|----------------------|------------------------------|---------------------------|
| Year | 1949–1950 | 1972–1974 | 1989 | 2015 |
| Sample plot/transect | 15 x (25 yd ²) | none | 2 x (2 m x 50 m) | 75 x (25 m ²) |
| Planar area used (ha) | 167 | 400 | 320 | 225 |
| Burrow densities (burrows·m⁻²) by habitat | | | | |
| <i>Scirpus</i> meadows | 1.79 | - | - | 0.81 |
| <i>Phylica</i> | 0.72 | - | 0.86 | 0.22 |
| Tussock | 1.20 | - | 1.06 | 1.02 |
| Overall density | 1.20 | 1.00 | ~1.00 | 0.98 |
| Reported burrow estimate | | | | |
| Burrows | ~2 million | ~4 million | ~3 million | 2.3 million |
| Occupancy | ~1.00 ^a | - | 0.71 ^b | 0.70 |
| Comparison using a standardised planar area of 225 h (2.25 km²) of habitat | | | | |
| Burrow estimate | 2.7 million | 2.2 million | 2.1 million | 2.3 million |
| Pairs | 2.7 million | - | 1.6 million | 1.7 million |

^a Occupancy not reported, but assumed as ~1.00 since “each year many hundreds of birds fail to obtain burrows and deposit their eggs on the open soil” (*cf.* Rowan 1952).

^b Occupancy from Inaccessible Island at same time.

Landing in September 2012; no additional active burrows were located over the three field seasons. We crudely estimate a breeding population of 1 000 pairs.

Grey-backed Storm Petrel

Grey-backed Storm Petrels *Garrodia nereis* were not seen or found in skua remains on the island, but were occasionally seen offshore during boat transfers. Their distinctive ‘cicada cricket’ call was heard from the hut at night on numerous occasions in November 2016/2017, but we did not locate a bird despite repeated searches through the *Spartina* tussock.

DISCUSSION

Based on comparison of historical estimates of the number of Great Shearwater burrows, there appears to have been a steady decrease in Great Shearwater numbers since the 1950s (Table 4). However, when estimates are compared using a standardised planar area of 225 ha (2.25 km²) of habitat, the population appears to have been relatively stable since the 1980s. Rowan (1952) estimated that upwards of two million pairs bred on Nightingale in 1949, and that their burrows covered the island at a mean density of one burrow per square yard (i.e., 1.20 burrows·m⁻², Table 4). This is the highest burrow density recorded on Nightingale, suggesting that there may have been a decrease in numbers between the first (Rowan 1952) and the second estimate (Richardson 1984). Ryan *et al.* (1990) recorded slightly lower densities in tussock (1.06 burrows·m⁻²), which are comparable to our 2015 tussock estimates (1.02 burrows·m⁻²). Although based on only a few records, this apparent early decline is further supported by Rowan’s statement that “each year many hundreds of birds fail to obtain burrows and deposit their eggs on the open soil” (*cf.* Rowan 1952, pp. 101), suggesting that burrow occupancy was close to 100 % (Table 4). By contrast, in 2015 we found that 20 % of the burrows were unoccupied, and we only observed a few abandoned eggs on the surface. Overall breeding success was not recorded in this study, but most petrel breeding failures on rodent-free islands tend to occur during the incubation and small-chick periods (Brooke 1990, Warham 1996). Therefore, it is likely that breeding success at our study nests would have been >60 %, which is above the normal range for most shearwaters (see Cuthbert 2005).

The Great Shearwater burrows sampled in the tussock around the huts had the lowest density (5720 ± 905 burrows·ha⁻¹; 5720 ± 905 burrows·0.01 km⁻²) and the lowest occupancy rates (49 %) across the island (Table 2, Fig. 1); this is likely due to the ongoing exploitation of chicks from this area over the last few decades. Burrow densities in *Phylica* and *Scirpus* meadows also appear to have fallen since previous surveys (Table 4). Although exploitation is roughly monitored and the shearwater population at Nightingale Island appears to have been relatively stable since the 1980s, Nightingale and Inaccessible islands are the most important rodent-free breeding sites for this species (Gough Island also supports a large breeding population in the presence of house mice *Mus musculus*). We strongly recommend restricting the exploitation of shearwaters at Nightingale and introducing an annual quota.

Broad-billed Prions are the second-most abundant seabird species breeding on Nightingale Island. Although two species of prions breed on Gough Island (Broad-billed Prion and MacGillivray’s

Prion *P. macgillivrayi*; Ryan *et al.* 2014), which is 380 km to the southeast, the morphology and timing of breeding suggest that only Broad-billed Prions breed at Nightingale Island. The average bill width of MacGillivray’s Prions on Gough Island is <19 mm (Ryan *et al.* 2014). However, the bill width of prions measured on Nightingale Island in 2015 was >19 mm (average 21.0 ± 1.0 mm, range 19.0–23.1 mm, *n* = 79), similar to those reported by Fraser *et al.* (1988) for prions from Inaccessible Island (average 21.6 mm, range 20–23 mm, *n* = 12). MacGillivray’s Prions also breed three months later than Broad-billed Prions on Gough Island, but, on Nightingale Island, we found no signs of prions laying in late November, or of small prion chicks in January.

Nightingale Island and its two offshore islets are globally important breeding sites for more than four million seabirds. The islands are riddled with petrel burrows, and the safeguarding of these seabirds’ breeding sites should remain a top priority for Tristan da Cunha. The Nightingale Island group currently has no conservation status (unlike Gough and Inaccessible islands, which are a single World Heritage Site, individual Ramsar sites, and Tristan Nature Reserves), and we encourage the Tristan Administration to proclaim the two islets as nature reserves. The accidental introduction of mice or rats from neighbouring Tristan da Cunha Island (where both currently occur) poses the greatest threat to these birds, and biosecurity measures need to be strictly enforced for visiting tourists, scientists, and islanders to avoid such a catastrophe.

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ENERGY INTAKE RATE INFLUENCES SURVIVAL OF BLACK OYSTERCATCHER *HAEMATOPUS BACHMANI* BROODS

BRIAN H. ROBINSON^{1,4}, LAURA M. PHILLIPS² & ABBY N. POWELL^{3,5}

¹ Department of Biology and Wildlife, University of Alaska, Fairbanks, AK 99775, USA

² National Park Service, Denali National Park and Preserve, Denali Park, AK 99775, USA

³ US Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, Fairbanks, AK 99775, USA

⁴ Current Address: US Geological Survey, Alaska Science Center, Anchorage, AK 99508, USA

⁵ Current Address: US Geological Survey, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville, FL 32611, USA (abbypowell@ufl.edu)

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ABSTRACT

ROBINSON, B.H., PHILLIPS, L.M. & POWELL, A.N. 2019. Energy intake rate influences survival of Black Oystercatcher *Haematopus bachmani* broods. *Marine Ornithology* 47: 277–283.

The Black Oystercatcher *Haematopus bachmani* is a species of conservation concern that depends on marine intertidal prey resources. We examined diet, feeding rates, growth, and survival of Black Oystercatcher broods in southcentral Alaska, 2013–2014. To determine the importance of diet for brood survival, we modeled daily survival rates of broods as a function of energy intake rate and other ecological factors. We hypothesized that broods fed at higher energy intake rates would grow faster and fly earlier, and thus be less vulnerable to predators and have higher rates of survival. Consistent with our prediction, broods with higher energy intake rates had higher rates of growth and daily survival. Our best-supported model indicated that brood survival varied by energy intake rate and brood age. To understand how adults meet the increasing nutritional needs of developing chicks, we examined delivery rates, prey type, and prey size as a function of brood age. Delivery rates differed by age, but composition and size classes of prey items did not, indicating that adults respond to the rising energetic needs of broods by increasing parental effort rather than by switching prey. These findings demonstrate the importance of diet and provisioning to broods and, given the consequences of reduced energy intake on survival, indicate that climate change–related shifts in intertidal invertebrates could significantly impact Black Oystercatcher populations.

Key words: Alaska, brood survival, chick diet, growth, parental care, provisioning rates

INTRODUCTION

The Black Oystercatcher *Haematopus bachmani* has been designated as a species of conservation concern due to its small population size, unknown population trends, and limited distribution (Tessler *et al.* 2014). They range from Baja California, Mexico to the Aleutian Islands of Alaska and are reliant on nearshore marine habitats for all life history components, including feeding, nesting, and raising their semi-precocial young (Andres & Falxa 1995). This reliance on the nearshore environment throughout their annual life cycle has made them vulnerable to a number of threats such as predation of eggs and young; human disturbance; coastal infrastructure development; direct and indirect effects of shoreline contamination, including reduced food availability; and climate change, with resultant effects on nesting and feeding resources (Tessler *et al.* 2010).

Despite considerable research effort examining threats to nest survival, our understanding of factors influencing Black Oystercatcher post-hatch survival is limited (Vermeer *et al.* 1992, Gill *et al.* 2004). Although predation is thought to be the major cause of mortality in Black Oystercatcher broods (Tessler *et al.* 2014), there is some evidence to suggest that diet plays an important role in brood survival. For example, in a study in British Columbia, heavier Black Oystercatcher chicks had a better chance of survival than lighter chicks (Groves 1984). Similar patterns were documented for Eurasian Oystercatchers *H. ostralegus*, in that fledging success was positively correlated with growth rate (Kersten

& Brenninkmeijer 1995). Furthermore, in years of lower food availability, brood survival of Eurasian Oystercatchers decreased (Heg & van der Velde 2001).

Given the potential relationship between diet and brood survival, climate-induced changes in the abundance or composition of marine intertidal invertebrates may significantly affect Black Oystercatchers. Warming ocean temperatures alter the behavior, physiology, and demography of many invertebrates on which Black Oystercatchers depend (Grenon & Walker 1981, Menge *et al.* 2008). The breeding propensity of Black Oystercatchers is negatively correlated with sea-surface temperature, presumably due to warmer sea temperatures creating deficient feeding conditions that result in poor body condition of breeding adults (Hipfner & Elner 2013). Ocean acidification, sea level rise, and increased storm frequency may also affect marine invertebrate communities (Harley *et al.* 2006, Fabry *et al.* 2008). These changes may have profound implications for Black Oystercatchers, considering that their diet is relatively specialized and has remained constant over the past century (Carney 2013).

To assess the importance of diet on brood survival of Black Oystercatchers, we modeled daily survival rates of broods as a function of energy intake rate and other ecological factors. We hypothesized that broods fed a similar diet but at a greater frequency would grow faster and fly earlier, and thereby be less vulnerable to predators. Assuming that diet is an important factor influencing brood survival, we predicted that the energy intake rate of broods

would be positively correlated with survival rates. To understand how adults meet the increasing nutritional needs of developing chicks, we examined how delivery rates, prey composition, and prey size varied with chick age. Collectively, these findings will identify the importance of diet and provisioning to the survival of Black Oystercatcher broods in a rapidly changing marine ecosystem.

STUDY AREA AND METHODS

Our field site was located within Kenai Fjords National Park in southcentral Alaska, USA, (59°51'18"N, 149°42'14"W). Specifically, we studied Black Oystercatchers (hereafter referred to as oystercatchers) nesting in Aialik Bay, a deep, glacially forged inlet in-cut by smaller coves and bounded by steep mountains (Cook & Norris 1998, Spencer & Irvine 2004). Shoreline topography varies from gravel beaches of low wave energy to rocky cliffs of high wave energy with a mean tide range of 1.7 m (NOAA 2008).

Field methods

From May to August in 2013 and 2014, we conducted systematic boat-based surveys of historically known nesting sites to locate breeding territories and oystercatcher broods. Upon detecting a territorial pair, we searched the surrounding area on foot. For all nests found, we recorded location and clutch size, and we floated eggs to determine the stage of incubation to estimate hatch dates (Mabee *et al.* 2006). To detect new nests throughout the breeding season, we periodically revisited sites where nests had failed, sites where territorial pairs were observed but had yet to initiate a nest, and historical breeding sites. Once nests were located, we monitored them every 3–5 d throughout the nesting period. As nests approached the estimated day of hatch, we visited them daily. After eggs hatched, we visited broods every 3–5 d until they fledged or failed, to determine growth rates, energy intake rates, and fledging success. We monitored six broods in 2013 and fourteen broods in 2014. Chicks were considered to have fledged when they were fully capable of sustained flight, which occurred at ~40 d after hatch.

We marked chicks with colored tape or colored plastic bands until their tarsi were large enough to be fitted with a metal band and two plastic alpha-numeric bands. We recaptured chicks every 3–5 d until they fledged or died, to measure relaxed wing length and thus determine growth rates. We used wing growth rather than body mass in our growth rate analysis because wing length determines when chicks can fly (Tjørve *et al.* 2007).

To estimate energy intake rates, we observed adults provisioning their broods for two hours at low tide, when intertidal feeding grounds

became exposed. Upon arriving at a territory, we used binoculars to locate the brood from our boat. During the first few days after hatch, most broods remained at the nest. Later, they moved with their parents to intertidal feeding areas and throughout their territory. Broods stayed with and were fed by their parents throughout the entire chick-rearing period. After a brood was located, we set up a 20–60× spotting scope in a camouflaged blind ~50 m away and waited for the birds to resume normal activity, which typically occurred within minutes of us entering the blind. We recorded the taxa and size class of each prey item fed to a chick and the time at which the provisioning event occurred. We assigned prey items to a size class in relation to adult bill length, using four size classes: 1) less than one eighth of the bill length, 2) between one eighth and one quarter, 3) between one quarter and one half, and 4) one half or more. Prey items, in general, were easily identifiable to the genus or species level based on shape, size, and color, as well as on the handling behavior of the adults. If the observer was unsure of the prey or if vision was obstructed during a feeding event, the prey item was listed as 'unknown.' Two observers worked together throughout the study to reduce observer bias. All fieldwork was conducted under appropriate permits and with approval from the University of Alaska, Fairbanks, Institutional Animal Care and Use Committee (#436591).

Energy analysis

We collected intertidal invertebrates to measure the energy content of oystercatcher prey. In July 2014, we sampled from five intertidal feeding areas within our study site. We collected the four most common prey items that we observed being fed to chicks: limpets *Lottia* spp. ($n = 22$), mussels *Mytilus trossulus* ($n = 45$), barnacles *Semibalanus cariosus* ($n = 15$), and chitons *Katharina tunicata* ($n = 10$; Table 1). Samples were frozen at $-4\text{ }^{\circ}\text{C}$ for approximately one month prior to analysis. In the lab, we measured the length and mass of each frozen sample, then dried them in a freeze drier at $-40\text{ }^{\circ}\text{C}$ for at least 48 hours. After freeze-drying, we weighed the samples, removed shells, and reweighed the samples to determine dry mass. We combined samples of the same prey type to obtain three composite samples with minimum of 1 g of homogenized dry mass for each prey item; samples were then homogenized using scissors and a mortar and pestle. Energy content of composite samples was measured using a bomb calorimeter and corrected for the unburned fuse and acid by titration. We calculated the energy density of composite samples as kilojoules per gram dry mass ($\text{kJ}\cdot\text{g}^{-1}\text{ DM}$) and averaged composite samples of the same prey type to obtain mean energy densities.

Since not all organic compounds in the diet are available to the consumer, we conducted a pepsin digestibility assay to determine

TABLE 1
Energy density ($\text{kJ}\cdot\text{g}^{-1}$) and digestibility ($\text{g digested}\cdot\text{g}^{-1}$ dry mass (DM)) of intertidal marine invertebrates collected in Kenai Fjords National Park, Alaska, July 2014

| Prey type | Energy density of composite samples | | | | | | Mean energy density ($\text{kJ}\cdot\text{g}^{-1}$) \pm SD | Mean digestibility ($\text{g digested}\cdot\text{g}^{-1}$ DM) \pm SD | Mean digestible energy density ($\text{kJ}\cdot\text{g}^{-1}$ DM) |
|-----------|-------------------------------------|-----|-------------------------------|-----|-------------------------------|-----|--|---|--|
| | $\text{kJ}\cdot\text{g}^{-1}$ | n | $\text{kJ}\cdot\text{g}^{-1}$ | n | $\text{kJ}\cdot\text{g}^{-1}$ | n | | | |
| Barnacle | 18.64 | 5 | 16.96 | 5 | 17.58 | 5 | 17.73 ± 0.69 | 0.49 ± 0.02 | 8.64 |
| Chiton | 18.68 | 3 | 18.38 | 3 | 19.65 | 4 | 18.90 ± 0.54 | 0.73 ± 0.11 | 13.75 |
| Limpet | 19.59 | 10 | 20.39 | 12 | - | - | 19.99 ± 0.40 | 0.78 ± 0.08 | 15.57 |
| Mussel | 17.84 | 15 | 18.06 | 15 | 17.94 | 15 | 17.95 ± 0.09 | 0.89 ± 0.04 | 16.02 |

the digestible energy density of prey items (Barboza *et al.* 2009). Approximately 1 g of homogenized dry mass of each prey type was placed in synthetic filter bags, inserted in jars, and immersed in an acid-pepsin solution of pH 1 in a 0.1 mol/L HCl solution containing 2 g/L pepsin (VanSomeren *et al.* 2015). The jars were placed in an incubator for six hours, then filter bags were removed, rinsed, and dried in an oven. We reweighed the samples to determine the remaining mass. Digestibility of prey was calculated by dividing the difference between total dry mass and remaining dry mass by the total dry mass. We calculated digestible energy density of prey items as the product of energy density and digestibility.

We estimated the energy intake rates of broods based on data from our provisioning observations and estimates of digestible energy density. For each prey type, we estimated the energy content of the four size classes to which observed prey was assigned. Energy content (kJ) of size classes was calculated as the product of digestible energy density ($\text{kJ}\cdot\text{g}^{-1}$) for each prey type and dry mass (g). We estimated the dry mass of size classes using the length-to-mass regression of each prey type and the proportion of bill length that each size class represented. We used adult bill length data (see Jehl 1985 in Andres & Falxa 1995) and calculated length-to-mass regressions from our measurements (see Burgherr & Meyer 1997 in Baumgärtner & Rothhaupt 2003). The energy intake rate was calculated as the total energy content of prey fed to chicks per time observed ($\text{kJ}\cdot\text{min}^{-1}$). Delivery rate was calculated as the total number of prey items fed to chicks per time observed. To account for variation in brood size, which ranged from one to three chicks, we divided energy intake and delivery rates by the number of chicks in a brood. We averaged energy intake rates to obtain a mean energy intake rate for each brood.

We calculated linear growth rate to quantify wing growth (Nisbet *et al.* 1995). Although birds exhibit a nonlinear pattern of growth (Ricklefs 1973), we were unable to capture chicks after they fledged, when growth rates begin to reach an asymptote. Therefore, we analyzed the linear phase of growth, which occurs when oystercatchers are 5–35 d old (Groves 1984, Hazlitt *et al.* 2002). Growth rate coefficients were calculated for broods by linear regression of age (in d) and wing length (in mm). Age and wing length values were log-transformed to meet assumptions of normality and equal variance. To test for a relationship between energy intake and wing growth, we conducted a linear regression of energy intake rate and wing growth rate coefficients.

We examined how delivery rate, prey composition, and prey size varied by chick age. We investigated these relationships by comparing between age classes: young (age ≤ 15 d) and old (> 15 d) chicks. We tested for a difference in delivery rates (number of prey items fed to chicks per minute) between the two age classes using a two-sample *t*-test. We conducted a chi-squared test of independence to determine if prey composition (limpets, mussels, barnacles, chitons, 'other' prey, unknown prey) differed between young and old chicks. We also conducted a chi-squared test to determine if the four size classes of prey consumed by chicks differed between age classes.

Survival analysis

We used an information-theoretic approach to examine the relative support for models that describe associations between daily survival rate of broods and variables of interest. A small set of candidate

models was selected from variables that we hypothesized might influence survival. These variables were age (as both a linear and quadratic trend), year (2013, 2014), minimum daily temperature, landform (island vs. mainland), and our primary variable of interest: energy intake rate. We included the landform covariate because we reasoned that: (1) survival would be higher for broods on islands than on the mainland due to the absence of mammalian predators on islands in our study area (Morse *et al.* 2006) and (2) composition of prey items delivered to chicks reared on rocky islands would differ from prey provisioned on mainland beaches (Robinson *et al.* 2018). In addition to models with a single variable of interest, we included additive models consisting of all two-covariate combinations (Table 2). Given that energy intake rates increase with brood age (Hazlitt *et al.* 2002) and that we did not have intake rates for many broods 20–40 d old because they did not survive to fledge, we limited our energy intake rates of broods to observations that occurred when broods were 15 days old or younger. We were unable to obtain energy intake rates for 7 of the 20 broods studied; to account for these missing data in the models that included energy intake rate, we applied the energy intake rate covariate to only the broods with energy intake data, and we applied the other covariates in the model to all broods (Cooch & White 2002). We used Akaike's information criterion, adjusted for small sample size (AIC_c) and normalized Akaike weights (w_i), to select the top-supported model in the candidate set. We conducted our survival analysis using

TABLE 2
Model rankings for Black Oystercatcher brood survival at Kenai Fjords National Park, Alaska, 2013–2014

| Model ^a | ΔAIC_c^b | w_i | <i>K</i> | Deviance |
|---------------------------------------|------------------------|-------|----------|----------|
| Age ² + Energy Intake Rate | 0.00 | 0.95 | 7 | 62.29 |
| Age ² | 8.92 | 0.01 | 3 | 79.35 |
| Energy Intake Rate | 10.22 | 0.01 | 3 | 80.66 |
| Age ² + Year | 10.70 | <0.01 | 4 | 79.11 |
| Age ² + Min Daily Temp | 10.72 | <0.01 | 4 | 79.13 |
| Energy Intake Rate + Min Daily Temp | 10.87 | <0.01 | 5 | 77.24 |
| Age ² + Landform | 10.93 | <0.01 | 4 | 79.34 |
| Energy Intake Rate + Landform | 11.45 | <0.01 | 4 | 79.86 |
| Year | 11.94 | <0.01 | 2 | 84.40 |
| Constant | 12.12 | <0.01 | 1 | 86.59 |
| Energy Intake Rate + Year | 12.73 | <0.01 | 5 | 79.11 |
| Age | 13.28 | <0.01 | 2 | 85.73 |
| Landform | 13.96 | <0.01 | 3 | 84.40 |
| Min Daily Temp + Year | 13.96 | <0.01 | 3 | 84.40 |
| Min Daily Temp | 13.97 | <0.01 | 2 | 86.43 |
| Landform | 14.01 | <0.01 | 2 | 86.47 |
| Min Daily Temp + Landform | 15.87 | <0.01 | 3 | 86.31 |

^a Models were ranked by differences for small sample size (ΔAIC_c) values. Normalized Akaike weight (w_i), number of parameters (*K*), and model deviance (Deviance) are also shown for each model.

^b The lowest AIC_c score in the model set was 76.48.

the nest survival module in program MARK (White & Burnham 1999). All other statistical analyses were done in program R (R Development Core Team 2014).

RESULTS

We monitored 20 oystercatcher broods in 2013 and 2014. The mean brood size was 2.3 ± 0.7 chicks (mean \pm standard deviation (SD)), with a range of 1–3 chicks per brood. Of 20 nests that hatched, 10 fledged at least one chick (fledging success of 50 %).

We observed 1 979 prey items fed to chicks in the 20 broods. Limpets were the most common prey consumed, followed by mussels, barnacles, and chitons. Of the common prey consumed by oystercatcher broods, limpets had the highest energy density (mean \pm SD; 19.99 ± 0.40 kJ·g⁻¹ DM) of the four prey items we analyzed (Table 1). However, mussels had the highest digestibility (0.89 ± 0.04 g digested·g⁻¹ DM) and digestible energy density (16.02 kJ·g⁻¹ DM). Prey items of size class 2 (1/8–1/4 bill length) made up the majority (53 %) of prey items fed to chicks. Digestible energy content of this size class was highest for limpets (1.13 kJ), followed by chitons (0.66 kJ), barnacles (0.59 kJ), and mussels (0.35 kJ).

Delivery rates were higher for old chicks than for young chicks ($t_{17} = -3.39$, $P = 0.004$; Fig. 1). However, neither the composition ($X^2_{25} = 30$, $P = 0.22$) nor the size classes ($X^2_9 = 12$, $P = 0.21$) of prey items fed to chicks by their parents differed between old and young chicks.

We calculated wing growth rates for broods during the linear phase of growth. The mean wing growth rate coefficient was $1.12 (\pm 0.12$ SD) with a range of 0.87–1.27. Energy intake rate to day 15 varied among broods, ranging from 0.01–1.01 kJ·min⁻¹ with a mean of $0.28 (\pm 0.26$ SD; $n = 13$). Energy intake rates were positively correlated with wing growth rate coefficients ($F_{1,9} = 14.87$, $P = 0.004$; Fig. 2).

We modeled daily survival rates of 20 oystercatcher broods. The best-supported model indicated that brood survival varied by

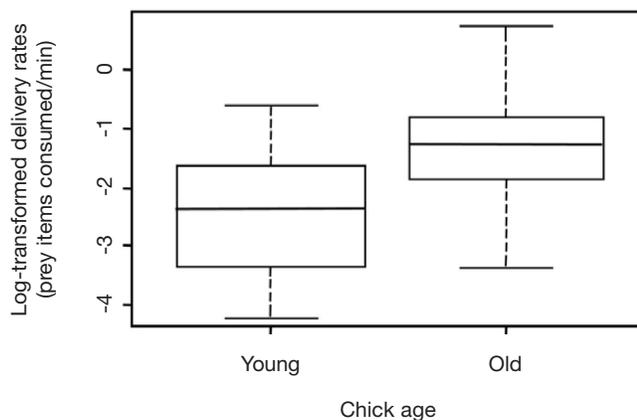


Fig. 1. Log-transformed delivery rates (prey items consumed per minute) differ between young (age ≤ 15 d) and old (> 15 d) Black Oystercatcher chicks in Kenai Fjords National Park, Alaska. Boxes represent the distances between the first and third quartiles; center bars represent the medians.

energy intake rate and brood age (Table 2). Support for a model with energy intake rate was strong; normalized Akaike weight indicated a 0.95 probability that it was the best of the candidate models. This model was 8.92 AIC_c units better than the next best model, which did not include energy intake rate. Energy intake rates were positively correlated with daily survival rates (Fig. 3). The age covariate in the top-ranking model was quadratic, with daily survival rates increasing for the first two weeks post-hatch and decreasing after three weeks (Fig. 4).

DISCUSSION

Our results supported our hypothesis that broods fed at higher energy intake rates would grow faster and have higher rates of survival. Consistent with our prediction, broods with higher energy intake rates had higher daily survival rates. The addition of an energy intake rate covariate to the top-ranked model improved fit and strongly decreased deviance. Broods provisioned at higher energetic rates had higher rates of wing growth, presumably enabling them to fly at an earlier age and possibly making them more adept at evading predators. In another study that examined chick survival of oystercatchers before and after fledging, all mortalities occurred before chicks began to fly (Groves 1984). Birds that can minimize the period in which they are most vulnerable to predators can increase their chances of survival. However, under conditions of restricted energy intake, growth is compromised, leading to negative effects on survival. Our results underscore the importance of diet and provisioning to the growth and survival of oystercatcher broods.

The relationship that we found between energy intake rate, growth, and survival is consistent with findings from other shorebird studies. Arctic shorebird chicks that had access to more prey had higher growth rates than chicks with lower prey availability (McKinnon *et al.* 2012). African Oystercatchers *H. moquini* with low biomass available in their territories had decreased energy intake rates and were less likely to successfully raise two chicks (Leseberg

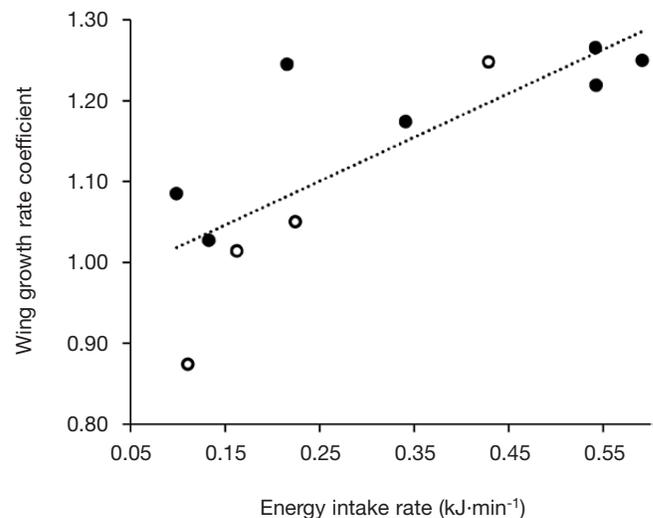


Fig. 2. Wing growth rate coefficients as a function of energy intake rate for Black Oystercatcher broods that survived to fledge (closed circles) and died before fledging (open circles) in Kenai Fjords National Park, Alaska, 2013–2014: slope = 0.55 (± 0.14 SD), $R^2 = 0.58$, $n = 11$).

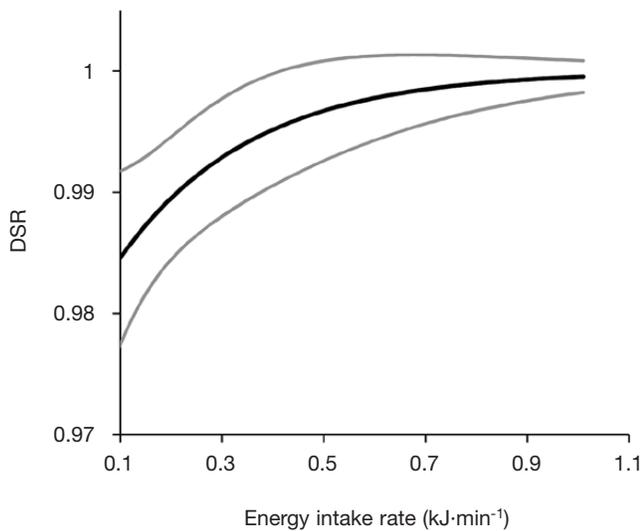


Fig. 3. Predicted daily survival rates (DSR) as a function of energy intake rate of Black Oystercatcher broods in Kenai Fjords National Park, Alaska, 2013–2014. Grey lines represent \pm SD.

et al. 2000). Food supply also strongly affected the growth and productivity of marine birds including kittiwakes *Rissa* spp. and skuas *Stercorarius* spp. (Gill & Hatch 2002, Ritz *et al.* 2005), and higher energy densities of Antarctic krill *Euphausia superba* result in higher growth rates and survival of Adelie Penguin *Pygoscelis adeliae* chicks (Chapman *et al.* 2010).

Although energy intake rates were positively correlated with wing growth, other mechanisms associated with feeding rates, aside from wing growth, may simultaneously influence survival. Chicks with higher energy intake rates may also have better body condition, making them more resistant to severe weather and disease (Møller *et al.* 1998); however, we did not encounter any diseased chicks. Additionally, parents that feed chicks at higher rates may attend to chicks more frequently and be able to defend them from predators more often. Since we were not able to test these hypotheses, we cannot rule out the possibility that additional mechanisms associated with intake rate, aside from growth, impact brood survival.

In addition to energy intake rate, brood age was a parameter in the best-supported survival model. The age trend in this model was quadratic, with low daily survival rates at hatch that increased for the first two weeks, then leveled off and decreased after three weeks. The pattern of lower survival among younger chicks has also been found in other shorebirds including American Oystercatchers *H. palliatus*, Snowy Plovers *Charadrius nivosus*, and Western Sandpipers *Calidris mauri* (Ruthrauff & McCaffery 2005, Colwell *et al.* 2007, Schulte & Simons 2015). Young chicks are slow and small, making them more vulnerable to predators and severe weather. Yet, in our study, after survival rates increased, they leveled off and decreased after three weeks. Chicks become less vulnerable to weather as they develop and begin to thermoregulate; however, they also become more active and conspicuous to predators. These combined factors may explain the quadratic relationship between age and survival.

Our findings also highlight how adults respond to the increasing nutritional needs of developing chicks. Adults did not adjust the types or size classes of prey brought to young versus old chicks;

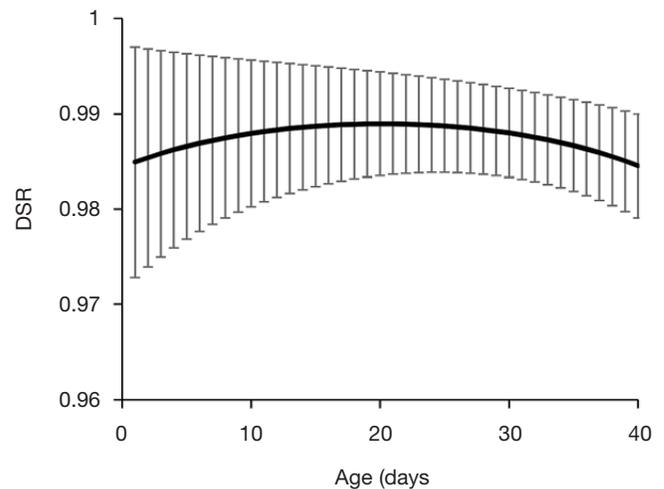


Fig. 4. Daily survival rates (DSR) of Black Oystercatcher broods by age in Kenai Fjords National Park, Alaska, 2013–2014. Intervals represent \pm SD.

instead they increased the frequency by which they delivered prey. Experimental studies of chick provisioning in other species revealed a similar trend: individuals adjusted their feeding rate to account for temporary changes in the energetic demands of broods but did not adjust the size of food items brought to the nestlings (Koenig & Walters 2012). Together, these results show that adults respond to the rising energetic needs of broods by increasing parental effort.

Our study demonstrates the importance of diet and provisioning to the survival of oystercatcher broods. In the Gulf of Alaska, mussel populations can undergo dramatic shifts in abundance across time (Bodkin *et al.* 2018). During years when mussel abundance is low, oystercatchers may have difficulty provisioning their young and survival may be compromised. Less is known about the population dynamics of other species of oystercatcher prey and the implications of changing ocean conditions. Given the consequences of reduced energy intake on brood survival, shifts in composition and abundance of intertidal invertebrates as a result of climate change may significantly affect oystercatcher populations. Brood survival, productivity, and recruitment into the breeding population may decline if marine intertidal invertebrates respond negatively to changing ocean conditions. To better understand the biology underlying oystercatcher conservation, future research should address how climate-driven changes in nearshore ecosystems will affect food resources and predator communities with respect to oystercatcher populations.

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THE HOME PLACE: MEMOIRS OF A COLORED MAN'S LOVE AFFAIR WITH NATURE

Lanham, J.D. 2017. Milkweed Editions, Minneapolis, USA, 240 pp. Paperback: ISBN 978-1571313508, US\$16.

Love for the land may be a form of religion, particularly for those who end up loving the great outdoors, from butterflies, birds and wolves, to seascapes. For those that admire a haunted hoot of an owl or wake up early to get their feet wet in a bog before dawn and watch flamingoes landing in the morning twilight, the land is the giver of all. Wild places can be a healer for those who seek comfort and a savior for those who seek salvation. Same goes for family—a form of rudimentary tribe, a religion, a church to find peace and a place to find oneness. Joseph Drew Lanham takes us on a journey through these deep valleys down memory lane. In the process he explores our human roots and the very foundation of our engagement with nature. It is not just Drew's story, it is a story about most naturalists, biologists, poets and painters, and those who feel 'out of place' in the hectic urban landscape. Drew's *The Home Place* is not painted in black and white; it is painted in color. Through color, the dark history of a continent is clinically exposed in a charming, soft, feathery tone. No harsh language or bitter examples; the somber darkness just there in the corner is seeping like a band of fog in a cold autumn evening.

The Home Place is a memoir of a farm boy of a unique phenotype, one prone to prejudice in his society who became an ornithologist. 'Colored' phenotype in American ornithology is as rare as a Spotted Owl in the old growth forests, a Short-tailed Albatross in the Pacific, or a Dovekie in the Atlantic. In a birder's eye though, the rarer the phenotype, the cooler it gets—the vagrants are sought after amongst the ubiquitous residents! Simply because we are oddities in the city-doused majority, biologists would share most of Drew's feelings more than once, irrespective of color, race, religion or status. A fear of the safety of your gear, your life, and the danger of losing your passport—strangled in a strange land. However, experiencing such fears in your homeland, amongst your own people, would be something of a whole different level. Through an eye of an ornithologist, Drew shows us the cruelty of racism.

Like many budding naturalists, the little Drew found his God and Heaven both in his backyard woodlands. In his own words "nature seems worthy of worship". *The Home Place* shows how childhood experiences, adventures, and imprinting could shape a 'wildling' into a scientist and conservationist. The urban sprawl and disappearing traditional ways of living bar today's majority from such experiences and advantages. The modern kids are imprinted to technology and a sterile world around them. What would be the path of a future conservationist in the decades to come? As for future seabird biologists, will they have enough puffins, fulmars and kittiwakes let alone, albatrosses, shearwaters and auklets left for them to inspire and imprint in their childhood?

The painting of the farmer—in Drew's dad—created a vivid picture of a man who ploughed, weeded, and fought with nature to control and tame it, so that the beef, the bacon, the cereal, and the pulses would come to the table to nourish. The smell of freshly ploughed earth and salty sweat are there all over the

pages providing a stunning description of wilderness and man's struggle to keep it at bay. Similar experiences made me a birder and a scientist many moons ago. I am sure such experiences are key in making wildlings into scientists across the globe. *The Home Place* talks about the importance of introducing birds into kids' routine as well. Most of Lanham's success in science and conservation had apparently begun from a few tiny childhood experiences; some were planned, such as getting a seven-year old to paint a mockingbird, and some were unplanned, such as seeing the grace of a soaring vulture.

A birder's taste for color depends on rarity. The red feet of the Red-legged Kittiwake in a Black-legged Kittiwake world is sought after and celebrated with the same enthusiasm as the black beak of the Aleutian Tern in a world of red-billed Arctic Terns. Throughout his *Memoirs of a Colored Man's Love Affair with Nature*, Drew talks about how the color of man is perceived differently. As a brown birder and an ornithologist, I, too, share similar feelings. At the seabird colonies in windswept Aleutians and in the barren, lichen-clad Labrador, my colleagues look colorless. It has not changed even in the city in bird conferences such as in IOC, NAOC or PSG – I am still surrounded by a sea of colorless colleagues. Sharing Drew's feelings, at times "*it is discouraging*". At the same time, as an immigrant grad student turned into an ornithologist without much social biases—I started to like it. After all I am the 'rare bird'. One of a kind..... an Asian vagrant in the Americas, far away from its native South Asian rainforests.

In North American woods or on a skiff, a brown birder with a pair of bins may be a less of a thing compared to that of a black birder. Though birding in Alaska, Labrador, Yellowknife, Florida and Texas has its own effects, mostly pleasant, where few were curious about what this brown-sugar lad is after. An occasional 'F' word or a middle finger from a truck just spiced up the moment...for me.

In his gentle feathery tone, the college professor preaches to us, urging us to reach out to paint a better picture for wild things and wild places in the minds of the public. The same way Aldo Leopold's *Sand Country Almanac* (Leopold 1949) inspired Lanham, a colored kid who already had enough nature in his nurture to become a wildlife biologist and a conservationist, *The Home Place*, a story of farmland turned into a childhood paradise, would be an inspiration for kids across the globe. Especially for kids of immigrant minorities who are craving a source of identity and inspiration, to become somebody significant, to get the recognition that their parents never had, and to be part of a community they were introduced to by forces alien to them in global politics and socioeconomics.

On a more personal note, as a brown farm boy turned into a birder, biologist and forester, I loved the gentle path that Drew took, from the family to the farm to the school and to the science of landscape restoration. My path has been, so far, surprisingly similar. The next step for me, I wonder, might lay in the Gulf

of Mannar in the Indian Ocean, where Jouanin's Petrels soar at night amongst thousands of breeding terns in sandy islands and the opportunity to convert the devilish concrete tide into a green veil! *The Home Place* is already churning something deeper in me. Would that be the same thing that E.O. Wilson had churned in a colored birder a few decades ago?

J. Drew Lanham's *The Home Place* is a stunning read, a masterpiece, a soft rebellion that touches the deepest of our instincts: love for the family, love for the wilderness, and our propensity for discriminative tribalism. *The Home Place* is a reminiscent first love of a farm boy who moved away from time and space. The adventures pursued, the lessons learnt and the

experiences gathered will continue to inspire all of us to see ourselves colored in nature's hues.

Sampath S. Seneviratne, *Avian Evolution Node*, Department of Zoology & Environment Sciences, University of Colombo, Colombo 03, Sri Lanka | Former Postdoctoral Fellow, Biodiversity Research Centre, University of British Columbia, Vancouver, BC and Bird Studies Canada. sam@sci.cmb.ac.lk | +94 710 821177

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THE SEABIRD'S CRY: THE LIVES AND LOVES OF THE PLANET'S GREAT OCEAN VOYAGERS

Nicholson, A. 2018. Henry Holt and Company, New York, USA, 400 pp. B&W illustrations. Hardcover: ISBN 978-1250134189, £65.00. Paperback: ISBN 978-1250181596, £29.95.

Most seabird ecologists can attest to the sense of wonder at their first encounter with a seabird colony. The deafening sound of seabird calls above pounding waves, the smell of salt and guano, and the breathtaking sight of thousands of birds coming in from or returning to the sea. *The Seabird's Cry* explores 10 seabirds: the fulmar, puffin, kittiwake, gull, guillemot, cormorant and shag, shearwater, gannet, great auk and its cousin razorbill, and albatross in the perfect marriage of seabird science and storytelling. "The astonishing findings of seabird scientists mean that a sense of wonder now emerges not from ignorance of the birds but from understanding them," says Nicholson. *The Seabird's Cry* eloquently captures the feeling of magic that seabirds inspire.

Nicholson, whose father bought the Shiant, a group of islands off the Scottish coast for 1 300 pounds in 1937, approaches the plight of seabirds from the perspective of a life-long admirer of the oceanic environment. Nicholson has a background in great literature and history, which is demonstrated as he weaves poetry throughout. As many of us have likely imagined when observing seabirds gracefully soaring around the hull of a ship—Nicholson describes seabirds as being otherworldly, transcendent—they are "a part of what we long for: beauty on the margins of understanding." From Homer to Milton, it will delight and perhaps surprise seabird ecologists to learn of the role of seabirds in mythology: kittiwake-like seabirds are portrayed as the bringers of salvation and a cormorant was sent by Satan to corrupt Eden.

Nicholson regales the reader with the classic revelations of seabird science. The chapter on shearwaters describes Ronald Lockley's eccentric experiments releasing Skokholm Island Manx Shearwaters at different locations around the Atlantic, from Devon to Venice. The journey that made Lockley famous was from the Boston harbor, where a shearwater flew over 3 000 miles back to Skokholm in 12 days, beating the mail sent from Boston by Lockley's correspondent who released the bird. In the chapter on albatross, Nicholson chronicles the efforts of Henri Weimerskirch and Pierre

Jouventin to track these enigmatic birds. The first tracking of a wandering albatross, flying over 10 000 miles from Crozet as far as Antarctica, is a "vision of life at sea which Coleridge would have loved." This referring to perhaps the most famous poem featuring a seabird: *Rime of the Ancient Mariner* by Samuel Coleridge.

As someone who has been battered by penguin flippers, soaked by a storm petrel's orange fish-smelling regurgitation, and covered in sticky guano after days of burrow-scoping, I commend Nicholson's ability to capture something that popular culture rarely reveals about seabirds—their malevolence. In the chapter on gannets, a gannetry is described vividly as a "monument to unkindness." When a researcher or lost chick wanders through a colony, gannets slash with "beaks of barbed wire." Between gannet nests, which are spaced a "beak thrust" apart, lies a "glutinous black ooze of mud, decayed seaweed, ordure, and spilt fish" that releases the foulest of smells when punctured by squabbling male gannets. In the chapter on gulls, the bird's existence is described as a "version of hell" in which cruelty and violence can be pervasive. Nicholson goes on to describe Jasper Parson's observations of herring gulls cannibalizing large numbers of neighboring chicks.

Where *The Seabird's Cry* truly shines is emphasizing seabird's beauty and wonder. In the chapter on fulmars, when observing the birds flying in loops above a colony, dancing on the wind, it inspires introspection: fulmars "make [us] wonder what life consists of." Nicholson borrows a term from philosophy to describe them: *inscendent*—the act of climbing into life and looking for its essence. The description of cormorant courtship and mating systems or *love* (as off-putting as that term may be for most scientists, in this context it seems almost natural) is sublime. Observe pair bonding between these "glamorous birds and you will witness a slow and careful ballet of tenderness and sweetness between them." Nicholson's description of Nathan Emery's study of the correlation between brain size and increasing lengths of monogamy are poetic in and of themselves. Birds need to be clever to understand their

mates; it's easy to anthropomorphize here. "Intimacy between shags is evidence of tight bonding between birds, [an elevated] principle of life and survival. Love matters for seabirds, because a harsh environment...can make raising healthy offspring more difficult" - could be a proverb.

Although the threats that seabirds face in a rapidly changing world are subtly present throughout the book, Nicholson underscores in the last chapter how dire the situation has become. Seabirds are more threatened than any other vertebrate and world populations have dropped by about 70 % in the past six decades, meaning there are one billion fewer seabirds now than in 1950 (Croxall *et al.* 2012). No surprises here, but the abrupt switch from magnificent stories of seabirds and their ecology to the grim conservation situation snap the reader to attention. As Nicholson correctly states, seabirds are indicators of ocean ecosystem health—if they are in trouble, life in the ocean is in trouble—and deep perturbations are evident around the world. After spending my entire adult life and over 300 pages reveling in my love for seabirds, my despair at this final chapter parallels my feelings about the current biodiversity conservation crisis we are facing.

Nicholson concludes on a reticently positive note. In 2016 he facilitated the removal of ship rats from his father's (now his) Shiant Islands, resulting in a recolonization of wren and

wheateaters and a new booming chorus of bird song. In a world of frightening human-caused global change, we could all show a little more love for nature. In *The Seabird's Cry*, Nicholson captures the enchanting world of seabirds, inspiring its readers to fall in love with these birds.

My hope is that in my time as book review editor for *Marine Ornithology*, I can help facilitate a collective celebration of love for nature, science, seabirds, and the marine environment. In this time of crisis, it's important as a scientific community to band together to solve problems—from mothers (Wang *et al.*, this issue) to "rare phenotypes" (Seneviratne, this issue) to those on the conservation front lines (Karnovsky, this issue). In Nicholson's words, seabirds 'display beauty in the most demanding moments life can offer'; perhaps we as scientists can do the same.

Rachel T. Buxton, PhD, Research Scientist, Carleton University, Department of Biology, Ottawa, Canada. Rachel.Buxton@colostate.edu

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THE END OF THE END OF THE EARTH

Franzen, J. 2018. Farrar, Straus and Giroux, New York, USA, 225 pp. Paperback: ISBN 978-0374906757.

Most people know Jonathan Franzen based on his brilliant novel *The Corrections*, and many of you are likely wondering why his book is being reviewed in *Marine Ornithology*. *The End of the Earth* is a collection of essays spanning diverse subjects, some of them addressing the conservation challenges facing birds across the globe, including a few on seabirds in particular.

Franzen begins with 'The Essay in Dark Times' about birdwatching in Ghana, the election of Donald Trump, climate change, and the nature of essays. He writes that essays are inherently deeply personal and, if done well, are a form of literature that "invites you to ask whether you might be somewhat wrong, maybe entirely wrong, and to imagine why someone else might hate you." Throughout this book he contemplates the right or wrong ways to respond to the dire state of our planet. Franzen's essays are all deeply personal and, truth be told, he often reveals parts of his personality that will make you cringe. He is completely aware of how these confessions sound and is mortified right along with you. Franzen reveals in his first essay that he is a compulsive lister, which he confesses makes him "morally inferior to birders who bird exclusively for the joy of it." His obsessive quest for counting species provides the backdrop for several of the incisive essays about the conservation of birds. For example, his quest to see the Crested Quail-Dove leads to a heartbreaking essay on habitat loss in Jamaica.

Franzen spends a lot of energy in his essays worrying that people hate him. One thing I have come to realize while writing this

review is that his anxiety is not unfounded: people have really strong opinions about him! Reading this book on an airplane, total strangers declared to me whether they loved or hated him. At the last Pacific Seabird Group meeting, Beth Flint received a well-deserved Lifetime Achievement Award for her work conserving seabirds. She gave an exquisite talk on new work being done to save seabirds from sea level rise. I ineloquently asked the question of how we can balance the need to be proactive about climate change with other impacts on seabirds, such as introduced species, mentioning Jonathan Franzen in reference to this debate. It was an eye-opening experience—this mention of his name resulted in me getting tracked down and yelled at by his supporters.

Franzen revisits the moment when he became a vilified target over the issue of climate change. His essay 'Carbon Capture,' originally published in *The New Yorker*, is reprinted in this book in the essay 'Save What You Love'. Franzen was a fierce critic of the National Audubon Society when it declared climate change as the primary threat to birds. He felt that this campaign would take away from support to combat other impacts on birds (e.g., introduced species, habitat loss) that have more tractable solutions. He skewers the National Audubon Society for what he saw as a hollow, money-making pitch. He goes on to highlight the work of two small-scale but enormously successful conservation projects: the work of Amazon Conservation in Manu National Park in Peru and of the Area de Conservacion

in Costa Rica. In the process he gives wonderful vignettes of conservation heroes Daniel Janzen, Winnie Hallwachs, and Don Alberto Manqueriapa.

After the original essay was published, many declared Franzen a climate denier and enemy of the National Audubon Society. Reading about what motivated him to write the essay and how the fallout affected him in 'The Essay in Dark Times' before reading 'Save What You Love' is illuminating and may make some critics soften their invective. The fact is, Franzen does not shy away from asking hard questions about how to best protect birds, given the many stressors on their populations. He asks the questions that we often ask ourselves.

One of the essays that I continue to be haunted by is called 'May Your Life Be Ruined'. In it, he travels to Egypt and Albania and witnesses the widespread and indiscriminate bird hunting. He gives an account of both the birds and the hunters who hunt them. I was left with a deep worry for the decoy kestrel that escaped, the young hunters, and the fragile bird populations who are funneled into bird traps during their migration across the Mediterranean. I had read an earlier version of this essay in *National Geographic* and assign this extraordinary piece of journalism in my undergraduate classes. In his essay 'Invisible Losses', Franzen describes the conservation challenges of many seabirds. He brings the reader into the 'murre blind' on the Farallon Islands where he beautifully describes watching the Common Murres return to their nest sites with food for chicks with seabird biologist Pete Warzybok. He recounts their long history of challenges, from egg collecting and gill nets to a changing ocean. He goes to South Africa and relays conversations between tuna-boat captain Deon van Antwerpen, seabird biologist Ross Wanless, and Andrea Angel, who leads BirdLife South Africa's Albatross Task Force, about how to best modify longlines to reduce bycatch of albatross. He describes in painful detail how mice are eating Tristan Albatrosses alive on Gough Island. It is not all bad news, however; he also reports on the rodent eradication success stories on South Georgia and Anacapa Island. It is a treat to read about conservation in action and to meet, through Franzen, the individuals who were responsible for these hard-won victories. The vignettes of Nick Holmes, science director of Island Conservation, and of Liz and Bruce Tuanui, founders of the Chatham Island Taiko Trust, show that profound changes can be made by dedicated, creative people who have managed to undo some of the harm caused by humans.

In his essay 'Postcards from East Africa', Franzen reluctantly goes to the Serengeti. He desperately wants to set himself apart from others who go on safari just to check off the trip on their bucket list. Franzen's whining about the trip and having to watch mammals (which he views as much less worthy) is hard to stomach as someone who would give my eye teeth for the chance to see a lion take down a

gazelle. He does come to appreciate the mammals ("Who could resist the sight of worried cheetah cubs? I couldn't, for about five minutes.") and his ecstatic descriptions of the birds makes you wish you could get there immediately with binoculars in hand.

Franzen describes his trip to Antarctica on a three-week-long cruise with Lindblad Expeditions and National Geographic in the essay that gives the book its name 'The End of the End of the Earth'. He gives a withering account of the Lindblad summer-camp type of experience. His journey from pariah to hero on the ship is very funny. Once again, as someone who has never seen the sublime King Penguins of South Georgia, his misery about the vacation is annoying. However, his description of the poorly attended final lecture onboard the ship on climate change is one of the most sobering parts of the book that will resonate with many readers.

This collection of essays will appeal to birders, conservationists, and lovers of literature. I enjoyed the parts of this book that had nothing to do with birds as much as the rest. Franzen often includes sentences with long lists of birds, which folks who are not interested in birds may struggle with. To me, these sentences read like a list of succulent treats.

This book is paean to birds. Franzen's passion is deeply infectious and non-birders will likely catch bird fever from reading this book. Birders will enjoy reading about his pursuit of lifers across the globe and his hilarious bird-spotting superstitions. Readers interested in Franzen's stunning prose will not be disappointed and will thrill to the essays about fellow writers such as the late David Foster Wallace and Edith Wharton.

Franzen provides several shocking statistics throughout the book. For example, "Every minute in America, thirty thousand paper cups are chucked." Franzen asks himself and the reader how to best cope with the overwhelming problems facing birds and planet earth. Fortunately, he provides many examples of people who are in the trenches making a difference. It is my hope that readers will use this book as a suggested guide to where donations could really make a difference in advancing conservation.

I am grateful that Franzen loves birds. His insights will be read by many who probably never thought about birds or climate change or loss of biodiversity across the globe before. How amazing that they now know of the Ashy Storm Petrel and the Magenta Petrel! In fact, I have thought of several areas of the planet that I hope he visits and will write about. I wonder what is left on his life list that might lead to a sequel to this book.

Nina J. Karnovsky, PhD, Willard George Halstead Zoology Professor, Pomona College, Department of Biology, Claremont, CA 91711, USA. Nina.Karnovsky@pomona.edu

MAKING MOTHERHOOD WORK: HOW WOMEN MANAGE CAREERS AND CAREGIVING

Collins, C. 2019. Princeton University Press, Princeton, USA, 360 pp. Hardcover: ISBN 978-0691178851, US\$29.95.

Making Motherhood Work is an insightful and eye-opening read on how mothers around the world try to balance family life and careers. Caitlyn Collins transports the reader into the homes and lives of working women in Sweden, Germany, Italy, and the United States. For scientist and seabird ecologist moms, *Making Motherhood Work* preaches to our choir and empowers us with knowledge of how policies and cultures in different parts of the world shape a working mom's struggle. Collins's book helps us take stock of how the culture within the scientific community perpetuates the conflict between science and motherhood (Buxton *et al.* 2019). Lack of support for scientist moms is one of the sources of the leaky pipeline for women in science (Cech and Blair-Loy 2019) and *Making Motherhood Work* offers demonstrable solutions through examples from other countries.

Collins introduces the concept of 'work-family justice' to replace the notion of work-family balance and the unattainable goal of 'having it all'. Framing the conflict between work and family life as an issue of 'balance' individualizes the problem, placing the blame on working mothers. This misguided framework suggests that working moms' stress is a result of our own shortcomings and mismanaged time commitments: if we could just work a little harder, we could 'have it all'. Instead, Collins argues, the onus should be placed on society—the conflict between work and family is not inevitable and it's not the fault of women or parents. To achieve work-family justice for working moms is to create a system where everyone has the support necessary to be successful in their careers and in motherhood.

The book presents many statistics that were surprising for us working moms in the US and Canada. For example, in Sweden, a 'dual-earner' career model is not only encouraged but expected of parents, which promotes equality between parents. Sweden is a social democratic country and Collins writes that there is a sense of collective responsibility to children, family, and to society as a whole. Parents in Sweden are legally allowed 240 days of *paid* leave to take care of a newborn, and if you're a single parent, you're allowed all 480 days (16 months) of leave! Moreover, Collins found that it is highly unusual—and even viewed as strange—for a parent to stay at home beyond the time allotted for parental leave after a baby is born. This is because of the strong support for free daycare options beginning at a young age. But the grass is not always greener on the other side of the world. In the former East Germany, although the 'dual-worker' family model resulted in women being encouraged to combine child-rearing with employment, women also are expected to maintain responsibility for the home. In combination with the tumultuous history of the fall of the Berlin Wall and mixing of west Germany's 'stay-at-home mom' culture, this has led to feelings of pressure for working moms to live up to an idealized version of motherhood: "the demand that society has for moms are that 'mom has to do everything perfectly...and [when there are problems], it's the mom's fault'". These sentiments echo what so many of us feel as working moms in the US and Canada.

At times it was disheartening to read the stories of other working moms' struggles. At the conclusion of the book, we felt frustrated

but cautiously hopeful that one day change may come to the US. Currently, the US does not have any nationwide policy on paid parental leave to take care of a newborn. The lack of formal policy across the nation leaves it up to employers to come up with their own policies, resulting in unequal opportunities for parental leave and childcare. In Canada, where policies fall somewhere between Sweden and the US, working moms receive up to 18 months maternity leave paid at 33 % (or 12 months paid at 55 %), with some employers topping-up salaries.

While we can relate to the feelings of pressure and stress from the professional moms interviewed in *Making Motherhood Work*, as scientist moms we face unique conflicts. For example, in many fieldwork-oriented careers (including seabird ecology), spending long weeks or even months in the field or at sea are often an important part of the job. As a result, many early-career female field ecologists report having to cope with being discouraged from getting married or having children. Furthermore, working moms are often removed from field projects without warning because they seem "no longer able or interested because they had a kid." As a working academic-scientist mom, there are many additional expectations including managing graduate and undergraduate students, serving on committees, writing grant applications, and the deeply entrenched 'publish or perish' mantra, all of which leave little room for maternity leave and family commitments. Yet seabird ecologist and conservation biologist moms offer a unique set of perspectives. Encouraging parents in field ecology and promoting gender diversity, which has a range of benefits in scientific endeavors (Nielsen *et al.* 2017), have the added benefit of demonstrating to children and young aspiring scientists that a career dedicated to the conservation of the natural world is feasible in combination with motherhood.

We were left wondering how we can promote the cultural change necessary for the scientific community to promote work-family justice. For starters, we, as a society, need to promote gender equality at work and at home; break down gender stereotypes; recognize the judgement that working moms experience from all facets of their community; and create flexible, workable solutions to accommodate the diversity of working scientist moms (Buxton *et al.* 2019). Working parents should lead by example and divide the labor of parenthood equally. In the US, policies are in dire need of change, but before nationwide policy changes can truly gain momentum, we need to radically evolve our cultural and societal perceptions of working moms. *Making Motherhood Work* is a good start, bringing to light a continuation of a fight that was started long ago by generations of working women before us.

All of us have spent weeks and months on seabird colonies, endured extreme remote conditions to count birds, dangled off cliffs in dank weather to capture birds for measurements, tissue sampling, and banding. The fragrant odor of seabird guano is a distant memory for most of us now that we have kids and can't be away for long periods of time. But that doesn't mean that we stopped contributing in our fields. On the contrary, we have adapted to our changing personal

environment, holding positions that allow us to direct research and science, ones that don't require long stints of field time. We are successful because we have persevered at finding a work-family balance that works for us on an individual level. However, achieving balance has not been easy and we have seen many bright scientist moms overwhelmed by the pressure. As we aim for inclusion that will benefit the field of ecology (and arguably the planet), there is value in shifting the paradigm—from balance to justice.

Shiway Wang, PhD, Science Coordinator, Exxon Valdez Oil Spill Trustee Council, Anchorage, USA (shiway@gmail.com). The views expressed here are her own and do not necessarily reflect the views or positions of the Trustee Council.

Holly Jones, PhD, Northern Illinois University, Biological Sciences and Institute for the Study of the Environment, Sustainability, and Energy, DeKalb, USA

Elizabeth Phillips, PhD, NOAA Fisheries Northwest Fisheries Science Center, Seattle, USA. The views expressed here are her own and do not necessarily reflect the views or position of NRC or NOAA.

Jennifer Provencher, PhD, Canadian Wildlife Service, Environment and Climate Change Canada, Gatineau, Canada.

Heather Major, PhD, University of New Brunswick, Saint John, Canada.

Rachel T. Buxton, PhD, Research Scientist, Carleton University, Department of Biology, Ottawa, Canada.

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¹ TAYLOR, B.N. & THOMPSON, A. (Eds.) 2008. *The International System of Units*. National Institute of Standards and Technology Special Publication 330, 2008 Edition. Gaithersburg, MD: National Institute of Standards and Technology, US Department of Commerce.

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² BOND, A.L. & HOBSON, K.A. 2012. Reporting stable-isotope ratios in ecology: Recommended terminology, guidelines and best practices. *Waterbirds* 35: 324–331. doi:10.1675/063.035.0213

³ BOND, A.L. & HOBSON, K.A. 2012. Authors' Erratum. *Waterbirds* 35(3). doi:10.1675/063.035.0318

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HAMMOND, R.L., CRAMPTON, L.H. & FOSTER, J.T. 2015. Breeding biology of two endangered forest birds on the island of Kauai, Hawaii. *The Condor* 117: 31–40. doi:10.1650/CONDOR-14-75.1

HUNT, G.L., JR. & HUNT, M.W. 1975. Reproductive ecology of the Western Gull: The importance of nest spacing. *The Auk* 92: 270–279. doi:10.2307/4084556

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R DEVELOPMENT CORE TEAM 2018. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: The R Foundation for Statistical Computing.

STRICKLAND, D. & OUELLET, H. 2011. Canada Jay (*Perisoreus canadensis*), version 2.1. In: POOLE, A. (Ed.) *The Birds of North America Online*. Ithaca, USA: Cornell Lab of Ornithology. [Accessed at <http://bna.birds.cornell.edu/bna/species/040> on 28 May 2015.] doi:10.2173/bna.gryjay.02.1

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