INCREASING USE OF ARTIFICIAL NEST CHAMBERS BY SEASONALLY SEGREGATED POPULATIONS OF BAND-RUMPED STORM PETRELS *HYDROBATES CASTRO* AT ST HELENA, SOUTH ATLANTIC OCEAN

ANNALEA BEARD[1]*, ROBERT J. THOMAS[1], ELIZABETH CLINGHAM[2], LEEANN HENRY[2],
RENATA MEDEIROS[3], STEFFEN OPPEL[4], ALISON SMALL[5] & FRANK HAILER[1]

[1]*School of Biosciences, Sir Martin Evans Building, Cardiff University, Cardiff, Wales CF10 3AX, United Kingdom*
*(annaleamichellebeard@yahoo.co.uk)
[2]*Environmental Management Division, Environmental and Natural Resources Directorate, St. Helena Government,
St. Helena Island STHL 1ZZ, South Atlantic Ocean*
[3]*School of Dentistry, College of Biomedical & Life Sciences, Cardiff University, Heath Park, Academic Avenue,
Cardiff, Wales CF14 4XY, United Kingdom*
[4]*Royal Society for the Protection of Birds Centre for Conservation Science, Cambridge, United Kingdom*
[5]*NatureSpace Partnership, 22 St. Peter's Street, Stamford, Lincolnshire PE9 2PF, United Kingdom*

ABSTRACT

BEARD, A., THOMAS, R.J., CLINGHAM, E., HENRY, L., MEDEIROS, R., OPPEL, S., SMALL, A. & HAILER, F. 2023. Increasing use of artificial nest chambers by seasonally segregated populations of Band-rumped Storm Petrels *Hydrobates castro* at St Helena, South Atlantic Ocean. *Marine Ornithology* 51: 85–96.

Artificial nest chambers have become a common management tool for monitoring nocturnal burrow-nesting seabirds, although their utility varies among species and locations. The widespread Band-rumped Storm Petrel *Hydrobates castro* species complex potentially harbours a cryptic species endemic to the South Atlantic. Here we evaluate the installation of artificial nest chambers as a tool for long-term conservation and monitoring of this species, which breeds in two distinct seasons on St Helena. Based on six years of observational data, we analysed factors affecting occupancy, mate and chamber fidelity, and reproductive success to optimise nest chamber installation and to enhance future management. Occupancy rates were high, increasing from 5% after the first season following installation to 85% after five years. Occupancy was positively associated with (1) the number of seasons since chamber installation, (2) whether the chamber was occupied in the previous season, and (3) whether the chamber was occupied in the same season in the previous year. Occupancy also varied with chamber location and lid construction material: chambers with wooden lids had 7% lower occupancy and 18% lower breeding success than chambers with other lid types. Lid replacement also negatively affected occupancy. Chamber monitoring revealed that individuals exhibited 93% mate fidelity and 86% chamber fidelity with little effect of previous breeding outcome. From 312 monitored nests, hatching success was 15% higher during the hot season, while fledging success was 28% higher during the cool season, leading to only 3.2% difference in overall productivity between seasons. Fledging success of each seasonal population varied by year. Chick mortality was considerably higher during the hot season (41% compared to 13% during the cool season), possibly reflecting different responses to temperature regime. We conclude that installation of artificial nest chambers represents an effective monitoring tool, and recommendations for the design and management of chambers are discussed.

Key words: Band-rumped Storm Petrel, artificial nest chambers, occupancy, productivity, fidelity, St Helena, seabirds

INTRODUCTION

Cavity-nesting seabirds spend much of the year out at sea and return to land only in darkness during the breeding season. Consequently, it is challenging to monitor such nocturnally active seabirds. Furthermore, seabirds often nest on steep cliffs and/or are restricted to offshore islands, which are difficult to access. The availability of suitable nesting cavities may be a limiting factor for many populations (Bolton *et al.* 2004). Providing nest boxes or artificial burrows has therefore become a common management tool for monitoring and conservation, especially of burrow-nesting seabirds (Bolton *et al.* 2004, Bourgeois *et al.* 2015, Bedolla-Guzmán *et al.* 2016).

The breeding success of seabirds in nest boxes has been shown to be generally higher than in natural sites, mainly due to more effective protection from predators (Libois *et al.* 2012) and reduction in

both egg damage and inter-/intra-specific interferences (Bolton *et al.* 2004). Nest-site characteristics and degree of competition can also affect breeding success (Warham 1990). However, nest boxes can potentially have undesirable negative effects on a population by acting as ecological traps (Mänd *et al.* 2005) through increasing attractiveness to predators (Sanz *et al.* 2003), reducing breeding success (Rodríguez *et al.* 2011), or reducing long-term survival of fledglings (Klein *et al.* 2007). The construction materials used can also affect the temperature inside the chamber, which can indirectly impact productivity (Carlile *et al.* 2012).

Artificial nest chambers have been used for several storm petrel species (Allan 1962, Ramos *et al.* 1997, Bolton *et al.* 2004, Bedolla-Guzmán *et al.* 2017) and can facilitate observation of nesting activities that would otherwise be difficult without disturbance. Storm petrels in particular are highly sensitive to disturbance

(including handling) at the nest, which can negatively affect reproductive success and site faithfulness, and can increase the likelihood of divorce (Carey 2009). The Band-rumped Storm Petrel species complex *Hydrobates castro* (also known as the Madeiran Storm Petrel) has a global conservation status of Least Concern, although it has a decreasing population trend (BirdLife International 2018). The species complex may include several cryptic and locally endemic species (Taylor *et al.* 2019).

At St Helena in the South Atlantic Ocean, *H. castro* usually breeds in two discrete periods: austral summer and austral winter (Bennett *et al.* 2009). The seasonally segregated populations of *H. castro* breeding on the Azores have warranted recognition of the hot season population as a separate species: Monteiro's Storm Petrel *H. monteiroi* (Bolton *et al.* 2008). A similar re-classification has been considered for *H. castro* at St Helena, dating back to 1935, when Mathews (1935) described a separate subspecies breeding on the island, *H. c. helena*, based on morphological differences. Recent research on *H. castro* by Taylor *et al.* (2019) found the South Atlantic (Ascension Island and St Helena) population, regardless of seasonality of breeding, to be significantly genetically divergent from other populations examined globally, and recent field identification guides have named the species as "St Helena Storm Petrel" *Thalobata* [*castro*] *helena* (Howell & Zufelt 2019).

Given the potential for the South Atlantic population to be a separate species or subspecies with a restricted range and thus of increased conservation concern, we aimed to increase our knowledge of its nesting behaviour. We began by installing artificial nest chambers at St Helena in a known breeding site. Our further aims were to (1) provide a convenient way of monitoring the breeding productivity of both seasonal sub-populations; (2) protect vulnerable nests from disturbance, e.g., from handling disturbance and from other competing species; (3) increase the availability of suitable nest sites; and (4) improve breeding success.

Here we present measures of occupancy levels, fidelity, and breeding success. We analysed factors to determine whether artificial nest chambers enhanced potential use for conservation. We broadly predicted a high occupancy level of nest chambers, especially if there is a shortage of nest sites on the island. Given that the sub-population breeding during the hot season is bigger than the one breeding during the cool season (AB unpubl. data), we explored the following hypotheses: (1) the rate of uptake of artificial nest chambers is higher in the hot season due to higher inter-specific competition for nesting cavities in this population; (2) the cool season population has a higher breeding success than the hot season population due to lower disturbance from other breeding seabird species and to lower inter- and intra-specific competition (testing the findings of Bennett *et al.* 2009); (3) if nest chamber characteristics are adequate for the protection of eggs and chicks, their use should result in a higher breeding success compared to storm petrels using natural cavities.

METHODS

Study site and species

This study was carried out on Egg Island (15°57′57″S, 005°46′39″W, Fig. 1), a small predator-free volcanic island off the northwestern coast of St Helena that harbours the largest sub-population of *H. castro* in the South Atlantic (AB unpubl. data). This study was conducted over six years, encompassed five hot seasons (2014–2018) and five cool seasons (2015–2019). The hot season occurs in the austral summer from late September to late December, and the cool season occurs in the austral winter from late March to early July (Bennett *et al.* 2009). The island is often used by different species overlapping in breeding phenology. Other burrow-nesting Procellariiformes known to occur in very small numbers on Egg Island are Bulwer's Petrel *Bulweria bulwerii* (Oppel *et al.* 2012) and White-faced Storm Petrel *Pelagodroma marina* (Bolton *et al.* 2010). During the hot season, Brown Noddies *Anous stolidus* and a small population of Sooty Terns *Onychoprion fuscatus* are the only other species that nest on the open slopes near storm petrel nesting cavities.

Artificial nest chambers

Artificial nest chambers (hereafter "chambers") were installed in early March 2014 (*n* = 40), early March 2015 (*n* = 50), late February 2017 (*n* = 20), and early April 2018 (*n* = 20). Installation was conducted during the day when most adults were at sea (AB pers. obs.). The chambers were positioned a minimum of two meters away from natural burrows in three areas on the island (Fig. 1c), in locations without previous presence of natural nests to reduce disturbance. All installation locations were in the open, as the island has limited vegetation cover or natural shelter. The chambers were made from polyvinyl chloride (PVC) plastic, following a simple design described by Bolton *et al.* (2004), but using two different lid materials: either PVC (circular; brown or green) or plywood (square, brown; Fig. 2).

Monitoring protocols

To determine chamber occupancy and nesting fate, chambers were inspected a minimum of four times during each season with a maximum interval of four weeks between these visits. Care was taken to leave the entrance as undisturbed as possible. We considered a chamber to be occupied if an adult was present on at least one occasion. All storm petrels present in a chamber were ringed for subsequent individual identification. If an egg (or incubating adult bird) was present on at least one of the visits, it was deemed a nesting attempt. Any chamber lids that were damaged or missing were noted and replaced with the same lid type within the same season. If replacement was not possible due to a lack of available materials, the chamber was considered unavailable for the season.

Data analysis

All statistical analyses were carried out in R 4.1.2 (R Development Core Team 2021). All generalised linear mixed models (GLMMs) were implemented in the "lme4" package (Bates *et al.* 2015), all general linear models (GLMs) and chi-squared tests in the "stats" package (R Development Core Team 2021), all likelihood-ratio tests (LRTs) in the "lmtest" package (Zeileis & Hothorn 2002), and all generalised additive mixed models (GAMMs) in the "gamm4" package (Wood & Scheipl 2020) following Thomas *et al.* (2017). Significant effects ($P < 0.05$) in all final models were plotted using the "ggplot2" package (Wickham 2016).

Breeding success and productivity

We excluded 15 of the original 327 nesting attempts because either fate or the failure stage could not be ascertained. Three re-nesting
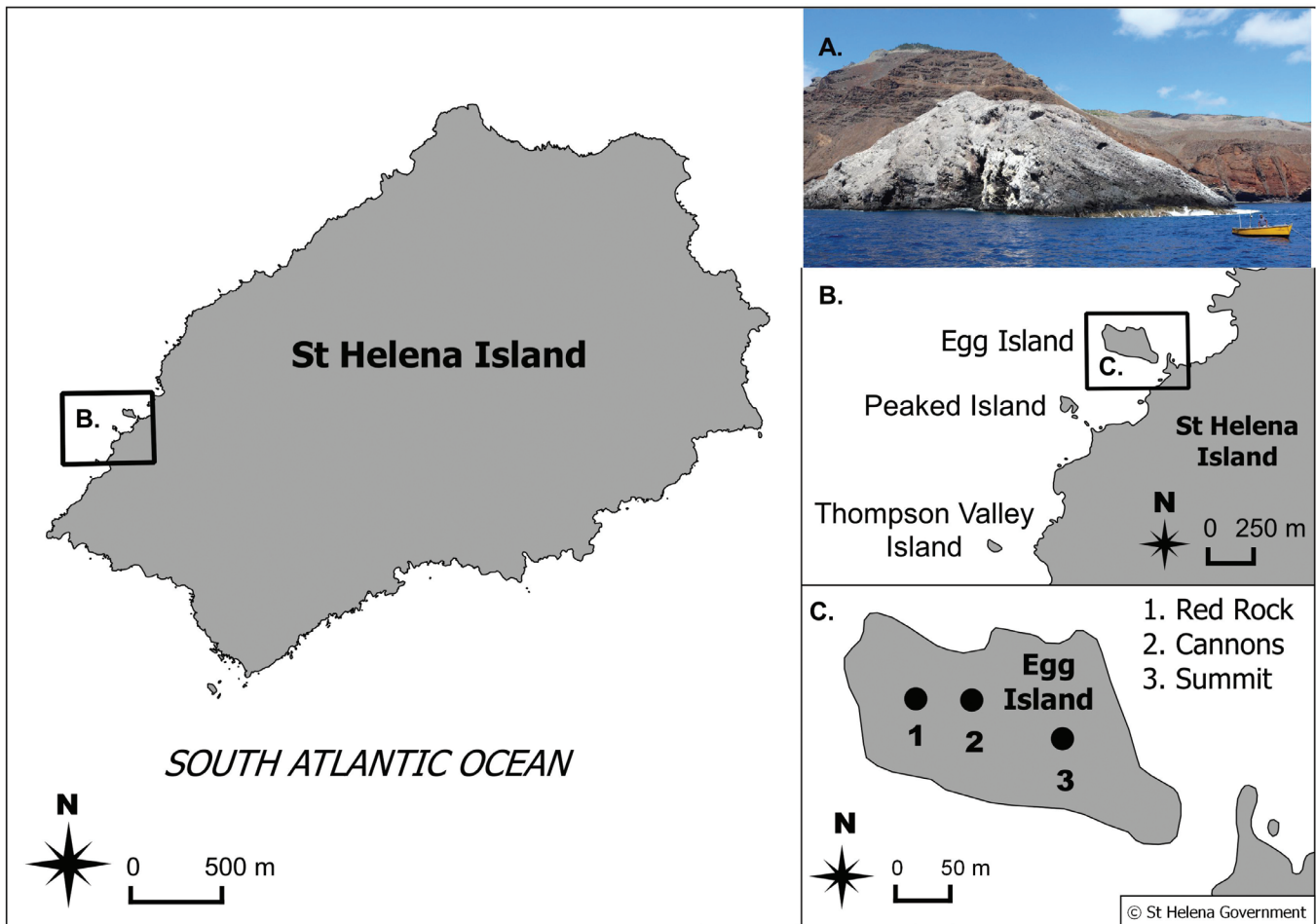
Fig. 1. Location of the study site at St Helena. (A) View of Egg Island from the sea (foreground) with St Helena in the background (Photo credit: St Helena Government). (B) Location of Egg Island in relation to other nearby offshore islands. (C) The three groupings of artificial nest chamber locations on Egg Island.

Fig. 2. Artificial nest chambers installed on Egg Island, St Helena, showing the different lid materials: plywood (bottom) and polyvinyl chloride (top) (Photo credit: Annalea Beard).

attempts following initial breeding failure in a season were pooled in the analysis. For ease of comparison between breeding success and productivity in natural nesting cavities and chambers, we closely followed the methods described by Bennett *et al.* (2009), which we summarise here: For each season and year, we estimated the daily egg survival rate and daily chick survival rate, both corrected for the exposure time of nests to account for nests being discovered at various stages (Mayfield 1975), and we reported the standard errors following Johnson (1979). Hatching success and fledging success were calculated assuming a 42-day incubation and a 70-day chick development period, respectively (Allan 1962, Harris 1969). Breeding success, defined as the proportion of eggs laid that result in a fledged chick, were calculated as a product of hatching and fledging success.

We tested for differences in hatching success and fledging success between each season, between each year, and within each season between years using logistic exposure GLMMs. Logistic exposure models are similar to logistic regression models in that the response variable is binomial (i.e., success or failure of nest occurred between nest checks), but the link function is modified from the logit link to consider nest exposure days (Shaffer 2004). We used chamber identity as a random effect to account for any environmental

stochasticity among the chambers, and we used a LRT (Lewis *et al.* 2011) to compare candidate models to a null model that lacked any covariates. We examined parameter estimates of significant terms to determine the direction of the effect. Comparisons of chick mortality between seasons were made using chi-squared tests.

Occupancy

We examined chamber use since installation by calculating the proportion of chambers either occupied or used for breeding out of the total number of chambers available for each season after installation. We used GLMMs to assess if occupancy and breeding use were associated with (1) the number of seasons since initial installation (installation length), (2) the year as a factor (2014–2019), (3) the season (hot vs. cool) as an independent variable, and (4) a two-way interaction (year × season). Both occupancy and breeding use were modelled as binary response variables (occupancy: 1 = occupied, 0 = unoccupied; breeding: 1 = used for breeding, 0 = not used for breeding) with a logit link function and binomial error distribution. Chamber location and identity were treated as nested random effects to account for repeated measures of the same individual chambers in the same locations. For the analysis of occupancy, we also included two additional variables: Previous Season Occupancy (PSO) and Previous Between-Season Occupancy (PBSO). PSO (true/false) was defined as whether the chamber was occupied in the previous season (e.g., hot season versus previous cool season and vice versa), while PBSO (true/false) was defined as whether the chamber was occupied in the same season the previous year (e.g., hot season versus previous hot season). For the analysis of breeding use, we included four additional variables. First, Previous Season Breeding Use (PSBU, true/false) was defined as whether the chamber was used for breeding during the previous season. Second, Previous Between-Season Breeding Use (PBSBU, true/false) was defined as whether the chamber was used for breeding in the same season the previous year. The last two variables were the chamber's Previous Season Breeding Outcome (PSBO, success = true/false) and Previous Between-Season Breeding Outcome (breeding outcome in the same season the previous year, PBSBO; success = true/false). For each variable and response variable, we constructed two models: one containing the variable as a fixed effect, and a null model without the variable as an effect. To assess each variable, we compared the two models using a LRT, and we determined variables to be a significant predictor of either occupancy or breeding use if the model containing the variable of interest was significantly better than the null model. We then further explored which of the candidate variables best explained the occupancy of a chamber by constructing a global model containing the year, season, year × season, PSO, PBSO, and installation length. Model selection was performed by removing variables that most reduced Akaike's Information Criterion adjusted for the effect of sample size (AICc) to identify the most parsimonious model (Burnham & Anderson 2002).

Chamber fidelity and mate fidelity

We calculated chamber location fidelity, chamber identity fidelity, and individual mate fidelity using the ringing data gathered from individuals identified using chambers during the study. The influence of previous breeding failure on chamber fidelity and mate fidelity was assessed by comparing the proportion of nesting attempts where at least one individual from the breeding pair was identified and bred more than once in successive years, versus the equivalent proportion of nesting attempts where at least one individual changed chamber or partner between successive years.

Location and lid

We used a GLM with a binomial distribution and log link function to test the effect of (1) chamber location (red rock, cannons, or summit; Fig. 1c) and (2) lid type (wood or PVC) on occupancy of chambers and reproductive performance. We first defined the overall occupancy for each chamber as the ratio of the number of breeding seasons the chamber was used by storm petrels out of the number of breeding seasons the chamber was available. We then defined the overall reproductive performance for each chamber as the ratio of the number of successful breeding attempts out of the number of breeding attempts that occurred in the chamber. We weighted these parameters with either the number of seasons the chamber was available or the total number of breeding attempts, respectively. For this analysis, we excluded chambers where the lid had been replaced, as we tested for any effect of replacing the lid separately. Results from the GLMs were presented using the full models, and predictions from these GLMs were plotted. To examine the effect of replacing a chamber lid on occupancy, we used a subset of chambers that had lids replaced during the study and excluded any seasons where the lid was absent. We then constructed two binominal GLMMs with logit link functions (as above) on the binary response variable (occupancy = true/false), with chamber location and chamber identity as nested random effects and installation length (the number of seasons the chamber had been installed) as a fixed factor in both models. One model was run with no explanatory variables (null model) and one was run with lid present/replaced as an explanatory variable. A LRT between the two models was then used to test whether replacing the lid in a given breeding season significantly influenced occupancy in that season.

Ethics statement

The fieldwork was approved by the St Helena Government Environmental Management Division, in accordance with the St Helena Government environmental ordinance and British Trust for Ornithology ringing permit no. S5526. Extreme care was taken to minimise stress of captured birds; handling time was kept to a minimum and never exceeded ten minutes.

RESULTS

Nest success and productivity

We obtained reliable data on breeding success from 312 nests, 187 during the cool season and 125 during the hot season (Table 1). Mayfield hatching success in chambers during the study was estimated at 47%. Mayfield hatching success during the hot season (pooled across years) was estimated at 55% (95% confidence interval (CI) 0.470–0.644) and was thus higher than during the cool season (40%, 95% CI 0.330–0.485; LRT $\chi_1^2 = 6.9247$, $P = 0.009$, $n = 285$; Fig. S1A). There was no indication that hatching success varied between years (LRT $\chi_1^2 = 0.0173$, $P = 0.895$, $n = 285$) or within each season between years (LRT $\chi_2^2 = 0.0816$, $P = 0.960$, $n = 285$).

Fledging success in chambers was estimated by the Mayfield method to be 68%. It was 28 percentage points higher during the

TABLE 1
Summary of breeding success for Band-rumped Storm Petrel *Hydrobates castro* nesting
in artificial nest chambers on Egg Island, St Helena, from 2014 to 2019

Year	*n*	*n* hatched	Daily nest survival	Hatching success	*n* fledged	Daily fledging survival	Fledging success	Productivity
Hot season (late September to late December)								
2014	7	3	0.969 ± 0.015	0.265	3	1.000 ± 0.000	1.000*	0.265
2015	9	4	0.985 ± 0.007	0.520	4	1.000 ± 0.000	1.000*	0.520
2016	27	18	0.987 ± 0.004	0.567	13	0.996 ± 0.002	0.778	0.447
2017	31	16	0.989 ± 0.003	0.623	12	0.975 ± 0.003	0.703	0.438
2018	51	29	0.985 ± 0.003	0.521	9	0.978 ± 0.005	0.210	0.109
Cool season (late March to early July)								
2015	16	10	0.987 ± 0.005	0.581	9	0.996 ± 0.004	0.750	0.429
2016	24	17	0.981 ± 0.007	0.456	14	0.997 ± 0.002	0.831	0.379
2017	44	28	0.971 ± 0.007	0.290	27	0.999 ± 0.001	0.958	0.278
2018	48	13	0.968 ± 0.005	0.250	9	0.996 ± 0.002	0.740	0.185
2019	55	33	0.986 ± 0.003	0.543	29	0.993 ± 0.003	0.618	0.336

* Mayfield fledging success in the 2014 and 2015 hot seasons was high, as all chicks survived to fledge. ***n* hatched** is the number of clutches that hatched, ***n* fledged** is the number of hatched chicks that survived to fledging, **Hot season** is late September to late December, **Cool season** is late March to early July.

cool season (82% estimated fledging success, 95% CI 0.912–0.733) due to higher daily chick survival rates (Table 1) compared to the hot season, for which fledging success was estimated to be 54% (95% CI 0.672–0.427; LRT $\chi_1^2 = 16.93$, $P < 0.001$, $n = 171$; Fig S1B). Fledging success was also significantly different between years when pooled across seasons (LRT $\chi_1^2 = 13.942$, $P < 0.001$, $n = 171$); 2014 showed the highest daily chick survival rates and fledging success estimates compared to other years. There was also evidence of differences in fledging success within each season between years (LRT $\chi_2^2 = 28.864$, $P < 0.001$, $n = 171$), with the hot season showing lower fledging success across years than the cool season (Table 1, Fig. S2). Productivity overall was estimated to be 32%, with a difference of only 3.2 percentage points between seasonal populations: cool season productivity was 32.7% while hot season productivity was 29.5%.

Causes of breeding failure

The cause of hatching failure (pooled across years) was undetermined for 104 of the 285 eggs monitored (36.5% of nests)—the egg disappeared from the chamber with no obvious signs of nest disturbance. Seventeen hatching failures (6.0%) were due to the egg being abandoned after initially being incubated. Egg damage caused by stones in the nest chamber floor cracking and breaking the shell accounted for 11 hatching failures (3.9%). A further three losses (1% of nests) were due to usurper events, where the egg from an active nest was evicted from the chamber and a different pair subsequently started a new nesting attempt. Two losses (0.7%) were due to an apparent absence of incubation, meaning that an egg was laid but no adults were ever observed incubating. There was one instance of a breeding adult dying in a chamber, which resulted in hatching failure, and there was one chick that died during hatching when it failed to emerge fully from the eggshell. For 41 of 171 (24%) chicks monitored, the cause of fledging failure was undetermined, meaning that the

chick died in a chamber with no apparent cause. Observed chick mortality pooled across seasons was significantly higher (i.e., 29 of 70 chicks or 41% failed to fledge) during the hot season than during the cool season (13 of 101 chicks or 13%, $\chi^2 = 9.6116$, $P = 0.002$). Only one chick disappeared from a chamber with no signs of disturbance and the cause of one other nestling failure was unknown.

Occupancy

Chambers on Egg Island were readily accepted by *H. castro*: 71% (92 of 130) of all installed chambers were occupied at least once during the study, 89% (82 of 92) of which were used at least once for breeding. In the 2015 and 2017 cool seasons, all occupied chambers were used for breeding. Both occupancy and use for breeding increased with time since the chamber had been installed (occupancy LRT $\chi_1^2 = 243.11$, $P < 0.001$, $n = 1050$; breeding LRT $\chi_1^2 = 128.39$, $P < 0.001$, $n = 920$). *H. castro* occupied 5.4% of chambers during the first season following installation, which increased to 85.0% after five years (10 seasons). Similarly, 4.6% of chambers were used for breeding after the first season following installation, reaching 72.5% after five years (Fig. 3).

Chamber occupancy also increased throughout the study period: 1.399 ± 0.125 (mean ± standard error), $z = 11.21$, $P < 0.001$, $R^{2m} = 0.171$, $R^{2c} = 0.713$; LRT $\chi_1^2 = 190.41$, $P < 0.001$, $n = 1050$. Although chamber occupancy was marginally higher in the hot season (38.48%) than in the cool season (36.61%), the difference was not significant: $R^{2m} < 0.001$, $R^{2c} = 0.426$, $z = 0.502$, $P = 0.616$; LRT $\chi_1^2 = 0.242$, $P = 0.622$, $n = 1050$. Chamber use in the previous season was positively related to current occupancy (1.958 ± 0.212, $z = 9.225$, $P < 0.001$, $R^{2m} = 0.171$, $R^{2c} = 0.353$; LRT $\chi_1^2 = 83.874$, $P < 0.001$, $n = 920$), as was occupancy in the same season of the previous year (1.846 ± 0.237, $z = 7.776$, $P < 0.001$, $R^{2m} = 0.137$, $R^{2c} = 0.397$; LRT $\chi_1^2 = 60.192$, $P < 0.001$, $n = 787$).
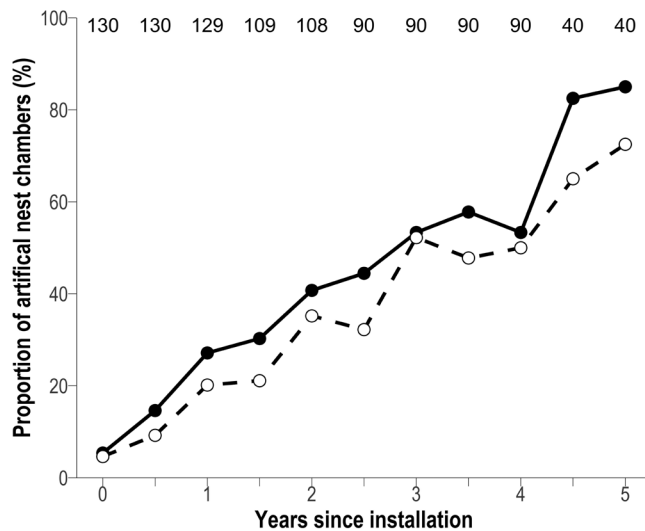
Fig. 3. Proportion of artificial nest chambers occupied (black points, solid line) and used for breeding (white points, dashed line) by Band-rumped Storm Petrel *Hydrobates castro* on Egg Island, St Helena, in relation to the number of years since their installation. Numbers at the top indicate the number of artificial nest chambers available for a given number of years.

After accounting for repeated observations of each location and chamber, the model that best explained whether a chamber was occupied or not in any given season (Table 2A) included the time since the chamber had been installed, whether the chamber had been occupied in the same season the previous year, and whether the chamber had been occupied in the previous season ($R^{2m} = 0.394$, $R^{2c} = 0.402$; Table 2B, Fig. S3).

Chamber use for breeding

The use of chambers for breeding increased significantly across the study period (1.212 ± 0.116, $R^{2m} = 0.147$, $R^{2c} = 0.670$, $z = 10.47$, $P < 0.001$; LRT $\chi_1^2 = 152.35$, $P < 0.001$, $n = 1050$). The number of chambers that were used for breeding were only marginally lower in the hot (29.91%) seasons compared to the cool seasons (32.37%), but not significantly so ($R^{2m} = 0.003$, $R^{2c} = 0.418$, $z = -1.668$, $P = 0.095$; LRT $\chi_1^2 = 2.803$, $P = 0.094$, $n = 1050$). The likelihood of chambers being used for breeding was positively related to both the previous season's breeding activity (1.846 ± 0.237, $z = 7.776$, $P < 0.001$, $R^{2m} = 0.150$, $R^{2c} = 0.299$; LRT $\chi_1^2 = 73.288$, $P < 0.001$, $n = 920$) and the breeding activity in the same season of the previous year (1.656 ± 0.233, $R^{2m} = 0.109$, $R^{2c} = 0.342$, $z = 7.094$, $P < 0.001$; LRT $\chi_1^2 = 49.646$, $P < 0.001$, $n = 787$). However, the breeding outcome in the same season of the previous year (success = true/false) was not related to whether a chamber was used for breeding in the following corresponding season (LRT $\chi_1^2 = 0.928$, $P = 0.335$, $n = 206$). Likewise, the previous season's breeding outcome was not related to the use of the chamber in the following breeding season (LRT $\chi_1^2 = 0.007$, $P = 0.931$, $n = 255$).

Site and chamber fidelity

In total, 302 adults were identified using chambers over the study, 83.3% (254) of which were using the chamber to breed. There was no overlap in individuals observed between seasons, i.e., no individuals found during the hot season were recorded subsequently in the cool season and vice versa. Among identified individuals, 50% (153) used the same chamber in more than one season and 62% (57) of used chambers were occupied by the same individual more than once. Of the 11 individuals recorded in all five years when chambers were used, four were recorded breeding in each season. Regarding the 27 individuals recorded in four years, 55.5% (15) were also breeding, 69.1% (29) of 42 individuals bred in all

TABLE 2

(A) Competing generalised linear mixed models used to assess which variables were associated with Band-rumped Storm Petrel *Hydrobates castro* occupancy of artificial nest chambers on Egg Island, St Helena, between 2014 and 2019. Chamber location and identification (LOC/ANC ID) were set as nested random effects. (B) Analysis of significance of variales in model 4.

A.	Competing models					
Model	Random effects	*k*	AICc	Delta AIC	AICcWt	Cum.Wt
(4) - Year	LOC/ANC ID	6	796.24	0.00	0.48	0.48
(3) - Year × Season	LOC/ANC ID	7	797.50	1.26	0.26	0.73
(2) - Season	LOC/ANC ID	8	798.07	1.82	0.19	0.93
(1) - Global[a]	LOC/ANC ID	9	799.95	3.71	0.07	1.00

B.	Significance of variables in model 4			
Variable	Estimate	Standard error	*z*	*P* value
PSO	1.698	0.194	8.751	**< 0.001**
PBSO	1.599	0.219	7.283	**< 0.001**
Installation length	0.070	0.041	1.721	0.085

[a] The global model contains all variables (year, season, year × season, previous season occupancy (PSO), previous between-season occupancy (PBSO), and installation length). Other models denote the interaction term that was removed from the global model and the resulting change in AICc. Model selection was based on AICc.

three years they were recorded, 64.4% (65) of 101 individuals bred in all two years recorded. Of the 121 individuals recorded using a chamber in only one year, 70.3% (85) were breeding.

Individuals showed strong site and chamber fidelity once they initiated occupation. Overall, 181 of 238 individuals (76.1%) that used a chamber for either roosting or breeding in successive years chose the same chamber. Among those that chose to use a different chamber during the study, 55 of 57 individuals (96.5%) chose chambers at the same overall location (Fig. 1C) within close proximity (< 2 m) to the original chamber. Two individuals that were found roosting in a chamber at a different chamber location were both using the nearest chamber location (red rock, cannons, or summit) to the previous location at which they had been recorded. Eight breeding individuals changed chambers more than once: upon observation in a new chamber, four individuals subsequently reverted to the chamber where they were initially breeding and four individuals changed to a different chamber again, but always within the same location (red rock, cannons, or summit) and in close proximity to the other chambers they were recorded using. Of the breeding attempts where at least one partner was identified and bred more than once in successive years, 153 of 187 individuals (81.82%) were faithful to their chamber: 60 of 70 individuals (85.71%) after breeding successfully in the previous year, 82 of 106 individuals (77.36%) after breeding failure (Fig. 4A), and 11 chamber-faithful individuals had an unknown previous breeding outcome.

Mate fidelity

Both partners were identified in 56.6% (194/327) of nesting attempts in chambers. Overall, 89.4% (143/160) of individuals from pairs who were found to nest more than once did so with the same mate: 88.1% (126/143) of individuals who were faithful to their mate were also faithful to the same chamber, while the remaining 11.9% (17/143) nested in a different chamber. Among individuals who were faithful to their mate, 13 of 17 individuals (76.5%) also chose a different chamber and the remaining four (23.5%) were

faithful to their original chamber. Of the breeding attempts in which both partners were identified in successive years and had at least one partner nest more than once, 110 of 120 individuals (92.4%) were faithful to their mate: 64 of 70 individuals (91.4%) after breeding failure, 38 of 41 individuals (92.7%) after breeding successfully in the previous year (Fig. 4B), and eight mate-faithful individuals had an unknown previous breeding outcome. Of the 10 individuals that were not faithful to their mate, seven swapped mates after a breeding failure and three swapped after a successful breeding attempt. We also found two incidences of temporary divorce where one of the mates breeding with a new partner chose to pair with its previous partner during the next breeding attempt.

Chamber lids and location

Chambers located at the cannons and red rock had higher overall occupancy than chambers at the summit (cannons: 0.511 ± 0.143, $t = 3.564$, $P < 0.001$; red rock: 0.168 ± 0.086, $t = 1.966$, $P = 0.049$; $R^2 = 0.018$; Fig. 5A). However breeding performance did not significantly differ between chamber locations ($R^2 < 0.001$, $\chi_2^2 = 0.088$, $P = 0.957$). Nine chambers had to have their lids replaced during the study, two of which were replaced twice. Occupancy in those chambers was significantly lower ($-31.3\% \pm 10.8\%$) in seasons during which the lid was replaced (LRT $\chi_1^2 = 11.512$, $P < 0.001$, $n = 79$) compared with chambers that had their lids continuously present during a season. Chambers with wooden and green plastic lids had a considerably lower occupancy than chambers with brown plastic lids (wood vs. brown plastic: -0.951 ± 0.158, $t = -6.026$, $P < 0.001$; green plastic vs. brown plastic: -0.278 ± 0.130, $t = -2.134$, $P < 0.05$; $R^2 = 0.140$; Fig. 5B). Chambers with wooden lids also had lower overall reproductive performance than chambers with brown plastic lids, equating to an approximately 18% lower breeding success (-0.774 ± 0.339, $t = -2.281$, $P = 0.022$; $R^2 = 0.066$, Fig. 5C), but green plastic lids only had a marginally lower average reproductive performance than brown plastic lids (-0.611 ± 0.334, $t = -1.826$, $P = 0.069$).

DISCUSSION

We show that artificial nest chambers offer an effective and convenient tool to monitor the breeding biology of burrow-nesting seabirds (Bolton *et al.* 2004; Bedolla-Guzmán *et al.* 2016, 2017). In our study, we found that occupancy of artificial nest chambers increases over time after their first installation. We also show that the two seasonal populations of the Band-rumped Storm Petrel complex of *H. castro* have very similar breeding performances. No apparent exchange or overlap of individuals among seasons was recorded, supporting the placement of these seasonal populations somewhere on the spectrum of other sympatric but temporally isolated storm petrel populations where allochronic speciation has occurred or is underway (Ainley 1980, Bolton *et al.* 2008, Taylor *et al.* 2019).

Reproductive performance

We found significant seasonal differences in success at different breeding stages, suggesting that different pressures exist between the hot and cool seasons. Our results can be compared with those of Bennett *et al.* (2009) who studied *H. castro* natural nest cavities at the same site, although their monitoring period was shorter and in an earlier series of years (2004–2007) than our study. Mayfield estimates for hatching success by Bennett *et al.* (2009) were 18%–
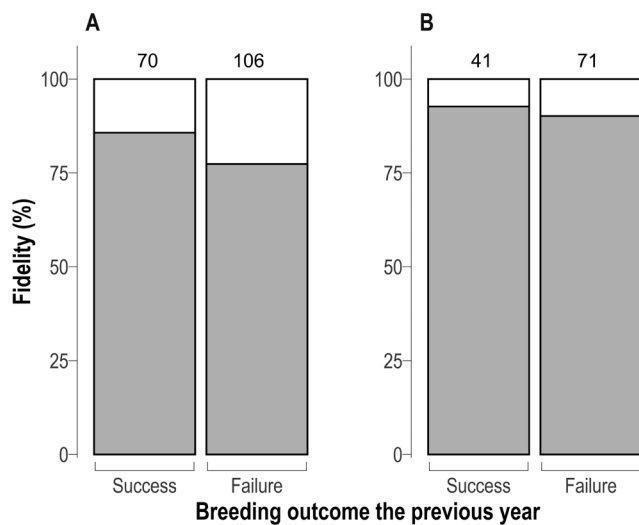
Fig. 4. Relationship between breeding outcome for Band-rumped Storm Petrel *Hydrobates castro* on Egg Island, St Helena, during the previous season and (A) chamber fidelity and (B) mate fidelity. Grey indicates fidelity, white indicates non-fidelity. Sample sizes are shown at the top.

A

B

C
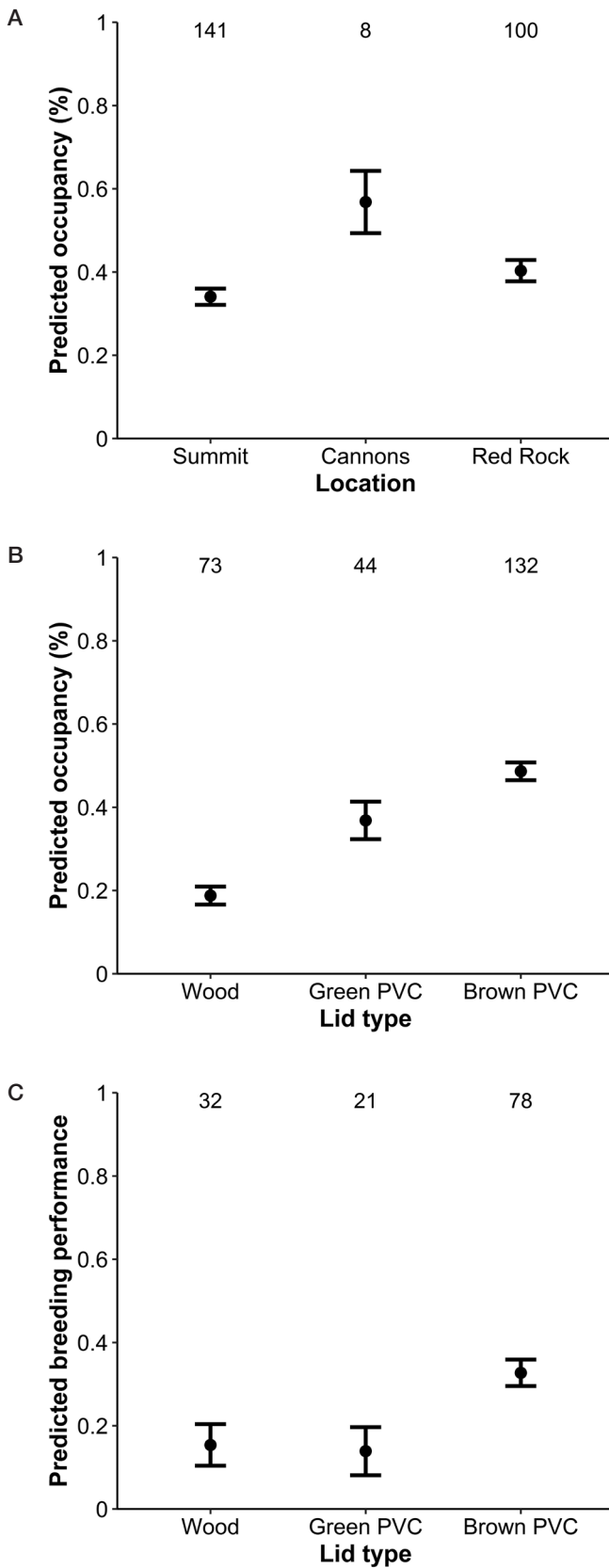
Fig. 5. Predicted effects of (A) chamber location on overall occupancy, (B) lid type on overall occupancy, and (C) lid type on breeding performance of Band-rumped Storm Petrel *Hydrobates castro* on Egg Island, St Helena. Values represent predicted occupancy and breeding performance ± one standard error. PVC = polyvinyl chloride.

43%, a lower range than the Mayfield estimates of hatching success observed in chambers during our study (25%–62%). Fledging success in natural nesting cavities in the Bennett *et al.* (2009) study also ranged from 1%–67%, compared to the higher 21%–100% fledging success observed in our chambers. Overall breeding success showed lower ranges: < 1%–27% in natural nest cavities vs. 11%–52% in chambers. These comparisons show that both the hot and cool seasonal populations of *H. castro* have considerable variation in success at all breeding stages (hatching, fledging, and overall productivity) between years, as is typical for marine seabirds (Schreiber & Burger 2002). Given the differences in study periods and the observed variation between years, it is impossible to say conclusively that chambers provided higher nesting success and productivity than natural cavities. However, it is encouraging that birds breeding in chambers have so far performed better than or equal to those breeding in natural cavities.

Occupancy

Chambers were occupied and used for breeding within the first season after installation, supporting either their preferential uptake or that there is a sizable 'floating population' suffering from a shortage of suitable nesting cavities on Egg Island (Ford *et al.* 2021). This is a fast uptake in comparison to another study of storm petrel breeding populations, in which it took three or more years to colonise new areas with additional methods such as acoustic attraction (Cruz & Cruz 1996). Occupancy was marginally higher in the hot season than in the cool season, but fewer chambers were used for breeding in the hot vs. cool season. Altogether this indicates that there may be more non-breeding storm petrels present during the hot than the cool season. The lower breeding occupancy in the hot season contradicts the hypothesis that there would be higher inter-specific competition for nesting cavities during the hot season due to the larger population size. Our results indicate that there is little (if any) difference between seasons in terms of the strength of competition for nesting chambers.

The significant positive influence of occupancy in the previous breeding season on the likelihood of chamber use is intriguing. It suggests that there are similarities between the seasons in terms of what attracts storm petrels to use chambers. It could be pure random chance that storm petrels in both seasons chose the same chambers, possibly due to having the same habitat preferences. However, the important role of olfaction in navigation to colony sites and nesting burrows in many petrel species has long been established, with individuals even being able to recognise the olfactory signature of their own nest and mate (Bonadonna 2009). Findings by Bonadonna & Bretagnolle (2002) showed that diurnal petrel species rely more on visual cues than olfactory cues, whereas nocturnal petrels returning to their nest sites in darkness rely on sense of smell to find burrows. If *H. castro* at St Helena are truly nocturnal, similar olfactory cues might be used by the two seasonal populations. This would explain the influence of between-season occupancy on chamber use. Of course, other influences on chamber choice (e.g., habitat quality around chamber locations, chamber quality, internal environment, etc.) may also influence occupancy. Although this study found no evidence of overlap in occurrence at the colony between the two seasonal populations (e.g., breeding hot-season storm petrels found in the colony during the cool season and vice versa), it may still occur and could further help to explain the influence of the previous breeding season on the likelihood of chamber use.

The significant negative effect of replacing a chamber lid on occupancy within a season was not surprising, given that Procellariiformes are well known for their acute olfactory senses (Bonadonna *et al.* 2003). This implies that storm petrels may not recognise their own chamber due to the difference in smell when returning to the colony the following season, and/or they may find the change in odour repellent, preferring to use a nearby chamber instead.

Fidelity

This study provides the first empirical evidence of high levels of both chamber and mate fidelity in *H. castro*, despite inherent limitations in the data. For example, not all of the individuals that were identified in more than one season were observed breeding in the same chamber as previously, nor were they identified in the subsequent season. It is therefore not known whether those individuals died, emigrated, chose to nest in a natural cavity, skipped breeding in one or more cycles, or went undetected due to insufficient frequency of monitoring visits. Likewise, individuals that were only identified once during the study could have died or emigrated. Contrary to common behaviour among petrels (Bried & Jouventin 1999, Mariné & Cadiou 2019), storm petrels in our study did not necessarily switch nest chamber or overall chamber location following nest failure. Although there was a slight negative effect of previous breeding failure on mate and chamber fidelity (Fig. 4), chamber use for breeding was unaffected and > 70% of failed individuals still bred in the same chamber. Our results indicate that individuals may be more likely to change their chamber following breeding failure the previous season than to change their mate, suggesting that the benefits of maintaining a pair bond may outweigh the cost of pair-bond disruption in *H. castro*, even after breeding failure. Mate fidelity is common in Procellariiformes (Warham 1990), a strategy thought to avoid missing breeding seasons owing to pair-bond disruption and re-mating and to avoid an initial decrease in reproductive performance with the new mate (Bried & Jouventin 2002).

Although it was not possible in this study to ascertain an individual's level of breeding experience, it is known to influence mate faithfulness: experienced breeders generally have better breeding success than inexperienced breeders, and in turn, unsuccessful breeders in some species are more likely to change their mates (Bradley *et al.* 1990, Weimerskirch 1990, Naves *et al.* 2006). Mate fidelity can also sometimes depend on site fidelity in some Procellariiformes, e.g., Cory's Shearwater *Calonectris borealis* (Thibault 1994). However, in other species such as Leach's Storm Petrel *Hydrobates leucorhous*, mate and site fidelity are not necessarily related (Morse & Kress 1984). It is unclear from our study if mate fidelity is a by-product of site fidelity or whether site fidelity is a strategy to maintain pair bonds. Site fidelity can serve as a meeting point for pairs to reunite (Morse & Kress 1984). If there is high competition for nest sites, as suggested by the high occupancy rate observed early after installation on Egg Island, site fidelity may ensure successful retention of the sites in the face of strong competition that poses a risk of usurpation. Site fidelity also allows individuals to be more efficient at finding a new mate, as they have better knowledge of potential mates in the area (Bried & Jouventin 2002). The very limited movement observed in this study between overall chamber locations while not breeding and restricted 'dispersal' between chambers while breeding has also been documented in other seabirds (González-Solís *et al.* 1999). This supports the theory that an individual's knowledge of the surrounding site may influence its choice of site and nest (chamber).

Causes of failure

Egg neglect is common in storm petrels (Boersma & Wheelwright 1979) and may have occurred during the study, thus explaining several failures during the incubation period. Monitoring was conducted during the day when adults are most likely to be foraging at sea. The periodical nature of checks also implies that the timing of nest checks may not have coincided with the presence of the adults. Another potential cause of egg failure is heat stress, which is known to be a significant cause of death in Grey-faced Petrel *Pterodroma gouldi* chicks in exposed artificial chambers in New Zealand (Miskelly *et al.* 2009). Differences in temperature regulation could therefore account for varying chick survival between seasons, given that air temperatures at St Helena during the cool season range between 16 °C and 18 °C, whereas temperatures in the hot season are more variable, ranging between 16 °C and 21 °C (Feistel *et al.* 2003). It may be more difficult for the parents and/or chick to regulate the temperature of the chick in the chamber during the hot season, potentially augmenting chick mortality. We found that the construction material of the chamber lids influences reproductive performance. While the colour of plastic lids did not significantly impact overall reproductive performance, wooden lids reduced nest success. This could be a consequence of the thermal properties of wood versus plastic, given that the type of construction material used for artificial burrows is known to affect temperatures inside (Carlile *et al.* 2012). It could also be related to the differences in how the flat wooden lids fitted on top of the chamber compared to the plastic lids, which have an overlapping edge. Regardless, the lid is the most exposed part of the chamber to direct sunlight and inclement weather, rendering it plausible that this component of chambers may be particularly relevant to breeding success in the chambers.

As expected, there was little evidence of inter-specific competition within the chambers during the study, although the hot season coincides with the Brown Noddy breeding season. Brown Noddy chicks were frequently found blocking chamber entrances, presumably seeking shelter from direct sunlight during the hot season. Small noddy chicks were also observed inside the chamber with incubating storm petrels or storm petrel chicks (see Fig. S4). This could influence the ability of parent storm petrels to attend to the nest, feeding frequency of chicks, and ultimately nesting outcome.

This study could not attribute any causes of breeding failure to predation. Although Egg Island is indeed currently free from invasive feral cats, rats, and mice, other resident species may predate on storm petrels. For example, Ascension Sally Lightfoot Crabs *Grapsus adscensionis* commonly predate bird eggs, causing clutch failure in Brown Noddies on Egg Island (Rowlands *et al.* 1998). Storm petrel eggs may likewise be targeted, if accessible. Furthermore, Common Mynas *Acridotheres tristis* were frequently observed around the colony during monitoring and were seen entering nesting cavities (AB pers. obs.). While mynas are a significant predator of endemic St. Helena Plover *Charadrius sanctaehelenae* eggs (Burns *et al.* 2013), we did not observe any clear evidence of egg predation. Invertebrate predation of storm petrel eggs and chicks is also conceivable. Centipedes were found to predate Black-winged Petrel *Pterodroma nigripennis* chicks,

specifically targeting the hind neck, on Phillip Island in the South Pacific (Halpin *et al.* 2021). Red-headed Centipedes *Scolopendra morsitans* were often seen hunting at night in the open on Egg Island, and some storm petrel chicks were observed with damage to the head and neck (AB pers. obs.) during this study. Similar injuries to storm petrel chicks have been observed in the Azores (H. Hereward pers. comm.) and on Ascension Island, where Allan (1962) referred to scars and the absence of down on the head as "mohawks," attributing the damage to low ceilings of certain natural chambers and/or other petrels. Therefore, such damage to chicks is more likely to have occurred from inter-specific competition with other pairs trying to evict a chick from its chamber rather than caused by centipedes. In addition, ants are known to predate St. Helena Plover nests (Burns *et al.* 2013) and have been observed swamping White Tern *Gygis alba* chicks (AB pers. obs.). Although predation by ants is uncommon, they could also affect storm petrels.

Management implications

The range of hatching success, fledging success, and overall productivity observed in artificial nest chambers in this study compared with the same measures in natural nest cavities monitored 10 years previously on St Helena (Bennett *et al.* 2009) indicates that chamber provisioning on Egg Island does not reduce storm petrel productivity or constitute an ecological trap. This is further supported by the high occupancy rate observed early after installation, indicating that storm petrels on Egg Island have a shortage of available nest sites. In future studies, it would be advantageous to monitor both a subset of natural nests and chambers simultaneously for a more detailed analysis of differences in productivity between natural and artificial nesting attempts and of variations between years. We tentatively conclude that provisioning of artificial nest chambers is an effective conservation management tool for storm petrels at St Helena, as they provide easy access to monitor breeding productivity and they increase the availability of suitable nest sites.

Reinforcement of current bio-security protocols would be beneficial to ensure that new and potentially harmful invasive species do not become established on the island. To ensure that the island remains free from predators, it may be prudent to include as part of the routine monitoring programme additional invasive species checks to enable early detection of new invasions (especially mammals). Given the observed negative effect of replacing a chamber lid on occupancy, it would be sensible to ensure that protocols are adhered to during monitoring checks. This could include verification that lids have been secured to the chamber adequately upon completion of the monitoring procedure, reducing the risk of lids being lost due to strong winds. It would also be advantageous to investigate other methods of securing lids to chambers in the long term. If lids are lost or new chambers are installed, then lids (replacements or otherwise) should be ideally constructed of PVC, preferably brown in colour, as we found those to be associated with significantly higher overall occupancy and breeding performance compared with other lid types and colours. Future chamber installations should carefully consider the choice of site location. On Egg Island, preference should be given first to cannons, then red rock, then summit, although it is recognised that there may be limitations in availability of suitable areas at each site for installation. Other small islands nearby known to contain seasonally breeding *H. castro*, e.g., Peaked Island and

Thompson Valley Island, may also be options for future chamber installation. To reduce the risk of egg breakage, installation of new or replacement chambers should ensure that the material used to pack the inside of the nest chambers follows guidance from Bolton *et al.* (2004): gravel at the bottom to facilitate drainage, topped with soil or small stones. Finally, it may be helpful to provide larger shelters using natural stone near storm petrel nest chambers located in Brown Noddy colonies, to mitigate against disturbance from noddy chicks during the hot season.

ACKNOWLEDGEMENTS

REFERENCES

AINLEY, D.G. 1980. Geographic variation in Leach's Storm-Petrel. *The Auk* 97: 837–853. doi:10.1093/auk/97.4.837

ALLAN, R.G. 1962. The Madeiran Storm Petrel *Oceanodroma castro*. *Ibis* 103B: 274–295. doi:10.1111/j.1474-919X.1962.tb07247.x

BATES, D., MÄCHLER, M., BOLKER, B. & WALKER, S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48. doi:10.18637/jss.v067.i01

BEDOLLA-GUZMÁN, Y., MASELLO J.F., AGUIRRE-MUÑOZ, A., LAVANIEGOS, B.E. & QUILLFELDT, P. 2017. Breeding biology, chick growth, and diet of the Least Storm-Petrel *Oceanodroma microsoma* on Islas San Benito, Mexico. *Marine Ornithology* 45: 129–138.

BEDOLLA-GUZMÁN, Y., MASELLO, J.F., AGUIRRE-MUÑOZ, A., & QUILLFELDT, P. 2016. A wood-concrete nest box to study burrow-nesting petrels. *Marine Ornithology* 44: 249–252.

BENNETT, E., BOLTON, M. & HILTON, G. 2009. Temporal segregation of breeding by storm petrels *Oceanodroma castro* (*sensu lato*) on St Helena, South Atlantic. *Bulletin of the British Ornithologists' Club* 129: 92–97.

BIRDLIFE INTERNATIONAL. 2018. *Hydrobates castro*. *The IUCN Red List of Threatened Species* 2018: e.T132341128A132433305. doi:10.2305/IUCN.UK.2018-2.RLTS.T132341128A132433305.en [Accessed on 22 July 2021.]

BOERSMA, P.D. & WHEELWRIGHT, N.T. 1979. Egg neglect in the Procellariiformes: Reproductive adaptations in the *Fork-tailed Storm-Petrel*. *The Condor* 81: 157–165. doi:10.2307/1367282

BOLTON, M., MEDEIROS, R., HOTHERSALL, B. & CAMPOS, A. 2004. The use of artificial breeding chambers as a conservation measure for cavity-nesting procellariiform seabirds: A case study of the Madeiran Storm Petrel (*Oceanodroma castro*). *Biological Conservation* 116: 73–80. doi:10.1016/s0006-3207(03)00178-2

BOLTON, M., SMITH, A.L., GÓMES-DÍAZ, E. ET AL. 2008. Monteiro's Storm-petrel *Oceanodroma monteiroi*: A new species from the Azores. *Ibis* 150: 717–727. doi:10.1111/j.1474-919X.2008.00854.x

BOLTON, M., WATT, R., ELLICK, G. & SCOFIELD, P. 2010. Evidence of breeding White-faced Storm Petrel *Pelagodroma marina* on St Helena Island, South Atlantic: Vagrancy or a relict from human pre-colonisation? *Seabird* 23: 135–138.

BONADONNA, F. 2009. Olfaction in petrels: From homing to self-odor avoidance. *Annals of the New York Academy of Sciences* 1170: 428–433. doi:10.1111/j.1749-6632.2009.03890.x

BONADONNA, F. & BRETAGNOLLE, V. 2002. Smelling home: A good solution for burrow-finding in nocturnal petrels? *Journal of Experimental Biology* 205: 2519–2523. doi:10.1242/jeb.205.16.2519

BONADONNA, F., CUNNINGHAM, G.B., JOUVENTIN, P., HESTERS, F. & NEVITT, G.A. 2003. Evidence for nest-odour recognition in two species of diving petrel. *Journal of Experimental Biology* 206: 3719–3722. doi:10.1242/jeb.00610

BOURGEOIS, K., DROMZÉE, S. & VIDAL, E. 2015. Are artificial burrows efficient conservation tools for seabirds? A case study of two sympatric shearwaters on neighbouring islands and guidelines for improvement. *Biological Conservation* 191: 282–290. doi:10.1016/j.biocon.2015.07.002

BRADLEY, J.S., WOOLLER, R.D., SKIRA, I.J. & SERVENTY, D.L. 1990. The influence of mate retention and divorce upon reproductive success in Short-tailed Shearwaters *Puffinus tenuirostris*. *Journal of Animal Ecology* 59: 487–496. doi:10.2307/4876

BRIED, J. & JOUVENTIN, P. 1999. Influence of breeding success on fidelity in long-lived birds: An experimental study. *Journal of Avian Biology* 30: 392–398. doi:10.2307/3677011

BRIED, J. & JOUVENTIN, P. 2002. Site and mate choice in seabirds: An evolutionary approach. In: SCHREIBER, E.A. & BURGER, J. (Eds.) *Biology of Marine Birds*. Boca Raton, USA: CRC Press.

BURNHAM, K.P. & ANDERSON, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd Edition*. New York, USA: Springer.

BURNS, F., MCCULLOCH, N., SZÉKELY, T. & BOLTON, M. 2013. The impact of introduced predators on an island endemic, the St Helena Plover, *Charadrius sanctaehelenae*. *Bird Conservation International* 23: 125–135. doi:10.1017/S0959270913000245

CAREY, M.J. 2009. The effects of investigator disturbance on procellariiform seabirds: A review. *New Zealand Journal of Zoology* 36: 367–377. doi:10.1080/03014220909510161

CARLILE, N., PRIDDEL, D. & MADEIROS, J. 2012. Establishment of a new, secure colony of Endangered Bermuda Petrel *Pterodroma cahow* by translocation of near-fledged nestlings. *Bird Conservation International* 22: 46–58. doi:10.1017/S0959270911000372

CRUZ, J.B. & CRUZ, F. 1996. Conservation of the Dark-rumped Petrel *Pterodroma phaeopygia* of the Galápagos Islands, 1982–1991. *Bird Conservation International* 6: 23–32. doi:10.1017/S0959270900001283

FEISTEL, R., HAGEN, E. & GRANT, K. 2003. Climatic changes in the subtropical Southeast Atlantic: The St. Helena Island Climate Index (1893–1999). *Progress in Oceanography* 59: 321–337. doi:10.1016/j.pocean.2003.07.002

FORD, R.G., TERRILL, S., CASEY, J. ET AL. 2021. Distribution patterns and population size of the Ashy Storm Petrel *Oceanodroma homochroa*. *Marine Ornithology*. 49: 193–204.

GONZÁLEZ-SOLÍS, J., WENDELN, H. & BECKER, P.H. 1999. Within and between season nest-site and mate fidelity in Common Terns (*Sterna hirundo*). *Journal für Ornithologie* 140: 491–498. doi:10.1007/BF01650993

HALPIN, L.R., TERRINGTON, D.I., JONES, H.P. ET AL. 2021. Arthropod predation of vertebrates structures trophic dynamics in island ecosystems. *The American Naturalist* 198: 540–550. doi:10.1086/715702

HARRIS, M. 1969. The biology of storm petrels in the Galápagos Islands. *Proceedings of the California Academy of Sciences* 37: 95–166.

HOWELL, S.N.G. & ZUFELT, K. 2019. *Oceanic Birds of the World: A Photo Guide*. Princeton, USA: Princeton University Press.

JOHNSON, D.H. 1979. Estimating nest success: The Mayfield method and an alternative. *The Auk* 96: 651–661.

KLEIN, Á., NAGY, T., CSÖRGŐ, T. & MÁTICS, R. 2007. Exterior nest-boxes may negatively affect Barn Owl *Tyto alba* survival: An ecological trap. *Bird Conservation International* 17: 273–281. doi:10.1017/S0959270907000792

LEWIS, F., BUTLER, A. & GILBERT, L. 2011. A unified approach to model selection using the likelihood ratio test. *Methods in Ecology and Evolution* 2: 155–162. doi:10.1111/j.2041-210X.2010.00063.x

LIBOIS, E., GIMENEZ, O., ORO, D., MÍNGUEZ, E., PRADEL, R. & SANZ-AGUILAR, A. 2012. Nest boxes: A successful management tool for the conservation of an endangered seabird. *Biological Conservation* 155: 39–43. doi:10.1016/j.biocon.2012.05.020

MÄND, R., TILGAR, V., LÕHMUS, A. & LEIVITS, A. 2005. Providing nest boxes for hole-nesting birds – Does habitat matter? *Biodiversity & Conservation* 14: 1823–1840. doi:10.1007/s10531-004-1039-7

MARINÉ, M. & CADIOU, B. 2019. Breeding success, nest site fidelity and mate fidelity in the European Storm-petrel *Hydrobates pelagicus*. *Seabird* 32: 46–58.

MATHEWS, G. 1935. *Cymochorea castro helena*. In: LOW, G. (Ed.) *Bulletin of the British Ornithologists' Club*. Volume 35. London, UK: H.F.G. Witherby.

MAYFIELD, H.F. 1975. Suggestions for calculating nest success. *The Wilson Bulletin* 87: 456–466.

MISKELLY, C.M., TAYLOR, G.A., GUMMER, H. & WILLIAMS, R. 2009. Translocations of eight species of burrow-nesting seabirds (genera *Pterodroma*, *Pelecanoides*, *Pachyptila* and *Puffinus*: Family Procellariidae). *Biological Conservation* 142: 1965–1980. doi:10.1016/j.biocon.2009.03.027

MORSE, D.H. & KRESS, S.W. 1984. The effect of burrow loss on mate choice in the Leach's Storm-Petrel. *The Auk* 101: 158–160. doi:10.1093/auk/101.1.158

NAVES, L.C., MONNAT, J.Y. & CAM, E. 2006. Breeding performance, mate fidelity, and nest site fidelity in a long-lived seabird: Behaving against the current? *Oikos* 115: 263–276. doi:10.1111/j.2006.0030-1299.14883.x

OPPEL, S., BURNS, F., ELLICK, G. ET AL. 2012. Recent observations suggest Bulwer's Petrel *Bulweria bulwerii* might breed on St Helena. *Marine Ornithology* 40: 67–68.

R DEVELOPMENT CORE TEAM. 2021. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. [Accessed at http://www.r-project.org/ on 04 December 2021.]

RAMOS, J.A., MONTEIRO, L.R., SOLA, E. & MONIZ, Z. 1997. Characteristics and competition for nest cavities in burrowing Procellariiformes. *The Condor* 99: 634–641. doi:10.2307/1370475

RODRÍGUEZ, J., AVILÉS, J.M. & PAREJO, D. 2011. The value of nestboxes in the conservation of Eurasian Rollers *Coracias garrulus* in southern Spain. *Ibis* 153: 735–745. doi:10.1111/j.1474-919X.2011.01161.x

ROWLANDS, B.W., TRUEMAN, T., OLSON, S.L., MCCULLOCH, N. & BROOKE, R.K. 1998. *The Birds of St Helena: An Annotated Checklist*. BOU Checklist no. 16. Tring, UK: British Ornithologists' Union.

SANZ, V., RODRÍGUEZ-FERRARO, A., ALBORNOZ, M. & BERTSCH, C. 2003. Use of artificial nests by the Yellow-shouldered Parrot (*Amazona barbadensis*). *Ornitologia Neotropical* 14: 345–351.

SCHREIBER, E.A. & BURGER, J. 2002. *Biology of Marine Birds*. Boca Raton, USA: CRC Press.

SHAFFER, T.L. 2004. A unified approach to analyzing nest success. *The Auk* 121: 526–540. doi:10.1642/0004-8038(2004)121[0526:AUATAN]2.0.CO;2

TAYLOR, R.S., BOLTON, M., BEARD, A. ET AL. 2019. Cryptic species and independent origins of allochronic populations within a seabird species complex (*Hydrobates* spp.). *Molecular Phylogenetics and Evolution* 139: 106552. doi:10.1016/j.ympev.2019.106552

THIBAULT, J.-C. 1994. Nest-site tenacity and mate fidelity in relation to breeding success in Cory's Shearwater *Calonectris diomedea*. *Bird Study* 41: 25–28. doi:10.1080/00063659409477193

THOMAS, R., LELLO, J., MEDEIROS, R. ET AL. 2017. *Data Analysis with R Statistical Software: A Guidebook for Scientists, 2nd Edition*. Cardiff, Wales: Eco-explore.

WARHAM, J. 1990. *The Petrels: Their Ecology and Breeding Systems*. San Diego, USA: Academic Press.

WEIMERSKIRCH, H. 1990. The influence of age and experience on breeding performance of the Antarctic Fulmar, *Fulmarus glacialoides*. *Journal of Animal Ecology* 59: 867–875. doi:10.2307/5019

WICKHAM, H. 2016. *ggplot2: Elegant graphics for data analysis, 2nd Edition*. New York, USA: Springer-Verlag. [Accessed at https://ggplot2.tidyverse.org on 10 May 2022.]

WOOD, S. & SCHEIPL, F. 2020. *gamm4: Generalized Additive Mixed Models using 'mgcv' and 'lme4'*. Version 0.2-6. [Accessed at https://cran.r-project.org/package=gamm4 on 10 May 2022.]

ZEILEIS, A. & HOTHORN, T. 2002. Diagnostic checking in regression relationships. *R News*. 2: 7–10. [Accessed at https://cran.r-project.org/doc/Rnews/ on 06 September 2021.]